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Investigating emerging self-awareness: its neural underpinnings, the significance of self-recognition, and the relationship with social interactions

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Originality Statement

'I hereby declare that this submission is my own work and to the best of my knowledge it contains no materials previously published or written by another person, or substantial proportions of material which have been accepted for the award of any other degree or diploma at the University of London or any other educational institution, except where due acknowledgment is made in the thesis. Any contribution made to the research by others, with whom I have worked at University of London or elsewhere, is explicitly acknowledged in the thesis. I also declare that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project's design and conception or in style, presentation and linguistic expression is acknowledged.'

This thesis includes work that appears in the following article:

Bulgarelli, C., Blasi, A., Arridge, S.R., Powell, S., de Klerk, C. C. J. M., Southgate, V., Brigadoi, S., Penny, W., Tak, S., Hamilton, A. (2018). Dynamic causal modelling on infant fNIRS data: A validation study on a simultaneously recorded fNIRS-fMRI dataset. *NeuroImage.*

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Abstract

Up until now, self-recognition in the mirror, achieved at around 18 months, has been used to assess self-awareness in infancy. Even though the significance of this test is not universally accepted, this field has progressed very little over the last decades, in contrast to a broad volume of literature on the self in adults. However, a relationship between self-other differentiation and social cognitive abilities has been recently hypothesized, renewing the interest in mechanisms underlying emerging self-awareness.

Adult studies have highlighted that brain networks, instead of isolated brain areas, support self-processing. Therefore, the first two studies of this thesis validated the use of advanced connectivity analyses on infant fNIRS data. Making use of these methods, one study demonstrated that functional connectivity between regions belonging to a network that has been related to abstract self-processing in adults gradually increases over the first two years of life. The same network was found to characterise infants who recognise themselves in the mirror. In another study, crucial regions of this network were shown to be engaged during self-recognition in 18-month-olds.

As social interactions have been suggested to be fundamental for the construction of the self, the last two studies of this thesis investigated the relationship between emerging self-awareness and social interactions. To test this, I focused on mimicry, known to play an important role in affiliation and in mediating relationships. One study demonstrated that emerging self-awareness may affect infants' tendency to selectively mimic in-group members, which may indicate a possible role of self-comparison and identification processes. The last study did not find evidence for a relationship between mothers' tendency to imitate their infants at 4 months and emerging self-awareness.

Taken together, these studies enrich our understanding of the mechanisms underlying emerging self-awareness and they represent a pioneering starting point for further investigations into this topic.

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List of Abbreviations

MSR   Mirror self-recognition

mPFC   Medial prefrontal cortex

TPJ   Temporo-parietal junction

fNIRS   Functional near-infrared spectroscopy

EMG   Electromyography

MRI   Magnetic resonance imaging

STS   Superior temporal sulcus

ERP   Event-related potentials

EEG   Electroencephalography

PCC   Posterior cingulate cortex

MNS   Mirror neuron system

IFG   Inferior frontal gyrus

IPL   Inferior parietal lobe

DMN   Default mode network

ACC   Anterior cingulate cortex

fMRI   Functional magnetic resonance imaging

CMS   Cortical midline structures

BOLD   Blood Oxygen Level Dependent

HbO_2 Oxygenated blood

HHb   Deoxygenated blood

DPF   Differential pathlength factor

S-D   Source-detector separation

ROI   Region of interest

STG   Superior temporal gyrus

SPM   Statistical Parametric Mapping

GLM   General Linear Model

ANOVA   Analysis of variance

HRF   Haemodynamic response function

DTI   Diffusion Tensor Imaging

PPI   Psychophysiological Interaction

GC   Granger Causality

DCM   Dynamic Causal Modelling

FDR   False Discovery Rate

PCI   Parent-child interaction

Chapter 1

Becoming a Self

1.1 Introduction: Motivation and aims

The sense of self is a person's essential being that makes them different from others. It is our 'inner movie' and the deepest part of ourselves. As adults, we tend to take our self-concepts for granted, but the mechanisms behind their development are unknown. Infants come into the world highly dependent on their caregivers, but they can also interact with others from a very early age, which may lead one to think that infants have self and other concepts from early in life. Does this mean that young infants have self-awareness? If not, when do infants become aware of themselves?

So far, there has been a little systematic investigation into the topic of the development of the sense of self and the abstract nature of this theme presents a challenge for scientific investigation. Some might think that a science of the self is impossible as science is, by definition, objective, while the self is subjective. With this PhD thesis, I hope to take a step towards demonstrating that a science of the self and a science of the development of the self is possible, even though there are many challenges that need to be overcome. One of the primary obstacles when facing this topic is the lack of agreement and inconsistency in the definition of what is the 'self', and the use of several different but related terms. Investigation into how a sense of self and self-awareness develops is hampered by the numerous definitions and multifaceted abilities that scientists have attributed to these concepts. Researchers in this field have to disregard the idea of having only one notion of selfhood, as there are several features of the self that commonly conflate under the same term. However, they also recognise the need for consistency between the different aspects and definitions. A *glossary of the self* is the focus of the next section, so as to clarify the terms used in this thesis.

Until now, the assessment of the sense of self in infants has been performed with the mirror self-recognition (MSR) task, a test developed in the early '70s, where infants had a dot of red lipstick covertly marked on their face. Their detection (revealed by touching) in the mirror of something unusual on their face is thought to be an index of some level of a sense of self (Amsterdam, 1972; Rochat, 2003). Self-recognition in the mirror emerges between 18 and 24 months of age, but what does this test measure? What skills are required to pass the test? And more importantly, which aspects of the self does this test assess?

Some researchers have argued against an in-depth interpretation of visual self-recognition, suggesting that successful self-recognition is an index of the mere detection of matching visual and kinaesthetic information (Heyes, 1996; Mitchell, 1993), or the understanding of the mirror's proprieties, related to cognitive development (Loveland, 1986). Many others have proposed that visual self-recognition indicates a broader sense of self, which goes beyond the recognition of physical features, encompassing a knowledge of self-other distinction and abstract self-representations (Brandl, 2016; Rochat, Broesch, & Jayne, 2012; Rochat & Zahavi, 2011). Additionally, it has been hypothesized that self-recognition in the mirror may highlight the ability to understand how others perceive us. This idea is consistent with a social construction of the development of the sense of self, where others play the role of *social mirrors* (Prinz, 2012; Rochat et al., 2012; Rochat & Zahavi, 2011; Zahavi, 2009). According to this view, emerging self-awareness is highly interconnected with social cognitive abilities that develop during the first years of life. However, despite the universal importance of the sense of self, the mechanisms behind its development and its relationship with social cognitive abilities are still unclear.

This field of research has progressed very little since the development of the MSR task in 1972. Despite the controversy surrounding this task, no real alternative test to assess self-awareness in infancy has been developed, and our knowledge of this topic is still very limited to what has been studied decades ago. A lack of tasks to assess the level of self-awareness in infancy, a lack of agreement over what the self 'is', and the abstract nature of the topic are factors that have likely limited the progress on understanding the mechanisms underlying the development of the self. However, this is in contrast to a broad volume of literature on the self in adults, mostly in terms of neuroimaging studies. Work in adults has demonstrated that there are a variety of brain regions (which are most often organised in brain networks) responding to, and associated with, physical and abstract self-awareness. Two regions in particular seem to play a fundamental role in self-processing in adulthood as part of more complex brain networks: the prefrontal cortex and the temporoparietal junction. However, whether these same regions are engaged in emerging self-awareness is yet to be investigated. Nonetheless, tools to explore brain connectivity development in infancy are limited.

Some researchers have recently hypothesized a relationship between self-other differentiation and social cognitive abilities (Santiesteban et al., 2012; Southgate, 2018; Steinbeis, 2016), which has renewed interest in exploring mechanisms underlying emerging self-awareness. For example, it has been shown that imitation–inhibition training, where participants were instructed to lift a different finger from the one displayed on the screen, enhances self-other processes in adults (Santiesteban, White, et al., 2012). In fact, the authors suggested that inhibition of imitation requires a clear distinction between self and other, as the participants must perform their own

motor intention rather than the one of the observed person (Brass & Heyes, 2005; Santiesteban, White, et al., 2012). Moreover, Santiesteban suggested that the same process of distinguishing between self and other intentions is necessary for higher cognitive processes, such as theory of mind, which is the ability to represent others' mental states (Santiesteban, White, et al., 2012). Along this line, it has been hypothesized that a lack of self-perspective in young infants, and therefore the absence of a conflict between self and other perspectives, may be a possible explanation for young infants' successful performance on tasks requiring them to take the others' perspective (Southgate, 2018). Given this, a deeper understanding of the development of the sense of self is needed, and this PhD work aims to fill some of this gap. The purpose of this thesis is to bring the topic of the development of the sense of self into research again, providing evidence for the validity of the MSR task, exploring neural underpinnings of the emerging self-awareness, and understanding how the development of the sense of self is related to social interactions early in life.

1.1.1 Glossary of the self, a note on terminology

The disagreement and confusion regarding the terminology related to the topic of the self is one of the biggest issues in this field of research. Therefore, the present section aims to clarify the uses and meanings of the different terms commonly associated with sense-of-self research. This glossary is intended as a guide for the terms used in this PhD thesis.

The term *sense of self* encompasses all the different aspects and features of the self, which are summarised hereafter. Sometimes researchers

use this term to describe only a particular component of the self-concept, and generalise this single aspect to the entire sense of self.

Bodily self-perception (or bodily self-awareness) describes the perceptual feeling that one's body belongs to oneself. As soon as we pay attention to our own body, we become aware of our own physical sensations, feelings, and pain. This term also refers to the perception of one's own body in space (De Vignemont, 2013). Bodily self-perception appears to be achieved early in development. For example, it has been shown that immediately after birth, infants are able to differentiate between self-touch and non-self touch (Rochat & Hespos, 1997), and there is evidence for cortical activation in response to body-related contingencies similar to that observed in adults, also in infants as young as 5 months of age (Filippetti, Lloyd-Fox, Longo, Farroni, & Johnson, 2015). Bodily self-awareness overlaps with what some researchers consider a *core self*, which has been hypothesized to be present from birth, suggesting an early differentiation between the individual and the environment (Gallagher, 2000; Zahavi, 2003, 2010). This topic is the focus of section 1.2.

Self-recognition has been originally defined as the recognition of one's own physical features (Brooks-Gunn & Lewis, 1984). However, self-recognition in the mirror, which emerges at around 18 months (Amsterdam, 1972; Rochat, 2003) has been argued to be an indicator of the development of a broader, more abstract sense of self, so-called *self-awareness* (Prinz, 2012; Rochat, 2003; Rochat & Zahavi, 2011) (the debate about the significance of visual self-recognition is broadly discussed in section 1.3). *Self-awareness* is defined as conscious knowledge of oneself as a particular individual with specific physical and mental features (Rochat, 2003). One may wonder whether there are any stages where the infants are able to recognise themselves without having

necessarily achieved a broader level of self-awareness. However, to date there is no evidence for self-recognition without self-awareness.

In line with this, the term *self-representation* is a term used to describe the idea of 'me', which is achieved with self-awareness. Having a form of self-representation means becoming the object of one's own attention (Lewis & Carmody, 2008). Consistent with a richer interpretation of the MSR task, infants that exhibit self-recognition have self-representation as well, and therefore they are able to perceive themselves not only as subjects, but also as objects of observation (Lewis & Carmody, 2008; Rochat, 2003; Rochat & Zahavi, 2011).

The term *self-consciousness* is sometimes used as synonymous with self-awareness, meaning the abstract and mental components of one's own features, such as mental states, inner feelings, and thoughts (Mead, 1934; Rochat 2009). However, others have used self-consciousness to describe the *strong first-person phenomena*, where one is able to think of and reflect about oneself (Baker, 2000, p.68). In this view, self-consciousness is achieved only when the child is able to refer to oneself. Therefore linguistic abilities and the use of the personal pronouns are necessary developmental steps for being considered self-conscious (Baker, 2000; Zahavi, Grünbaum, & Parnas, 2004).

The *sense of agency* is considered to be the perception of oneself as an executor of actions, i.e. having a sense of control over one's actions (Moore, 2016). There are different shades of the terms sense of agency, as some consider this to develop along with bodily self-perception, as it involves a feeling of control over one's own body (Gallagher, 2012; Tsakiris, Longo, & Haggard, 2010). However, others consider the sense of agency as linked to higher-order cognitive processes, with capacities of reflection on one's own

actions (Stephens & Graham, 1994), therefore achieved only later in the development.

Table 1.1 summarises the research terms used throughout this thesis.

Aspects of the sense of self	Definition
Bodily self-perception	The perceptual feeling that one's body belongs to oneself
Self-recognition	Recognition of one's own physical features
Self-awareness	Conscious knowledge of oneself as a particular individual with specific physical and mental features
Self-representation	the idea of 'me', being an object of one's own attention
Self-consciousness	Awareness of one's own mental states / the ability to refer to oneself
Sense of agency	Perception of oneself as an executor of actions and as having control over one's own actions

Table 1.1. Summary of the terminology used in this PhD thesis.

1.1.2 Research aims

The overall aim of the current PhD thesis is to try to elucidate the mechanisms underlying emerging self-awareness. To do this, I will focus on the exploration of its neural underpinnings in the first years of life, with an emphasis on brain networks to help describe the complexity of this phenomenon. This is motivated by the fact that much work has explored the neural underpinnings of self-awareness in adults, and thus investigating the brain regions recruited during tasks proposed to measure self-awareness in infants has the potential to shed light on both the phenomenon of self-awareness early in development,

and on the validity of the tasks that are believed to index self-awareness. To explore brain activation and networks involved in emerging self-awareness, I used functional near-infrared spectroscopy (fNIRS), a neuroimaging technique suitable for awake infants and toddlers. A background to this method is provided in Chapter 2. The development of techniques for connectivity analyses, which were previously underdeveloped for this neuroimaging method was an important aim of this PhD project, with the ultimate aim of applying them to understanding the development of self-awareness. Chapter 3 describes two preliminary studies aimed at developing techniques for investigating functional connectivity with fNIRS data. While ultimately, time did not permit one of these methodological advancements to be applied to our own data, it is hoped that such techniques provide a valuable contribution to the tools available to the field. Nonetheless, the second study in Chapter 3 presents a longitudinal investigation into the development of the spontaneous functional connectivity, providing a data analysis pipeline that is used in Chapter 4.

Chapter 4 is the first chapter aimed at investigating the neural underpinning of self-awareness. The previous adult literature has revealed a link between a functional network of brain regions engaged during rest and self-processing (Davey, Pujol, & Harrison, 2016; Kelley et al., 2002; Kircher et al., 2000; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005). fNIRS allowed the recording of spontaneous blood fluctuations in the brain in awake infants at rest to investigate the relationship between self-awareness and connectivity between crucial areas of the functional network previously explored in adults. Moreover, there is substantial adult literature showing that core brain regions of the Default Mode Network (DMN) are engaged in self-processing, for example, while subjects are looking at their own image or

listening to their own voice (for some examples see Committeri et al., 2007; Kampe, Frith, & Frith, 2003; Mort et al., 2003; Platek et al., 2006; Staffen, Kronbichler, Aichhorn, Mair, & Ladurner, 2006; Sugiura et al., 2008, 2012). However, what is happening in the developing brain during self-recognition has yet to be investigated. During the first years of life, the detection of temporal contingency between observed and performed movements has been suggested to be an important cue for self-recognition (Rochat, 2003). Therefore, in Chapter 5, I took advantage of fNIRS to acquire brain responses while 18-month-olds were looking at themselves. This was one of the first investigations into the neural correlates of self-processing in the developing brain.

As already mentioned, some researchers have highlighted the fundamental role of others in the construction of the self and how they act as *social mirrors* (Prinz, 2012; Rochat, 2003; Rochat & Zahavi, 2011). Based on this approach, a further aim of this work was to explore how self-awareness can influence social interactions. To test this, I focused on mimicry, the spontaneous tendency to copy others, which is known to play an important role in affiliation and in mediating social relationships. In Chapter 6, I explored how mimicry of models belonging to in-group or out-group might be mediated by emerging self-awareness. Furthermore, I investigated whether the mothers' tendency to imitate their 4-month-olds' facial actions is a predictor of emerging self-awareness at 18 months. For this part of the thesis, I integrated the use of fNIRS with electromyography (EMG) to record subtle muscle activation.

This PhD thesis can be divided into three main sections: i) methodological improvements of fNIRS analysis techniques to explore the brain networks supporting the emergence of self-awareness; ii) an investigation of the neuronal underpinnings of emerging self-awareness in

awake infants; iii) an investigation of how others interact with an infant's emerging self-awareness and their possible influence on its development.

In summary, this PhD thesis addresses the following questions:

- What is the significance of visual self-recognition in infancy?

- May functional connections in brain networks at rest be a marker of self-awareness in infants, as it is in adults?

- Are the brain areas that are typically engaged in adult self-processing also engaged in emerging self-awareness?

- What role do others play in the construction of our sense of self? How does self-awareness influence how infants interact with the social world?

- Which is the relationship between emerging self-awareness and mimicry?

The remainder of this chapter provides an overview of the psychological theories concerning the development of the sense of self, and of the different views on the significance of visual self-recognition. I summarise the theories related to the self-other relationship and the impact of self-awareness on the development of social cognitive abilities in the first years of life with an emphasis on mimicry. Lastly, a literature overview of the neuronal correlates of the sense of self in infancy and in adulthood is presented.

1.2 Theories on the development of the sense of Self

1.2.1 Hypotheses regarding a minimal self

Do we have a sense of self from the moment we are born? Or do we instead gradually develop this through our experiences with the environment? This has been one of the burning questions since the origin of psychology as a science.

One of the first psychologists that described newborns' experiences with the environment was William James in 1890, who stated that "the baby, assailed by eyes, ears, nose, skin, and entrails at once, feels it all as one great blooming, buzzing confusion" (James, 1890, p.488). This 'confusion' suggests a disoriented infant, destitute of any sense of self, in an initial state of non-differentiation between themselves and the environment. Along these same lines, Jean Piaget spoke of newborns as "a visually perceiving two-dimensional tableaux that is completely undifferentiated as to components due to activity of self and components due to independent events in external reality" (Piaget, 1954).

This lack of differentiation between the infant and the environment has not been proven by empirical evidence and is mainly based on the idea of underdeveloped visual space perception at birth. This general framework, taken for granted in developmental psychology for several years, was challenged by James Gibson (1966), who affirmed that perceptual systems are the first vehicle for infants interacting with the world and that the perception of the world is their first step towards the perception of themselves (Gibson, 1966). This new proposal, extremely revolutionary for that time, helped to inspire the subsequent theories on the development of the sense of self.

Consistent with Gibson's (1996) theory, the past thirty years of neuroscientific and psychological research have demonstrated that newborns and infants have a more developed self-concept than previously thought. Nowadays, researchers agree that we come into the world with at least a 'minimal' sense of self; a foundation that allows us to interact with the environment (Gallagher, 2000; Zahavi, 2017). Despite some differences in terminology, the presence of a core self has been highlighted by many during the last decades. The biologist Edelman (1990) spoke about *primary consciousness,* which allows us to be mentally aware of the stimuli in our environment, and distinguished this from higher-order consciousness, which entails a more developed idea of our own self. Primary consciousness only provides a sense of ourselves in the measurable present, not in the past or future (Edelman, 1990, 2005; Edelman, Gally, & Baars, 2011).

Similarly, Neisser (1988) defined the core self as the *ecological self,* which is present from a very early age as a manifestation of our interactions with the world. This is the first of five self-related domains that form a complete self-concept, with the other four domains being the interpersonal self, which is engaged in social interactions; the conceptual self, which involves the mental representations of oneself; the temporally extended self, which comprehends one's own life story; and the private self, which provides insight into one's own thoughts (Neisser, 1988).

Contemporary philosophers and scientists have also supported the idea of a *core self* and many of them agree that there can be no experience without a sense of self (Gallagher, 2000; Zahavi, 2003, 2010, 2017). Gallagher (2000) and Zahavi (2003, 2010) argued that there has to be *something*, even if it is very basic and immediate*,* from the very beginning of life. Blanke and Metzinger

(2009) described the basic and pre-reflective experience of being a self as 'minimal phenomenal selfhood', but mainly related this to aspects of bodily self-awareness.

Recently Zahavi (2017, p.689) stated that, "it is a self-awareness rooted in the first-personal *givenness* of its experiences, in the intrinsic self-manifesting character of its experiential life". This precursor and primordial self might be considered the foundational part of selfhood. However, Zahavi does not intend this primordial self a fully-fledged sense of self, as the primordial self is still far removed from the complex components of the self, such as self-awareness, self-consciousness, and a sense of agency, which emerge later in development (Zahavi, 2017). Indeed, the label *minimal* is employed by Zahavi to highlight how limited this core is and how much more has to develop to account for a complete and multifaceted idea of the human self (Zahavi, 2014).

Infant studies showing a positive relationship between proprioceptive skills from birth are considered an evidence for a minimal self from birth (Rochat, 1995; Rochat & Striano, 1999, 2000; Zahavi et al., 2004). In this view, infants are described as behaving as actors in a meaningful environment from birth as opposed to being a mere collection of reflexes. Inter-sensory coordination and intermodal perception are known to exist right after birth (for a review see Lickliter, 2011), suggesting that the presence of a core self allows us to efficiently interact with the environment (Rochat, 1995). This theory is based on studies showing visual-auditory coordination (for some examples see Bremner et al., 2011; Castillo & Butterworth, 1981; Fenwick & Barbara, 1998) and visual-tactile coordination (for some examples see Bower, Broughton, & Moore, 1970; Freier, Mason, & Bremner, 2016; Meltzoff & Borton, 1979; Streri,

1993) in very young infants, indicating that they can integrate information from different perceptual systems concerning the same external objects. Further evidence to support the existence of a minimal self from a very young age is based on their ability to perform and their preference to look at goal-oriented actions, and the active exploration of the environment, which rely on bodily self-awareness and the perception of self-produced movements (Butterworth & Hopkins, 1988; Craighero, Leo, Umiltà, & Simion, 2011; Rochat, 1995; Rochat & Striano, 2000). Other researchers belonging to this tradition often refer to Meltzoff and Moore's (1977, 1983, 1989) works, which argued that neonatal imitation provides evidence of innate self-awareness (Gallagher & Meltzoff, 1996; Meltzoff, 1988; Meltzoff & Moore, 1977, 1983, 1989). However, further studies failed to replicate these findings, suggesting that the innate nature of imitation is controversial and questionable (Anisfeld, 1996; Anisfeld et al., 2001; Welsh, 2006; for a recent review on this topic see Oostenbroek, Slaughter, Nielsen, & Suddendorf, 2013).

It has also been also shown that infants are able to seek and explore contingent stimulations, argued to have evolved in order to provide input for a developing rudimentary representation of their bodily self (Gergely, 2004). This so-called 'contingency detection module', aimed to analyse the temporal conditional probabilities of stimuli and responses, has been hypothesised as innate and it would give raise to a *primary subjectivity* in the infant (Gergely & Watson, 1996, 1999). Empirical research seems to support this idea, showing that very young infants are able to appreciate differences between contingent and non-contingent movements, even from one month of age (van der Meer, van der Weel, & Lee, 1995). By two months, infants seem to explore the auditory effects of their actions (Rochat & Striano, 1999) and show a higher level of

interaction with a self-live video rather than a self-delayed one (Reddy, Chisholm, Forrester, Conforti, & Maniatopoulou, 2007). These findings support the idea of an inborn tendency to discriminate temporally contingent and non-contingent stimuli and might support the presence of an early 'ecological self', a term from Neisser's (1988) theory, that suggests a perception of oneself as an entity distinct from the environment. However, despite the fact that the ability to detect contingencies between performed and observed movements is present from early on (Reddy et al., 2007; Rochat & Striano, 1999), children do not appear to use this information for self-awareness until around 18 months of age, as evidenced by the mirror-self-recognition task (Amsterdam, 1972; Rochat, 2003).

This first section provided an overview of the evidence for a minimal sense of self from very early in life. This seems to be the crucial core of one's own selfhood that allows the interactions with others (Zahavi, 2017). With evidence of efficient interactions with the world (Neisser, 1998; Rochat, 1995), capabilities of integrating multisensory information (Lickliter, 2011), and preference for self-contingence stimuli (Gergely, 2004; Rochat & Striano, 1999) from very early after birth, James's (1980) idea of an infant undifferentiated from the environment has been largely rejected during the last few decades. Although these results support a minimal self in young infants, they do not explain the mechanisms underlying a more advanced sense of self and self-awareness, which are the main focus of this PhD project.

In fact, with this thesis, I aimed to go beyond the understanding of the development of this first core-self and explore the mechanisms that could contribute to self-awareness. As self-awareness is conceived as *the conscious knowledge of oneself as a peculiar individual with specific physical and mental*

features (Rochat, 2003), it encompasses but is not limited to the minimal sense of self. This suggests that to speak of self-awareness, evidence of abstract self-representation and knowledge of one's own mental features is needed. As the last few decades of research on the development of the sense of self have mostly focused on bodily self-perception and rudimental minimal self, there is a clear need for a deeper understanding of the mechanisms underlying the development of awareness of one's own person and features, which this PhD work aims to investigate.

1.2.2 How social interaction contributes to defining one's own sense of self

In the more recent updates to the *minimal self* theories, it has been proposed that a social component of the self, i.e. interaction with others, plays a fundamental role in the emergence of the self from very early in life (Kyselo, 2016; Zahavi, 2017). This is supported by evidence showing that self and other representations share neural correlates (Decety & Sommerville, 2003) (see section 1.5.3 for more details). However, how perceptions of the self and of others are integrated, and which lead to the understanding of the other perspective, is still unclear.

The relationship between self- and other-concepts, and which of these two aspects develops first has been a much debated topic in developmental psychology. The idea of the sense of self as a social construct found its origins in the early 20th century, when social psychologists advanced the idea of a *social genesis of the self*. For example, Cooley proposed the concept of the *looking-glass self* (Cooley, 1902), where interpersonal interactions are fundamental for

the formation of the self. Consistent with this view, Mead talked about the importance of *being an object to oneself* and that the construction of the self happens only when the subject adopts the other's attitude to oneself (Mead 1934; Mead & Morris, 1962)*.*

Contrary to the idea of a socially shaped self proposed by Cooley and Mead, some other more recent theories have proposed that the understanding of one's own mental states and access to one's own mind were fundamental requirements for the understanding of, and interaction with, others. This approach is known as the *like-me* perspective, where knowledge of one's own inner states and feelings are considered to be fundamental tools to access perceptions of others (Gallese, 2005; Meltzoff, 2007; Meltzoff & Moore, 1997).

More recently, researchers such as Zahavi, Prinz, and Rochat referred back to Cooley and Mead's approach and, in contrast to the *like-me* perspective, they remarked the importance of social interactions for the formation of the self (Prinz, 2012; Rochat & Zahavi, 2011). In this approach, minds are viewed as open and interchangeable systems and the development of subjectivity is defined through communication and social interactions. Compared to the view presented by the *like-me* perspective, where each mind is considered an isolated and closed system, the *open minds* theory supports the idea of a self that is socially shaped, with others being necessary for the understanding and development of our inner states and minds (Hauf & Prinz, 2005; Prinz, 2003, 2012). As others' minds are used to reflect and explore our own subjectivity, proponents of this view consider others to be *social mirrors* (Prinz, 2012; Rochat & Zahavi, 2011)*.* As with the reflection of one's own image in the mirror individuals detect their own movements and physical appearance, similarly through the relationships with others, individuals experience how others

perceive themselves in terms of mental and inner features. In fact, while acting in the social environment, infants learn from others' responses how their own actions and inner states are perceived by others (Rochat, 1995). This process is vital to the formation of the self and to helping us perceive ourselves as objects of observation, rather than simply subjects (Rochat, 2003; Rochat & Zahavi, 2011). Prinz described the *like-me perspective* as a *self-naturalism* approach, as in this view the self seems 'an organ of the mind' that develops with the brain (Prinz, 2012). The *like-me* perspective does not take into account the role of others in shaping the self, but instead the interactions with others are actually a product of the development of the self (Prinz, 2012). On the contrary, the *open minds* paradigm alternatively suggests a *like-you* perspective, characterised by a constant relationship with others, which acts as a foundation for the gradual construction of one's own self (*self-constructivism*) (Hauf & Prinz, 2005).

The first fundamental *other* interacting with ourselves in early life is our mother or carer, who has a particular influence on shaping our sense of self. Early social exchanges, such as proto-conversations, taking turns, early imitations, and action understanding are the foundations of the dynamic interchanges between *open minds* (Prinz, 2012). It is worth mentioning, however, that both the *like-me* and the *like-you* perspectives consider active interactions with the mother as empirical support for their approaches. While the *like-me* perspective considers early social exchanges as evidence of self-awareness that has already been shaped, the *like-you* perspective thinks of these exchanges as evidence of an on-going process that indicates the gradual development of self-awareness (Meltzoff & Moore, 1997; Prinz, 2012).

More research is needed to clarify whether relationships with others are causes or consequences of emerging self-awareness and to provide further

empirical evidence for the social nature of the self. Table 1.2 summarises the main characteristics of the *like-me* and the *like-you* perspectives discussed in this section.

	Like-me perspective (Meltzoff, Gallese)	Like-you perspective (Rochat, Prinz, Zahavi)
Development of one's own mind	Self-naturalism: the self develops first and it is based on self-knowledge that one can understand others	Self-constructivism: through interactions with others, one can construct the self
Relationship between own mind and other minds	Closed minds: individuals develop subjectivity by themselves and each mind is an isolated system	Open minds: social shaping of the mind, others act as social mirrors

Table 1.2. Summary of the two main views of self-other interactions.

1.3 Visual self-recognition and the mirror-self-recognition task

1.3.1 The mirror self-recognition task, its development and procedure

Visual self-recognition has been proposed by many as a possible indicator of self-awareness (for a review see Suddendorf & Butler, 2013), and thus the so-called Mirror Self-Recognition test has become the primary indicator of self-awareness in early life. In a landmark paper in 1970, Gallup showed self-recognition in non-human primates for the first time (Gallup, 1970). In this original experiment, Gallup tested four chimpanzees who had never been

exposed to a mirror. After some days of habituation with the mirror, mirror-aided self-directed behaviours were observed, which were interpreted by Gallup as evidence for self-recognition in chimpanzees (Gallup, 1970). In a second version of this experiment, Gallup (1977) introduced a new procedure where the faces of the chimpanzees were marked while they were under anaesthesia and their reactions in front of the mirror were tested again. Mark-directed responses were observed, such as attempts to touch the marked area on their faces through visually guided mirror feedback (Gallup, 1977). Self-recognition using this task has been demonstrated in several other great apes (Anderson & Gallup, 2011; Hauser, Kralik, Botto-Mahan, Garrett, & Oser, 1995; Rajala, Reininger, Lancaster, & Populin, 2010; Schilhab, 2004; Suarez & Gallup, 1981). Evidence for self-recognition has been observed also in dolphins (Marino, Reiss, & Gallup, 1994; Reiss & Marino, 2001), birds (Prior, Schwarz, & Güntürkün, 2008), and elephants (Plotnik, de Waal, & Reiss, 2006). However, while the findings on great apes have been widely replicated, there is very little evidence for replication on dolphins, birds and elephants, therefore these results must be interpreted with caution. Interestingly, it is those species closest to humans (i.e. gorillas, chimpanzees, and orangutans) that pass the MSR task, while the less related groups (e.g. gibbons and monkeys) failed to pass. This finding suggests that self-recognition may have evolved relatively recently (Schilhab, 2004; Suddendorf & Butler, 2013).

Scepticism as to whether non-human primates can really recognise themselves has been shown by Heyes (1994, 1995), who argued that self-recognition depends only on artefacts related to the anaesthetic recovery. Heyes interpreted self-directed and mark-directed behaviours as mirror-independent behaviours rather than signs of self-recognition (Heyes, 1994a,

1995). However, further analyses of the temporal patterning of mark-directed and non-mark-directed behaviours showed an increase of mark-directed touches (Gallup et al., 1995; Povinelli et al., 1997. For critical reviews on methodology and interpretation of self-recognition in non-human primates see De Veer & Van Den Bos, 1999; van den Bos, 1999; Schilhab, 2004).

Using a similar procedure to the one used with animals, the MSR task (also known as the *rouge test*) was adapted for use with infants in 1972 by Amsterdam (Amsterdam, 1972). In this first study, 88 children aged between 3 and 24 months were tested to assess their self-image reactions in front of a mirror. During the first year of life, the image in the mirror is likely to be perceived as another infant, and it is only after the second year of life, particularly between 18 and 24 months of age, that toddlers start to show signs of self-recognition. While half of 18-month-olds tend to recognise themselves in the mirror, by 24 months, most of the children 'pass' the MSR task (Amsterdam, 1972; Rochat, 2003). For the MSR procedure used nowadays, the experimenter covertly marks the child's cheek or nose, usually using red lipstick. The children's reactions in front of the mirror after the mark has been placed are the focus of the test, as children with self-recognition capabilities should identify something unusual on their faces. The toddlers that exhibit mark-directed behaviours are categorised as 'recognisers', though the definition of mark-directed behaviour differs across studies (e.g. whether toddlers have to touch the mark exactly, touch in the vicinity of the mark, or simply touch their face) (for a review on different criteria for mark-directed behaviours Kärtner, Keller, Chaudhary, & Yovsi, 2012). It is also unclear whether toddlers should be classed as 'recognisers' if they show self-referential pointing gestures, if they stare at the marked face, or if they say their own name.

More commonly, toddlers that exhibit behaviours at the edge of self-recognition are categorised as 'ambiguous' (Kärtner, Keller, Chaudhary, & Yovsi, 2012). All other behaviours fell in the Non-Recognisers category. 'Non-recognisers' usually bang on the surface of the mirror, kiss or point at their mirror image, and laugh and interact with the reflected image. It is likely that looking behind the mirror indicates that the infant believes the reflected image belongs to another infant.

1.3.2 What does the mirror self-recognition task measure? Evidence for and against a measure of self-awareness

As previously mentioned, the MSR task provides an index of self-recognition in a mirror, but many researchers have suggested that successfully passing this test is an indicator of a broader sense of self (e.g. Suddendorf & Butler, 2013). Gallup (1998) was the first to claim that self-recognition in the mirror is an index of self-awareness, because to recognise yourself you need to become the object of one's own attention. In both developmental and comparative psychology, however, there is an ongoing debate about the real significance of this task. What type of sense of self do we measure with this test? What are the cognitive skills necessary to pass this task? How does the participants' motivation change the outcomes of this task? Are there any cultural differences affecting the successful outcomes of this task that suggest that exposure to mirrors can influence self-recognition?

These are some of the open questions and criticisms regarding the use of this task that mean that visual self-recognition is not universally accepted as an indicator of self-awareness. Arguing against any richer interpretation of the MSR task than simple visual self-recognition, Mitchell (1993) proposed two

hypotheses to explain what drives mirror self-recognition. One hypothesis argues that a successful outcome on the MSR task might indicate nothing more than the detection of matching visual and kinaesthetic information, and the understanding of the mirror correspondence (*inductive theory*). The second hypothesis argues that mirror self-recognition might be driven by object permanence, which relates self-recognition in the mirror merely to the identification of one's own body-parts in the mirror. In fact, if the infants see one part of the body reflected and they know it belongs to the entire body, than they understand that the mirror reflects both the body part and the entire body (*deductive theory*). Neither the inductive nor the deductive theory links mirror self-recognition to anything beyond basic physical self-recognition. Indeed, Mitchell claimed that some individuals may pass the MSR task without necessarily having recognised their own image. The possible emergence of self-awareness is not even debated in Mitchell's theory. Self-awareness can be achieved either before or after the recognition of one's own image in the mirror, but according to Mitchell this is an aspect not assessed by the MSR task in any way (Mitchell, 1993). Loveland (1986) argued that the understanding of the proprieties of the reflective surface is a necessary skill to pass the MSR task, via "a continuous process through which information about different properties of the mirror is picked up and its significance gradually appreciated"(Loveland, 1986, p.20). According to this view, self-recognition is driven by cognitive development and requires the child to have mastered perceptual problems related to the reflective surface, and is therefore not related to emerging self-awareness. The overcoming of perceptual challenges, such as the symmetry of the mirror and perceiving parts of one's own body that are not usually accessible (e.g. the face) might more accurately define the outcome of the MSR

task (Loveland, 1986). The criticisms of the MSR task appeared in the years immediately following its development. However, most of the recent empirical evidence seems to support the very first meaning attributed to the MSR task proposed by Gallup (1982), and suggests that a successful performance in self-recognition draws on the broader capacity to collate self-representations. (Brandl, 2016; Gallup, 1982; Kärtner et al., 2012).

Indeed, consistent with this more conceptually rich interpretation, several studies aimed to explore an association between self-recognition in the mirror and other indexes of self-awareness. For example, success in the MSR task has been associated with empathy (Bischof-Köhler, 2012), personal pronoun use and pretended play (Lewis & Ramsay, 2004), which have been argued to reflect awareness of a psychological self (Brandl, 2016). Self-recognition in the mirror has also been associated with a capacity for 'symbol-mindedness', with the mirror considered a symbol of the representations of one's own body (Savanah, 2013). It has been shown that self-recognition between 18 and 24 months of age is related to other body parts, not just the face (Nielsen, Suddendorf, & Slaughter, 2006). This suggests that self-recognition might be based on expectations about physical appearance that are not restricted to the face, raising doubt about those that suggested that the special status of the face may be the reason for success in the MSR task (Mitchell, 1993; Parker, Mitchell, & Boccia, 1995).

Recently, some authors inferred an even more multifaceted interpretation of the MSR task than the one initially proposed by Gallup (1982). According to this new theory, passing the MSR task might indicate that, "the mental state or the idea of 'me' is that part of the self that makes reference to itself" (Lewis, 2011, p. 127), i.e. the ability to understand how others see you

and that you are not only a subject but also an object of observation (Lewis, 2011; Rochat, 1995, 2003; Rochat & Zahavi, 2011). Lewis (2011) and Rochat (1995, 2003) are two of the main researchers who subscribed to this view and there is a strong link between their interpretation of the MSR task and the idea of others as fundamental scaffolds for the emerging sense of self (as mentioned in the previous section). Rochat (2011) described how in one of Gallup's studies (1977), the chimpanzees who grew up in isolation failed to exhibit self-directed behaviours in front of the mirror (even after extensive exposures). After three months of group experience, however, these same chimpanzees showed signs of self-recognition (Gallup, 1977). This finding is consistent with the idea of a fundamental role of social interactions in the emergence of a sense of self, and highlights the social nature of emerging self-awareness (Rochat & Zahavi, 2011).

It has recently been proposed that the MSR task also assesses the ability to experience social emotions and that it provides evidence for the social connotations associated with success in this test (Rochat et al., 2012). In fact, while a large amount of literature argues for the presence of basic emotions (such as happiness, sadness, fear, or surprise) from very early in life (Ekman, 1992), social emotions (such as pride, guilt, or shame) require interactions with others to be experienced (Rochat et al., 2012). In the MSR task, shame or puzzlement are sometimes observed in some of the toddlers that exhibit self-recognition as soon as something unusual is detected on their faces. This is consistent with the idea of the MSR task as a test for understanding others' perceptions of oneself. To support this, Rochat et al. (2012) demonstrated the influence of the social environment on self-recognition by placing a sticker on the toddlers' face during the MSR task, with a similar sticker being worn by

everyone else in the room. Under this condition, participants were more hesitant to remove the sticker, whereas this hesitation was not exhibited when self-recognition was tested in a set-up in which the other people in the room did not wear the sticker (Rochat et al., 2012). Interestingly, children who have social impairments, such as autistic children, have also been shown to pass the mirror self-recognition task. However, these children show self-recognition with a flat affect and neutral expression, and do not display any sign of the embarrassment or perplexity often associated with a successful outcome of this test (Dawson & McKissick, 1984; Neuman & Hill, 1978; Rochat & Zahavi, 2011; Spiker & Ricks, 1984). However, Rochat's hypothesis about the development of social emotions associated with emerging self-awareness leaves unexplained why autistic children, who notoriously have deficits in recognizing other's perspectives (Frith & Happe, 1999), have no difficulties in passing the mirror test. To my knowledge, a systematic and objective assessment of the shame reaction during the MSR task has not been performed yet, therefore empirical evidence supporting the association between social emotions and emerging self-awareness are still needed, both in typical and in atypical development.

The MSR has been so influential within this field that Rochat's (2003) theory of the development of the sense of self is almost entirely based on his observations of behaviour in this context. His theory identified five stages, each of which is characterised by different reactions when in front of the mirror. At birth, the mirror is conceived as an extension of the environment (*confusion,* level 0), but the infant soon starts to perceive the peculiarity of this object (*differentiation,* level 1). During the first year of life, there is exploration of seen and felt movements (*situation,* level 2), culminating in self-recognition between 18 and 24 months of age (*identification,* level 3). The self then moves beyond

the here and now of mirror experience after the second year of life (*permanence,* level 4) and a completely abstract sense of self develops around 4-5 years of age (*self-consciousness,* level 5) (Rochat, 2003).

1.3.3 Cultural differences in the mirror self-recognition task

Despite some researchers suggesting that familiarity with mirrors does not correlate with the age at which children pass the MSR task (Priel & de Schonen, 1986), more recent cross-cultural studies have highlighted significant variation in the age at which visual self-recognition in the mirror is achieved. Infants between 18 and 20 months of age from urban Greece, Costa Rica, and Germany were compared to infants of the same age in a rural community in Cameroon (Keller et al., 2004). A greater proportion of urban children passed the test (more than 50%) compared to the rural children (less than 4%). However, these differences have been attributed to different parenting styles present in different cultures. In fact, a distal parenting style typical of urban societies, characterised by a high level of face-to-face interactions, emphasising autonomy and separateness, is more likely to lead to self-recognition rather than a proximal parenting style typical of rural societies, characterised by a high level of body contact, which promotes bodily closeness and interpersonal fusion (Keller et al., 2004, 2005). In line with this finding, a more recent study compared the level of self-awareness of infants from Scotland, who were exposed to distal parental style, Zambia, who were exposed to proximal parental style, and Turkey, who were exposed to a mixture of both. Scottish infants exhibited a higher success rate at the MSR task than infants from other cultures (Ross et al., 2017). Consistent with the findings of Keller and Ross, a study performed by Broesch, Callaghan, Henrich, Murphy and Rochat (2011)

showed absent or delayed signs of self-recognition in infants from Kenya, Fiji, Saint Lucia, Grenada, and Peru compared to urban and rural Canadians and Americans (Broesch, Callaghan, Henrich, Murphy, & Rochat, 2011). These finding seem to suggest that there are environmental factors that influence the emergence of self-awareness, which might not depend on cultural differences *per se*, but more on different parental styles related to the difference cultures. Therefore, it might be interesting to explore which other factors of the early parental-child relationship can influence the emergence of self-awareness.

However, a similar study performed with infants from urban German middle-class, rural Indian, rural Cameroonian, and urban Indian middle-class families suggested that success on the MSR task increased with age in all the sociocultural contexts, but that success rates were higher in urban families compared to rural ones (Kärtner et al., 2012). Contrary to the studies from Keller (2004, 2005) and Broesch (2011), Kartner et al. (2012) inferred that sociocultural differences do not explain variations in onset on the MSR task, but it is familiarity with the mirror or cultural norms that account for success on the task. As the interpretation of how cultural differences affect performance on the MSR task is quite controversial, further research is needed to clarify which other variables affect MSR task outcomes in different sociocultural contexts.

1.3.4 The role of different media and temporal contingency on visual self-recognition

Some studies have aimed to explore whether findings from the MSR task can be generalised to other methods of presenting one's own image, e.g. pictures and videos. Self-recognition in videos has been found to be more difficult than self-

recognition in mirrors (Suddendorf, Simcock, & Nielsen, 2007). It has been shown that self-recognition in videos delayed in time, or pictures, does not occur until around four years of age, suggesting children master the understanding of the self's endurance across time later on in their development (Povinelli, Landau, Perilloux, Landau, & Perilloux, 1996; Povinelli & Simon, 1998). A more recent study showed that self-recognition in delayed videos occurred at around 2.5 years of age (Skouteris, Boscaglia, & Searl, 2009).

These findings could suggest that successful visual self-recognition in the mirror indicates a *present self*, whereas passing the delayed video version of the test could demonstrate the presence of a *temporally extended self* (Suddendorf & Butler, 2013). The lack of eye-contact in the delayed videos has been proposed as a reason for the failure to self-recognise. Indeed, other non-human species who generally avoid eye-contact, such as monkeys, fail the classic mirror version of the self-recognition task (Hauser et al., 1995). The same asynchrony between the mirror and video versions of the MSR task has been replicated in infants tested on a video of their own leg, even though no eye-contact was required to succeed at the task (Suddendorf et al., 2007).

Moreover, a study in adults showed that there are different brain responses to self-live and self-delayed videos, supporting the peculiarity of the detection of temporal contingency when processing information about oneself (Sugiura et al., 2015).

1.3.5 An attempt at an alternative to the MSR task

To my knowledge, only one other task has been developed to assess self-awareness in infancy, known as the *trolley task* (Moore, Mealiea, Garon, & Povinelli, 2007). The idea came from Piaget's (1954) early observation of his

daughter sitting on a rag. She was trying to pick it up but was prevented from doing so by her own weight. Piaget suggested that objectification of the bodily self is reached when the infant develops the ability "to represent the body's spatial and causal relations with the external world" (Piaget, 1954). Similar to the challenge experienced by Piaget's daughter, in the trolley task, the child is required to push a toy shopping cart with a mat attached at the back of the cart. If the child steps on the mat to grasp the handle, the child's weight will impede the forward motion of the cart. Passing the task involves folding or moving the mat to the side and avoiding stepping on it so the trolley can be pushed.

The findings of the trolley task are consistent with those shown by the literature on the MSR task, with infants around 18 months of age successfully pushing the trolley, requiring the infants to master the contingent motion relationships between themselves and world (Moore, Mealiea, Garon, & Povinelli, 2007). Even though Moore et al. (2007) suggested that success at this task might underlie the presence of a broader self-concept than just bodily self-perception, no association between success at the trolley task and other more abstract self-awareness indicators has been tested for. Moreover, not many other studies have used the trolley task to assess emerging-self-awareness. A recent study found an association between a successful performance on the trolley task and a parenting style characterized by proximal contact (Ross et al., 2017). However, as mentioned in the previous section, this style of parenting has also been associated with a lower successful rate on the MSR task compared to other parenting styles (Ross et al., 2017). This might be consistent with the idea that this test assesses bodily self-awareness, with little implications for a broader sense of self.

1.4 The relationship between self-awareness and social interaction during the first years of life

1.4.1 Self-other distinction and self-other integration: two sides of the same coin

As described in section 1.2, recent theories in developmental psychology have suggested the importance of social interactions in relation to emerging self-awareness. Many social processes require human beings to understand and share others' perspective and feelings (i.e. self-other integration), while some other contexts necessitate a more clear separation between self and others' perspective in order to achieve an efficient social interaction (i.e. self-other distinction) (Decety & Sommerville, 2003; Sowden & Shah, 2014; Steinbeis, 2016) . Therefore, self-other distinction and integration are often conceived as two sides of the same coin (Santiesteban, 2014).

A shared representation between self and other is supported by a variety of empirical evidence. For example, it has been shown that people confuse their own traits with those of in-group members (Coats, Smith, Claypool, & Banner, 2000) and that others' performances might influence one's self-evaluation (Buckingham & Alicke, 2002). More importantly, shared representation between self and other seems to be the foundation of empathy, i.e. the ability to share others' affective experience (Decety & Jackson, 2006; Shamay-Tsoory, 2011; Singer & Lamm, 2009). However, having a shared representation does not imply a complete overlap, which would lead to confusion and emotional contagion (Decety & Sommerville, 2003). Therefore a distinction between self and other perspectives is also necessary, and there are

recent studies that provide evidence for this process, as well during social interactions.

Self-other distinction has been proposed to be the mechanism that underlies both processes at the perceptual-motor level, such as imitation, and also higher cognitive processes, such as theory of mind (Santiesteban, White, et al., 2012). Santiesteban exploited the inhibition of imitation, where participants were instructed to lift a different finger from the one displayed on the screen, to explore the relationship between self- and other- perspectives. It has been shown that training the inhibition of imitation facilitates a distinction between one's own actions and other' actions, where the ability to adopt the perspective of others was enhanced (Brass, Derrfuss, & Von Cramon, 2005; Santiesteban, 2014; Santiesteban, White, et al., 2012). Recently Tomova et al. investigated the role of oxytocin, a peptide known to increase salience of social signals (Bartz, Zaki, Bolger, & Ochsner, 2011), and therefore possibly implicated in social processes (Domes, Heinrichs, Michel, Berger, & Herpertz, 2007; Shamay-Tsoory & Abu-Akel, 2016). In Tomova's study, oxytocin has been found to improve self-other distinction in higher cognitive processes, i.e. a perspective taking task, but it had no effect on a perceptual-motor level, i.e. an inhibition-imitation task (Tomova, Heinrichs, & Lamm, 2018). However, a previous study that has been able to show an effect of oxytocin even on a perceptual-motor level (De Coster, Mueller, T'Sjoen, De Saedeleer, & Brass, 2014), therefore this topic would benefit of more research to clarify the role of oxytocin in self-other distinction.

While self-other integration and distinction in relation to social interactions have been widely explored in adults, we know very little about how these aspects are intertwined during ontogeny. However, as suggested by the

like-you perspective, one may think that others play a fundamental role in constructing one's own self-concept by acting as *social mirrors* (Prinz, 2012; Rochat, 2003; Rochat & Zahavi, 2011). This social construction of the sense of self is consistent with the rich interpretation of visual self-recognition (Rochat & Zahavi, 2011), as described in the previous paragraph. Therefore, it seems artificial to disentangle emerging self-awareness from interactions with others and the social environment. In fact, it is likely that the emerging sense of self might have implications for other social cognitive abilities, which are interactive by definition, and *vice versa.* Perspective taking, imitation, empathy, and emotional recognition are some of the important social cognitive abilities known to develop during the first years of life (Carpendale & Lewis, 2006). For example, evidence of young infants passing preverbal versions of the false-belief task, may be explained by the absence of a conflict between self and other perspectives, characterizing infants who have not yet developed self-awareness. Therefore, these infants may not be required to inhibit a self-perspective in order to focus on the other's perspective, as children with a clear self-other distinction should need to be able to do (Southgate, 2018). This is consistent with the idea that successful performance on a false-belief task in childhood might be related to a continuous balancing of mechanisms underlying self–other distinction, more than the child representing only the other's mental state (Steinbeis, 2016). The link between emerging self-awareness and the development of social cognitive abilities in the first years of life is still poorly understood, but studying how these two processes are related from early in life could elucidate how mechanisms of self-other integration and distinction interact in social interaction from the first years of life.

1.4.2 Emerging self-awareness and the development of mimicry

In this PhD thesis, I explore the relationship between emerging self-awareness and social interactions by focusing on mimicry, a form of imitation. Mimicry is the spontaneous tendency to copy others' actions and has been suggested to play a pivotal role in shaping social interactions and building relational bonds in everyday life (Lakin & Chartrand, 2003; Lakin, Jefferis, Cheng, & Chartrand, 2003). Mimicry has been extensively recognised as increasing affiliation and cooperation (Chartrand, Maddux, & Lakin, 2012; Cheng & Chartrand, 2003; Fischer et al., 2013; Stel et al., 2010) and as a modality of non-verbal communication (Bavelas, Black, Lemery, & Mullett, 1986). Therefore, although mimicry by definition constitutes the reproduction of others' actions, it has also been shown to serve important social functions (Trevarthen & Aitken, 2001).

While several studies have explored the social modulation of mimicry in adulthood (for some examples see Downing, Dodds, & Bray, 2004; Janina Neufeld, Ioannou, Korb, Schilbach, & Chakrabarti, 2015; Likowski, Mühlberger, Seibt, Pauli, & Weyers, 2008; Neufeld & Chakrabarti, 2016; Rauchbauer, Majdandžic, Stieger, & Lamm, 2016; Tramacere, Ferrari, Gentilucci, Giuffrida, & De Marco, 2018), research has only recently started to elucidate how social factors influence mimicry throughout the first years of life (de Klerk, Hamilton, & Southgate, 2018).

The link between emerging-self-awareness and imitation has been investigated by some. It has been demonstrated that there is a positive association between testing behaviours in front of the mirror during the MSR task and the tendency to imitate salient parts of observed actions at 14 months (Zmyj, Prinz, & Daum, 2013). Similarly, 18-month-olds that exhibited self-recognition in the mirror imitated more salient parts of the observed actions

than infants that did not exhibit self-recognition (Zmyj et al., 2013). In this study, the relationship between imitation and the detection of matching movements in the mirror is thought to be mediated by the detection of visual-motor contingencies. Moreover, it has been shown that the 18-month-olds that recognised themselves in the mirror imitated peers and models more synchronically than infants with a less developed sense of self, suggesting that emerging self-awareness allows the child to master self and other perspectives (Asendorpf & Baudonnière, 1994; Asendorpf, Warkentin, & Baudonni, 1996). However, an alternative account proposed a negative association between imitation and self-other processing, where the boundaries between self and other become blurred during mimicry (Georgieff & Jeannerod, 1998; Hale & Hamilton, 2016). Moreover, being mimicked might increase the overlap between self and other, where the other is perceived with more proximity (Ashton–James, van Baaren, Chartrand, Decety, & Karremans, 2007). From a developmental perspective, this hypothesis would predict that infants with a less advanced sense of self show a greater tendency to mimic others, as their self-other boundaries are weaker compared with infants with a more advanced sense of self. However, this would be in contrast with Zmyj (2013) and Asendorpf (1994, 1996) studies that showed a positive association between emerging self-awareness and imitation[1]. Therefore, more studies are needed to expand our knowledge of the relationship between self-awareness and social interactions, such as imitation and mimicry. On this respect, developmental

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[1] It is worth acknowledging that imitation and mimicry are not completely overlapping. Imitation is not only the mirroring of the other's actions, but it requires cognitive processes, such as the representation of action goals, which are not associated with mimicry, which is a spontaneous phenomenon (Southgate & Hamilton, 2008).

studies can inform our understanding of how these two processes are entangled from the first years of life.

1.5 Imaging the Self

The study of the neural correlates of self-awareness has been a target of interest for recent adult neuroimaging research. Studying the neural underpinnings of emerging self-awareness might shed light on the mechanisms underlying its development, and its link with social interactions. Moreover, as studies in adults have been able to identify different neural substrates in relation to different component of the self, investigating whether the same brain regions are engaged in the development of the sense of self might elucidate which components of the self are emerging in the first years of life.

While neuroimaging studies aimed to investigate neural underpinnings of self-awareness in development are limited, research with adults has progressed in identifying several areas of our brain that are engaged in self-processing. However, as discussed in the first paragraph, the existence of multiple definitions and the multifaceted nature of the sense of self complicates the operationalisation of the variable of interest. Our knowledge of the neuronal substrates of self-awareness is still limited compared to other psychological domains, and not always consistent. The next section provides an overview of the few developmental studies performed in infancy and a literature review of the neural underpinnings of self-awareness based on adult research.

It is worth noting that a review of the adult studies on the neural underpinnings of the sense of self is not performed here with the intent of equating the infant brain to the adult brain. There is evidence of some infant

brain networks that are highly specialised from very early in life and that have similar functions and connections to adult brain networks (although not without further changes related to age and experience), such as the brain regions related to auditory and visual networks (Gao, Alcauter, Smith, Gilmore, & Lin, 2015; Lin et al., 2008; Liu, Flax, Guise, Sukul, & Benasich, 2008), language (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; May, Byers-Heinlein, Gervain, & Werker, 2011), and social perception (Blasi et al., 2011; Sarah Lloyd-Fox et al., 2009).

Many more networks gradually develop with the progressive specialisation of their brain regions' roles, however, and each network component adjusts its response to optimise the overall network functioning (Johnson, 2011), e.g. the brain regions supporting executive and cognitive functions (Diamond, 2009; Durston et al., 2006). Moreover, when approaching the study of brain function in developmental neuroscience, one has to acknowledge that the infant brain undergoes several changes in shape and morphology that are likely to affect its function (Johnson, 1997). Therefore, when planning developmental studies, an accurate literature review should not be based only on previous adult findings.

Due to the very limited number of studies that investigate the neural underpinnings of self-awareness in infancy, however, it was necessary to look at the adult research and this constituted a valuable starting point for this PhD work. Research investigating the neural correlates of the self in infancy is limited to three studies and it is summarised hereafter.

1.5.1 Neuroimaging research in infancy

To my knowledge, little research has been done into the neural correlates of self-recognition in the developing brain. Therefore, one of the aims of this PhD project was to shed light on the brain areas engaged in the developing sense of self.

The first study that aimed to define the neural markers of the emerging sense of self was performed by Lewis et al. (2008). Infants between 15 and 30 months of age were tested for grey matter maturation in the brain regions associated with the development of the sense of self and self-representation using MRI. The MSR task, a measure of personal pronouns use, and pretend play, assessed the participants' levels of self-representation, intended as the idea of 'me', as object of observation in others' minds (Lewis & Carmody, 2008). Left TPJ maturation was significantly correlated with self-representation, particularly the results of the MSR task, and with other-directed pretend play. This was the first study to confirm the fundamental role of the TPJ in self-processing in infancy. Interestingly, this effect is not age-dependent as self-representation still accounts for most of the variance in TPJ maturation even when age is placed as a covariate in the model (Lewis & Carmody, 2008). Lewis and Carmody (2008) did not find any effect of self-representation related to maturation of other brain regions, highlighting the specificity of the TPJ in self-related processing. The non-significant relationship between brain maturation and self-processing was expected for regions outside the 'social brain'; however, frontal lobe maturation was reasonably expected to be associated with the development of the sense of self, as suggested by most of the adult studies (for some examples see D'Argembeau, 2013; Gusnard, Akbudak, Shulman, & Raichle, 2001; Heatherton et al., 2006; Qin & Northoff, 2011).

Despite this, Lewis and Carmody's study represented the first investigation into the neural correlates of the emergent sense of self and provided evidence for the TPJ as a key brain region in this process.

A second study investigated the neural correlates of self-processing in infancy with a focus on bodily self-representation. Using fNIRS, Filippetti (2015) showed the engagement of the STS and the TPJ when infants saw their own bodies in a live video compared to a delayed video. These results suggests the possible presence of precursors to bodily representation even in very young infants (Filippetti et al., 2015).

A recent study investigated the brain responses of 18-month-olds when they were looking at their own faces (Stapel, van Wijk, Bekkering, & Hunnius, 2016). Thirteen infants were presented with a picture of their own face, their caregiver's face, another participant's face, and the face of another participant's caregiver and their ERP responses were measured using EEG. The classic MSR task was also used to assess self-recognition in the mirror. The results showed that the N290 component, known to be related to face processing in infancy, was significantly different when the infants observed their own face compared to another infant's face. This result suggests that there are different patterns of response related to self and other-processing in infanthood, as highlighted by differences in the ERP components (Stapel, van Wijk, Bekkering, & Hunnius, 2016). In this study, no significant interaction between brain responses and MSR task outcomes was found. Stapel et al. (2016) argued that this was due to the inaccuracy of the MSR test in assessing self-recognition. However, it is possible that because the comparison between infants who recognised themselves and infants who did not was performed on a very restricted sample

of just 11 children, there might not have been sufficient power for a statistically meaningful comparison.

Although these findings suggest an early specialisation of the infant cortex for self-processing stimuli, our knowledge of the neural underpinnings of the sense of self in the developing brain is still very limited. To investigate the validity of our behavioural indicators of early self-awareness, it would be fruitful to explore whether the same brain regions related to self-processing in adults are engaged also in emerging self-awareness. Moreover, the investigation into the neural underpinnings shared between emerging self-processing and social cognitive abilities may inform the link between these two processes during the first years of life. Given the limited research performed so far on the developing brain, a look into the adult neuroimaging research is necessary. The next three sections present a literature review of the adult neuroimaging studies, focusing on physical self-awareness, self-other distinction and integration, and abstract self-processing.

1.5.2 Physical self-recognition

Several studies have explored the neural correlates of the self by investigating brain activation in response to one's own physical features, e.g. face or voice. An early study testing the brain's responses to self-processing found that participants' own faces elicited the P300 event related potential (ERP) component (Ninomiya, Onitsuka, Chen, Sato, & Tashiro, 1998). Previous findings have shown that the P300 component is enhanced for salient and motivationally relevant stimuli (Polich & Kok, 1995), suggesting the high relevance attributed by our brain to our own face. Several studies further replicated this finding, showing a higher P300 in response to both the

participants' own faces (Scott, Luciana, & Wewerka, 2005; Sui, Zhu, & Han, 2006) and to their names (Holeckova, Fischer, Giard, Delpuech, & Morlet, 2006; Müller & Kutas, 1996). This means that the P300 characterises the brain's response to general self-processing and is not dependent on the modality of the stimulus. Similarly, in a combined ERP and positron-emission tomography (PET)[2] study, the P300 amplitude in response to the participants' own names was shown to be highly correlated to the blood flow in the core regions of the DMN (Perrin et al., 2005), which is a network that has been associated with self-processing (Raichle et al., 2015).

Activation of the medial prefrontal cortex (mPFC) and the precuneus/posterior cingulate cortex (PCC) has been shown in self-recognition tasks (Kampe, Frith, & Frith, 2003; Platek et al., 2006; Staffen, Kronbichler, Aichhorn, Mair, & Ladurner, 2006; Sugiura et al., 2008, 2012), while the temporoparietal junction (TPJ) has been found to be engaged mainly in bodily self-perception (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke, 2005; Chen & Huang, 2017). TPJ activation has also been shown during the integration of multisensory events attributed to our body and as part of the building of an internal model of body awareness (for some examples see Bottini, Bisiach, Sterzi, & Vallar, 2002; Committeri et al., 2007; Mort et al., 2003; Tsakiris, Costantin, & Haggard, 2008).

There is an ongoing debate in the literature regarding the neural correlates of the self and their possible hemispheric specialisation, especially for self-face recognition (Gillihan & Farah, 2005). The results are inconsistent, with some studies showing that self-recognition is supported by both

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[2] Positron-emission tomography (PET) is a nuclear functional imaging technique. It detects brain activation based on the assumption that areas of high radioactivity are associated with brain activity (Kim et al., 2006).

hemispheres (Sperry, Zaidel, & Zaidel, 1979; Sugiura et al., 2005), while others suggest it is supported predominantly by the right hemisphere (Keenan, Wheeler, Platek, Lardi, & Lassonde, 2003; Preilowski, 1979) or the left hemisphere (Turk et al., 2002). Most of the recent adult research seems to confirm the superiority of the right hemisphere in self-recognition tasks, but with an engagement of complex bilateral networks as well (Devue & Brédart, 2011; Keenan, Nelson, O'Connor, & Pascual-Leone, 2001; Keenan, Wheeler, Gallup, & Pascual-Leone, 2000; Levine, Banich, & Koch-Weser, 1988; Uddin et al., 2005).

1.5.3 Self other-integration and distinction: the role of the mPFC and the TPJ, and of the Mirror Neuron System

As highlighted in section 1.4, self and other perspectives are likely to be highly interconnected due to our constant interaction with others. Social exchanges can be considered as a consequent chain of switch between self-other distinction and self-other integration (Decety & Sommerville, 2003; Santiesteban, 2014).

From a neural perspective, one of the systems that has been related to self-other integration is the Mirror Neuron System (MNS). The MNS is composed of the inferior frontal gyrus (IFG), the superior temporal sulcus (STS), the inferior parietal lobe (IPL), and the primary motor cortex (Rizzolatti & Craighero, 2004), and it responds when we perform and when we see an action (Iacoboni, 2005; Rizzolatti & Craighero, 2004). As this has been considered the functional link between other perspective (i.e. action understanding) and self-perspective (i.e. reproduction of action), the MNS has been thought to support not only behaviours at the perceptual-motor level,

such as imitation, but also other social cognitive abilities that require an interplay between self and other representations, such as theory of mind (Gallese & Goldman, 1998) and empathy (Baird, Scheffer, & Wilson, 2011)[3]. As an evidence to support this, areas belonging to the MNS have been found to be engaged in self-processing tasks, for example when participants hear their voice or they look at their face (Kaplan et al., 2008; Uddin, Iacoboni, Lange, & Keenan, 2007; Uddin et al., 2005). It has been shown that individuals with alexithymic traits, which appear to have some kind of deficit in self-awareness (Taylor & Bagby, 2004), displayed a greater activation of regions belonging to the MNS in a goal directed task (Moriguchi et al., 2009). This might appear at odds with the hypothesis of a relationship between self-other integration and the MNS activation. However, the author interpreted the greater activation of the MNS as a reflection of the low self-other discrimination abilities, which may lead individuals with alexithymic traits to overlap others' action onto their own (Moriguchi et al., 2009). According to the hypothesis of the MNS as a possible neural substrate of self-processing, given the link between imitation and emerging self-awareness (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013), and the functional activation of areas belonging to the MNS for self-related stimuli (Kaplan et al., 2008; Uddin et al., 2007, 2005), it has been proposed that the MNS may be the functional link between imitation and the sense of self even during the first years of life (Iacoboni & Dapretto, 2006; Iacoboni, 2009). However, to date there is no empirical evidence from developmental neuroscience to support this theory.

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[3] However, it is worth acknowledging that the role of the MNS in imitation and social cognitive abilities is not universally accepted (For a critical review of this see Hickok, 2009; Kosonogov, 2012; Southgate, 2013).

The MNS is not the only neural substrates which has been hypothesized to be related to self-other integration. Saxe et al. (2006) showed that reasoning about others' beliefs recruits the mPFC, the precuneus, and the TPJ, which are also core regions for self-processing (Saxe, Moran, Scholz, & Gabrieli, 2006). Other studies have supported this finding by showing that the ventral part of the PFC is engaged both by introspections about the self and about others' minds that are perceived as similar to the self (Jenkins, Macrae, & Mitchell, 2008). Again, it has been shown that a network involving the mPFC and the TPJ is activated when inferring representations on self and other during a task designed to measure empathy (Zaki, Weber, Bolger, & Ochsner, 2009)

Interestingly, while I have just discussed evidence for the role of the mPFC and the TPJ in shared representation between self and others, there are a variety of other works suggesting that these two brain regions are fundamental also in the self-other distinction process. Using transcranial direct current stimulation (tDCS)[4] of the right TPJ, Santiesteban showed that the right TPJ stimulation inhibited other-representations and enhanced self-representations during an imitation-inhibition task, where the participants were asked to perform a different finger movement from the one observed. On the contrary, the right TPJ stimulation inhibited self-representations but enhanced other-representations during a perspective-taking task, where participants were asked to adopt the viewpoint of a "director", instructing them on how to move objects on a shelf. Surprisingly, the stimulation of the right TPJ did not have any effect on the performance during a self-referential task, where

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[4] The tDCS is a method that can selectively neurostimulate brain regions by sending constant low direct current. This increases the neuronal excitability in the area stimulated, which leads to alterations of brain functions (Walsh & Cowey, 2000).

participants were asked to make judgements about themselves or other. As judgment on the self and on the other were presented one at the time, this condition did not require any conflict between self and other perspectives. These results taken together suggested that the right TPJ has a crucial role when self and other perspectives conflict and individuals are required to control such conflict in order to achieve successful social interactions (Santiesteban, Banissy, et al., 2012). Consistent with this, the mPFC and the TPJ have been extensively related to the control of imitation, suggesting that these areas are crucial for distinguishing self and other representation (Brass et al., 2005; Brass, Zysset, & von Cramon, 2001; Sowden & Catmur, 2015; Spengler, von Cramon, & Brass, 2010). In line with the role of TPJ in self-other distinction, the IPL, a portion of the TPJ, plays a fundamental role in avoiding confusion between the self and others, contributing especially to the sense of agency (Farrer, Franck, Georgieff, et al., 2003; Ruby & Decety, 2001).

This literature overview discussed evidence for the involvement of the mPFC and the TPJ in both self-other integration and self-other distinction, which might suggest an important role of these two regions in efficiently switching between self and other perspectives.

1.5.4 The abstract self-processing: the default mode network and cortical midline structures

Adult research has shown extensively that there is a positive association between self-processing and the DMN, which is a network of brain regions engaged during quiet rest (Davey et al., 2016; Kaplan et al., 2008; Kelley et al., 2002; Kircher et al., 2000; Uddin et al., 2005). This so-called 'resting state' is the acquisition of spontaneous fluctuations in the low-frequency range (<0.1 Hz)

in the absence of any cognitive, sensory, or social stimulation (Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995; Damoiseaux et al., 2006; van den Heuvel & Pol, 2010). The DMN is composed of the mPFC, the precuneus, the anterior cingulate cortex (ACC), the PCC, the medial temporal lobe, and the TPJ (Raichle, 2015). These brain regions have also been documented as involved in social cognitive processes (Greicius, Krasnow, Reiss, & Menon, 2003; Harrison et al., 2008; Mars et al., 2012; Molnar-Szakacs & Uddin, 2013; Raichle, 2015; Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008).

The DMN has been suggested to be our 'intrinsic system' that deals with inner-oriented and self-related signals. In fact, activity in these regions has been found to be 'internally driven' and present even without any external stimulation (Golland, Golland, Bentin, & Malach, 2008). The fact that activity in the DMN is remarkably similar to that shown in self-processing tasks, led to the hypothesis that during quiet rest, there is a shift from perceiving the external world to internal modes of cognition (Buckner & Carroll, 2007). This has been empirically supported by imaging studies that demonstrate that DMN activity at rest is positively correlated with participant reports of mind wandering and self-related thoughts (Mason et al., 2007; McKiernan, D'Angelo, Kaufman, & Binder, 2006). Consistent with this idea, recent fMRI studies have explored the engagement of the core areas of the DMN in self-processing tasks. In these studies, while TPJ activation is especially related to physical bodily awareness (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke, 2005; Chen & Huang, 2017), the mPFC is the main component of the DMN that has been demonstrated to be related to several forms of self-reflection (Jenkins & Mitchell, 2011). The PFC has high metabolic activity during rest and during self-referential tasks, which

is possibly further evidence of its importance in self-referential processes (Gusnard et al., 2001; Raichle et al., 2001; Yaoi, Osaka, & Osaka, 2009).

The central portion of the DMN is the cortical midline structure (CMS), which is composed of the mPFC, the ACC, and the PCC. This part of the DMN has been argued to be the nucleus of the neuronal substrates of the sense of self, processing abstract information about the self (Northoff & Bermpohl, 2004; Northoff et al., 2006; Uddin, Iacoboni, Lange, & Keenan, 2007). Several self-related processes, such as self-representation, self-evaluation, self-monitoring, and self-integration have been associated with the CMS (Northoff & Bermpohl, 2004). This has been confirmed by evidence showing an increase in activation in regions of the CMS during self-processing tasks, such as self-appraisal (Ochsner et al., 2005), self-referential judgments (Gusnard et al., 2001; Kelley et al., 2002), and self-reflection (Johnson, Baxter, Wilder, Pipe, Heiserman, Prigtano, 2002; Kjaer, Nowak, & Lou, 2002). This overlap between the regions of the CMS that respond to self-related stimuli and those that are engaged during resting-state supports the idea of the CMS as the *internal origin of the self* (Qin & Northoff, 2011). The strong link between the self and others in the brain has been highlighted in the previous section and consistent with this, it is worth mentioning that the CMS has been found to be activated not only when representing self-related mental states, but also when representing other-related states (Araujo, Kaplan, & Damasio, 2013; Frith, 1999; Iacoboni et al., 2004; Van Buuren, Gladwin, Zandbelt, Kahn, & Vink, 2010). Therefore, it has been suggested that the CMS is also involved in what is defined as the *social self* (Mitchell et al., 2005; Uddin et al., 2007).

Furthermore, alpha oscillations (8-12 Hz) recorded by EEG have been shown to reflect the activity of the DMN (Goldman, Stern, Engel, & Cohen, 2002)

and several studies have shown the relationship between self-referential thoughts and alpha oscillations (Cannon & Baldwin, 2012; Gonçalves et al., 2006; Jann et al., 2009; Knyazev, 2013; Knyazev, Slobodskoj-Plusnin, Bocharov, & Pylkova, 2011; Laufs et al., 2003), confirming the previous findings regarding the DMN.

Researchers belonging to the MNS tradition proposed a distinction between abstract cognitive processes related to the self, and physical self-recognition, which may be supported by two different brain networks (Molnar-Szakacs & Uddin, 2013). According to this idea, while the DMN is engaged in abstract and evaluative self-processing (i.e. reflecting about oneself), areas of the MNS are activated when physical self-processing is required, both for self-face recognition and self-voice recognition (Kaplan et al., 2008; Uddin et al., 2007, 2005). Therefore, a complete representation of the neural substrate of the sense of self conflates together the DMN and the MNS, with overlapping hubs and a high degree of functional connections (Molnar-Szakacs & Uddin, 2013).

The literature review on the neuronal correlates of self-awareness in adults has shown the implication of several brain regions, with some hubs consistently found to be crucial keys for different aspects of the self, such as the mPFC and the TPJ (see Figure 1.1. for a graphical representation of the main regions described as the neural correlates of the sense of self). Due to the complexity and multifaceted nature of this topic of research, it is likely that the engaged regions interact in sophisticated functional networks to support the emergence of self-awareness. Indeed, the adult literature widely documented networks such as the MNS, the DMN, and the CMS as the neural correlates of

physical and abstract self-awareness (Gusnard et al., 2001; Molnar-Szakacs & Uddin, 2013; Raichle et al., 2001; Yaoi et al., 2009). The recent approach of brain network adopted in neuroscience offers a new framework for approaching brain structures and functions as a multi-scale system, where cortical areas are integrated to create a network supporting complex psychological functions (Petersen & Sporns, 2015). Therefore, one may think that tracking the developmental trajectories of brain networks could provide information about the mechanisms underlying emerging self-awareness during the first years of life. In fact, the gradual emergence of self-awareness may reflect the early immaturity of brain networks which support neuronal processes related to self-processing and social interactions (Raichle et al., 2001). In this PhD work, I applied this novel approach to the investigation of the neural underpinnings of the development of self-awareness in infancy.

MIRROR NEURON SYSTEM (MNS)

STS
- Physical self-processing
- Self-voice recognition
- Self-face recognition
- Self-other integration
- Bodily self-awareness in infants

IPL
- Physical self-processing
- Self-voice recognition
- Self-face recognition
- Self-other integration

IFG
- Physical self-processing
- Self-voice recognition
- Self-face recognition
- Self-other integration

PCC
- Abstract information about the self
- Self-appraisal
- Judgment of personal traits
- Self-reflection
- Not only self but also other-related stimuli
- Self-recognition
- Reasoning about others

ACC
- Abstract information about the self
- Self-appraisal
- Judgment of personal traits
- Self-reflection
- Not only self-related but also other-related

mPFC
- Self-processing
- Self-awareness
- Self-other distinction
- Self-other integration
- Self-recognition
- Reasoning about others

TPJ
- Self-other distinction
- Self-other integration
- Bodily self-awareness in adults and in infants
- Reasoning about others
- Self-representation in infants

CORTICAL MIDLINE STRUCTURES (CMS)

DEFAULT MODE NETWORK (DMN)

Figure 1.1 Graphical representation of the main brain areas related to the sense of self.

1.6 Summary

Recent theories on the development of the sense of self suggest that i) infants are born with a core sense of self that allows them to interact with the environment; ii) the sense of self is socially constructed through interactions with others who serve as *social mirrors*. Self-recognition in the mirror, achieved at around 18 months, has been used to assess emerging self-awareness in infancy, even though the significance of this test is still not universally accepted. The reviewed evidence suggests that self-recognition may be an indicator not only of physical awareness, but of a broader sense of self, i.e. self-awareness. Consistent with theories that suggest a social shaping of the self, it is likely that the emergence of self-awareness is highly connected with some fundamental social cognitive abilities that develop early in life. Mimicry, the spontaneous tendency to copy others, might be influenced by emerging self-awareness and being mimicked early in life might affect self-awareness later on in development.

Knowledge of the neural correlates supporting self-awareness has come mainly from adult studies and suggests that i) the MNS, which is engaged when we see and perform actions, is activated in self-recognition tasks and in self-other integration; ii) the DMN is associated with abstract self-processing; iii) the TPJ and the mPFC, two core regions of the aforementioned networks, respond to self-processing tasks and to shared representations between self and other. The literature review highlighted several brain regions associated with self-awareness and the brain networks that have been found to support this complex phenomenon in adulthood. Therefore, connectivity analyses applied to infant brain data might provide a detailed picture of the neural underpinnings of emerging self-awareness.

1.7 Overview of the present work

This PhD thesis addresses the outstanding questions outlined above by investigating the neural correlates of emerging self-awareness using fNIRS and places an emphasis on the analyses of brain networks to help investigate this complex phenomenon. Moreover, this work explores how the development of self-awareness is related to other social cognitive abilities, and in particular, mimicry.

Chapter 2 summarises the advantages and disadvantages of using fNIRS in infancy. It highlights the pros and cons of this neuroimaging technique and describes the methodological approach to obtaining fNIRS data from young infants that was employed. This chapter also briefly describes the data analyses approach used in the following chapters.

The adult literature consistently highlights a wide set of brain regions and some networks as the neural correlates of the sense of self. Moreover, the complexity and the multifaceted nature of this topic of research requires more sophisticated analyses than a focus on the activation of single areas. **Chapter 3** is therefore dedicated to elucidating how fNIRS can be employed to assess functional connectivity in awake infants. This chapter also illustrates two connectivity techniques that were adapted to be used on the fNIRS infant data to enrich the description of the developing brain.

Taking advantage of one of the connectivity techniques explained in Chapter 3, **Chapter 4** presents an investigation of how the brain regions in a known network that is consistently described as being related to self-processing might be considered markers of emerging self-awareness in infancy as well. fNIRS has been employed here to record the brain activation in awake infants at rest, creating similar testing conditions to those used with adults.

Chapter 5 explores which brain areas are engaged during self-recognition in infancy and investigates whether the areas that may be related to self-processing at rest are also engaged in this task. This study manipulates the temporal contingency between observed and performed movements while brain responses are recorded with fNIRS.

Chapter 6 investigates how emerging self-awareness can influence infants' interactions with the social environment. Here, the focus is on the selective mimicry of in-group and out-group members, which was measured with EMG and fNIRS.

Chapter 7 tests the hypothesis of the important role of others in constructing the self, investigating the social nature of the self. It explores how the mothers' tendency to imitate their 4-month-olds' facial actions may be a predictor of self-awareness at 18-month-old.

Chapter 8 discusses how the work of this thesis provides insight into the mechanisms underlying developing self-awareness. This chapter also highlights how this work relates to and extends the previous work in this field. It acknowledges the limitations of the studies presented and gives potential directions for future research.

Figure 1.2 relates each chapter of this PhD work to the aims described at the beginning of the Introduction.

Which are the mechanisms underlying emerging self-awareness?

methodological improvements of the fNIRS analyses to explore brain networks

investigation of neuronal underpinnings of emerging self-awareness in awake infants

investigation of how others interact with emerging self-awareness, possibly influencing its development

Chapter 3
A measure for the complexity of the brain: connectivity analyses on infant fNIRS data

Chapter 4
Fronto-temporoparietal connectivity as a potential neural marker of self-awareness in 18-month-olds: a resting state fNIRS study

Chapter 5
Neural underpinnings of self-recognition in 18-month-olds

Chapter 6
The role of self-awareness in selective facial mimicry of linguistic in-group over out-group members.

Chapter 7
An investigation into the relationship between the mothers' tendency to imitate their 4-month-olds and emerging self-awareness at 18 months

Figure 1.2 Graphical representation of the aims of this PhD work and each chapter.

Chapter 2

Methodology:

functional-near infrared spectroscopy

2.1 General principals of functional near-infrared spectroscopy

2.1.1 Introduction to the fNIRS method

fNIRS is a relatively new non-invasive neuroimaging method, widely used in the developmental neuroscience field (Ferrari & Quaresima, 2012; S. Lloyd-Fox, Blasi, & Elwell, 2010). This method uses light to measure brain activation, taking advantages of the different optical proprieties of blood with and without oxygen (Villringer & Chance, 1997). The discovery of light as a possible way to study the brain is dated back in 1976, when the German biologist Frans Jobsis-vander Vliet realised that the light path was visible through a steak bone. Thus, he reasoned that if light in the visible spectrum could travel through the bone, light with a longer wavelength – i.e. the near-infrared light – should be able to travel through longer distances, providing access to the brain. After this discovery, it took another 20 years before the first studies using near-infrared light to explore brain responses in humans were published (Hoshi & Tamura, 1993a, 1993b; Villringer, Planck, Hock, Schleinkofer, & Dirnagl, 1993). However, in the past decades this method has been remarkably improved and its use is rapidly growing in several fields, and in particular, in the study of the developing brain (Hoshi, 2007; S. Lloyd-Fox et al., 2010).

The main principle underlying the use of fNIRS to detect brain activations relies on the fact that skin, biological tissues and bones are relatively transparent to light in the near-infrared band of the electromagnetic spectrum, while blood is a strong absorber (Jacques, 2013). In particular, oxygenated and deoxygenated blood present different proprieties of absorption in the near-infrared wavelength spectrum (700-1000 nm). When a brain region is

activated, a localised increase of oxygenation occurs in that tissue. This produces a change in the amount of light absorbed by this tissue which can be measured by near infrared spectroscopy systems, using it as an index of brain activation. Therefore, measuring differences in the absorption and scattering of the oxygenated and deoxygenated blood allow us to measure the difference in the haemoglobin concentration (Elwell, 1995; Hoshi, 2016). In the following paragraph, I describe the neural origins of the fNIRS signal and how the NIRS technology works to study it.

2.1.2 Neural origins of the fNIRS signal

With fNIRS, changes in the level of oxygenation associated with functional activation are measured by light injection and detection on the surface of the head. Brain activity and cognitive processes are associated with an increase in neuronal firing and consequently an increase in oxygen consumption. Because of the coupling with the vascular system, this leads to an increase in the transportation of oxygenated blood to this area (Hoge et al., 1999; Magistretti & Pellerin, 1999). Whereas neuronal activity might last milliseconds, the increase in blood flow in brain tissues takes from 5 to 10 seconds to reach its maximum (Poldrack & Nichols, 2011). This increase in blood flow to brain areas that are activated is commonly known as the 'haemodynamic response' (Attwell & Iadecola, 2002; Clarke & Sokoloff, 1999; Roy & Sherrington, 1890; Zheng et al., 2002).

Similar to fMRI, fNIRS measures the supply of oxygen in the brain. fMRI detects the Blood Oxygen Level Dependent (BOLD) signal, which primarily corresponds to the concentration of deoxyhaemoglobin (Arthurs & Boniface, 2002; Logothetis & Pfeuffer, 2004). fMRI takes advantages of the paramagnetic

proprieties of the deoxygenated blood, as an increase in the BOLD signal corresponds to a decrease in the concentration of deoxygenated blood, based on which an increase in the oxygenated blood is inferred (Heeger & Ress, 2002). In a similar way, fNIRS relies on the different proprieties of oxygenated (HbO_2) and deoxygenated (HHb) blood, but regarding their different absorption characteristics (Zhang, Brooks, & Boas, 2005). Both fMRI and fNIRS provide access to the haemodynamic response, but fNIRS informs about both chromophores of interest (i.e. HbO_2 and HHb). In fact, the vast majority of the NIRS systems acquire measurements using two wavelengths, each of which selectively sensitive to one chromophore (although both contribute to the measure of both signals). The two wavelengths can slightly vary across systems, but one is commonly above and one below the haemoglobin isobestic point at 805nm, where HbO_2 and HHb haemoglobin present the same absorption coefficient. In fact, HHb absorbs considerably more light at wavelengths below the isobestic point, while HbO_2 absorbs considerably more light at wavelengths above the isobestic point (see Figure 2.1) (Boas, Dale, & Franceschini, 2004).
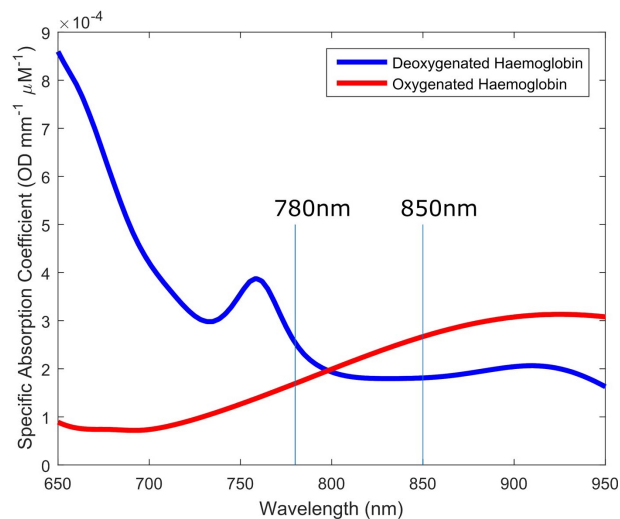
Figure 2.1 Absorption spectra of the oxygenated and deoxygenated haemoglobin. The red line represents the oxygenated haemoglobin and the blue line represents the deoxygenated haemoglobin (image reproduced with permission from

www.gowerlabs.co.uk). 780 and 850 nm are two wavelengths used by NIRS systems to detect HbO_2 and HHb signal.

The signal obtained with fNIRS contains more than just information about neuronal activation, as it also includes noise and physiological factors. Vasomotor waves, respiration signal, cardiac measures, experimental noise, and motion artefacts 'hide' the haemodynamic response (Bauernfeind, Wriessnegger, Daly, & Müller-Putz, 2014; Brigadoi et al., 2014). Therefore, pre-processing of the fNIRS signal is needed to measure the haemodynamic response, removing the noise caused by physiological factors (for more information about pre-processing and motion artefacts see paragraph 2.3.2). A typical haemodynamic response has a pattern of increasing HbO_2 and decreasing HHb, due to changes in the level of oxygen in the brain tissue (see Figure 2.2) (Cui, Bray, & Reiss, 2010; Kleinschmidt et al., 1996; Villringer & Chance, 1997). However, this canonical response is not always present in infants and young children (Issard & Gervain, 2018) , and studies in infancy often rely on the oxygenated signal only (for some examples see: Grossmann, Cross, Ticini, & Daum, 2013; Lloyd-Fox et al., 2010; Lloyd-Fox, Széplaki-Köllod, Yin, & Csibra, 2015; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014). Understanding the pattern of oxygenated/deoxygenated blood coupling is a topic of ongoing research in developmental neuroscience (for example see Issard & Gervain, 2018).
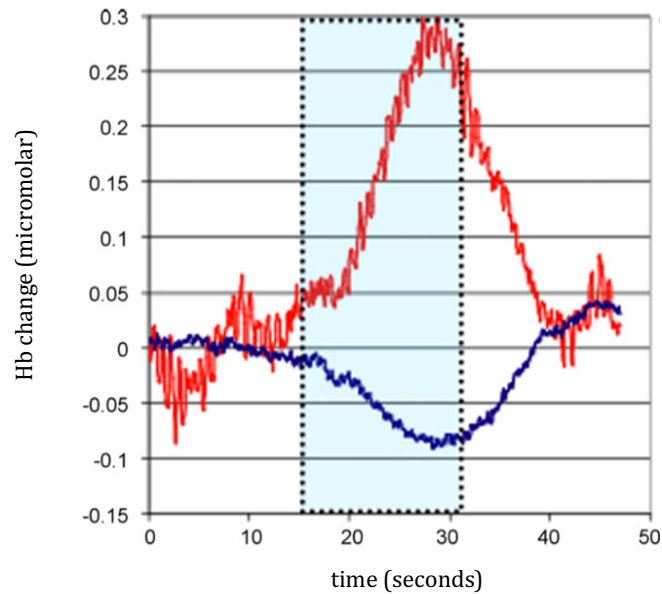
Figure 2.2 Typical haemodynamic response to cortical activation recorded with fNIRS. Red line represents HbO$_2$ and blue line represents Hbb (image reproduced with permission from Coutts et al., 2009).

Sources and detectors of near-infrared light are the main components of the NIRS system. When the near-infrared light is shone into the brain, only a portion of it reaches the detector, while the rest is scattered and diffused through the brain tissues (Elwell, 1995; Hoshi, 2016). The light attenuation is converted into relative concentrations of HbO$_2$ and HHb by the modified Beer Lambert Law:

$$OD = -log_{10}(I/I_0) = \varepsilon \Delta c.B.L + G$$

where OD is optical density (or attenuation of the light radiation), I is the intensity of the signal transmitted, I$_0$ is intensity of the incident light, ε is the molar extinction coefficient, Δc is the change in the concentration of the chromophore, and L is the optical pathlength (Boas et al., 2001).

The modified version of the Beer Lambert Law introduced two terms, B and G in the formula. The factor known as differential pathlength factor (DPF)

corrects for the increased optical pathlength due to scattering (B in the formula). As the estimation of the DPF value depend on both the scattering and the absorption proprieties of the tissue, this value is wavelength and age dependent, so it needs to be specified by the experimenter. There are some papers that researchers can take as a reference, suggesting age and wavelength dependent formula to calculate the DPF value (Duncan et al., 1995, 1996; Scholkmann & Wolf, 2013). In particular, the study performed by Duncan and colleagues provides valuable information on how absorbing and scattering proprieties of brain tissues change as the brain develops: i) the DPF values in newborns are generally lower than those in adults, suggesting that there is less scattering of the light at younger ages, due to a thinner skull and scalp compared to adults; ii) the standard deviations of the DPF values estimated in newborns are lower than those in adults, suggesting less variability in the optical proprieties of the various brain tissues in the developing brain than in the adult one[5] (Duncan et al., 1995).

The second term introduced in the modified version of the Beer Lambert Law accounts for the scattering losses due to photons never reaching the detector (G in the formula) (Arridge, Cope, & Delpy, 1992; Delpy, Cope, Van Der Zee, et al., 1988; Hiraoka et al., 1993). Note that G is unknown and it is dependent upon the scattering coefficient of the tissue interrogated. Therefore, this equation cannot provide a measure of the absolute concentration of the chromophore. However, if we assume G does not change during the measurement period, it is possible to determine a change in the concentration of the chromophore from a measured change in attenuation (Elwell, 1995). This

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[5] This is consistent with the less differentiation of white and grey matter in the first year of life (Weisenfeld & Warfield, 2009).

term in the formula highlights the importance of taking into account both absorption and scattering of the light when measuring light transportation through the brain. In fact, it is estimated that around 80% of the light emitted will be scattered, and only the remaining 20% will be absorbed (Elwell, 1995).

fNIRS measures changes in oxygenation levels in the cortical area between the sources and the detectors, so-called channel (Everdell et al., 2005). The light path between a source-detector pair is typically described as 'banana-shaped', based on the curved shape of the light sensitivity between the two optodes. The light cannot travel very deep into the brain, therefore fNIRS allows the access only to the superficial layers of the cortex. The profile of the spatial sensitivity, which indicates the volume of the tissue reached by the light, is characterized by the optical heterogeneity of the brain layers which the light goes through (Okada, Firbank, & Delpy, 1995). Several studies assessed the shape and the depth of this curve, and most important, which factors affect it, such as properties of the tissue or age (for some example see Arridge et al., 1992; Boas, Dale, & Franceschini, 2004; Hiraoka et al., 1993; Okada, Firbank, & Delpy, 1995; Okada & Delpy, 2003). As biological tissues absorb and scatter light differently, sensitivity maps of photon migration can be employed by fNIRS researchers to estimate the amount of light that each detector gets, given the light dispersion in different tissues and the possible contamination by hemodynamic processes in the extracerebral vasculature. The Monte Carlo simulation is often used to model light migration in human tissue, computing individual photon paths (Fang, 2010; Hasegawa, Yamada, Tamura, & Nomura, 1991; Wilson & Adam, 1983). An interesting study compared light propagation in adult and newborns head models. It showed that the photon migration changes in relation with age, with the neonatal brain absorbing more light than

the adult one, due to the difference in skull thickness and the optical proprieties

of white and grey matter (Fukui, Ajichi, & Okada, 2003).

Although calculating a sensitivity map of photon migration is not

commonly part of fNIRS data analysis pipelines in developmental science, in

this PhD work an estimation of light propagation was necessary to validate

effective connectivity methods on infant fNIRS data presented in the next

chapter (section 3.2).

2.1.3 Advantages and disadvantages of fNIRS and comparisons with other neuroimaging techniques used in developmental neuroscience

The increased use of fNIRS in experiments studying the developing human

brain is due to certain characteristics that make it an ideal neuroimaging

method to be used with developmental populations (S. Lloyd-Fox et al., 2010;

Wilcox & Biondi, 2015). First, infants present less hair and a thinner scalp

compared to adults (aspects that could affect the absorption and the scattering

of the light), enabling the near-infrared light to more effectively reach the grey

matter. Secondly, the fact that fNIRS is relatively robust to motion allows infants

and toddlers to be tested while they are awake and relatively free to move. In

fact, as long as the fNIRS headgear is securely positioned on the infant's head,

the infant is relatively free to move. This allows researchers to investigate

functional brain activation in a much wider range of experimental situations,

for example during live interactions (Canning & Scheutz, 2013; Holtzer et al.,

2011; Pan, Cheng, Zhang, Li, & Hu, 2017; Pinti et al., 2015, 2018; Solovey et al.,

2009), and on multiple participants simultaneous recorded (i.e.

hyperscanning) (Cui, Bryant, & Reiss, 2012; Pan et al., 2017). Thirdly, testing protocols with fNIRS are not restricted to a lying down posture, making it more participant friendly, as infants and children can sit on or close to their carer throughout the study. Lastly, the low cost, the portability and of this equipment has helped increase the use of fNIRS for neuroimaging over the last decade (Hoshi, 2007; Piper et al., 2014), allowing for it to be used in a wide variety of settings, including developing countries and hospitals (for examples see Lloyd-Fox et al., 2017; Meek et al., 1999)

However, fNIRS also has some disadvantages that need to be taken into account. First of all, as mentioned, the near-infrared light cannot penetrate very deep into the brain, preventing any measurements of change in blood oxygenation in subcortical structures. Therefore, neuroimaging studies can benefit from the use of fNIRS only if the brain areas of interest are on the outer layer of the cerebral cortex (Ferrari, Mottola, & Quaresima, 2004; Hoshi, 2003). Secondly, accuracy of the spatial localisation of the fNIRS signal is dependent on i) the positioning and stability of the fNIRS cap on the participants' head; ii) the shape and size of the participants' head; iii) an accurate co-registration with MRI templates in order to define the structure and the positioning of the fNIRS array (for some example see Lloyd-Fox et al., 2014; Tsuzuki & Dan, 2014). A third disadvantage is that the temporal resolution of fNIRS - allowing for data acquisition up to 100 hertz - is much lower than the resolution provided by EEG, usually reaching up to a thousand hertz (Luck, 2005). However, it has to be acknowledged that temporal resolution of fNIRS is faster than the resolution provided by fMRI, which typically reaches only 1 hertz or less (Kim, Richter, & Uğurbil, 1997; Huettel, Song, McCarthy et al., 2004; Weishaupt, Kochli, Marincek, & Kim, 2007). This enables fNIRS to provide more time-accurate

recordings of the blood fluctuations in the brain, which connectivity analyses can benefit from (see Chapter 3 for more details on this). Figure 2.3 gives a graphic summary of benefits and disadvantages of the various neuroimaging techniques used in developmental neuroscience (S. Lloyd-Fox et al., 2010).
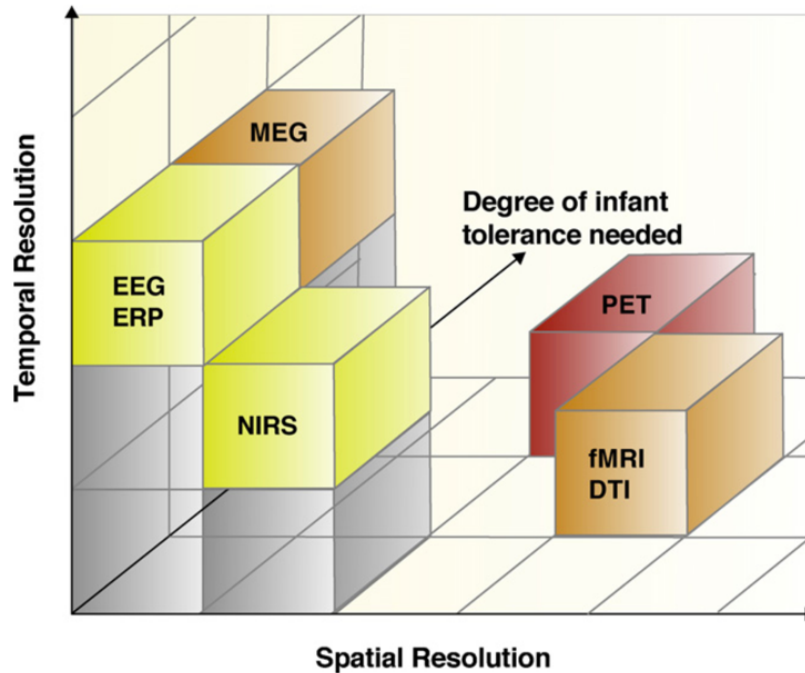
Figure 2.3. Graphical representation of the proprieties of the neuroimaging techniques used with infants. Degree of tolerance is ranked from a low (yellow), to medium (orange), till a high level (red). Spatial resolution and temporal resolution are plotted on the other axes. EEG, electroencephalography; ERP, event-related potential; MEG, magnetoencephalography; NIRS, near infrared spectroscopy; fMRI, functional magnetic resonance imaging; DTI, diffusion tensor imaging; PET, positron emission tomography (image reproduced with permission from Lloyd-Fox et al., 2010, p.271).

In this PhD work, particular attention was dedicated to limit the consequences of some of the disadvantages of fNIRS. In particular, participants' head measurements were acquired in order to choose a size of the fNIRS cap as close as possible to the head size of the participant (see next sections for more information about the fNIRS cap sizes and experimental procedures). Moreover, a study in collaboration with Dr. John Richards at the University of

South Carolina registered the fNIRS array structure used for this project on MRI scans of infants of a similar age and with a similar head shape and size, to estimate which brain areas were being measured (see section 2.2.2). Finally, I took advantage of the relatively good temporal resolution of fNIRS to adapt and validate some connectivity techniques to study developing brain networks (see the studies presented in sections 3.2 and 3.3).

2.2 The NIRS instrumentation and the NTS2 system

The NIRS system used at the Centre for Brain and Cognitive Development (CBCD) at Birkbeck College is called NTS2 optical imaging system. It has been developed at University College London (UCL) since 2005 (Everdell et al., 2005), and it is currently used in several European and international laboratories (see Figure 2.4). The NTS2 is a continuous wave system, which uses a continuous emission of light from the sources, measuring changes over time, not absolute values of attenuation. It enables the data acquisition with a high sampling rate and it can record from several channels simultaneously. The NTS2 is composed of 32 laser diodes sources (16 at 780 nm and 16 at 850 nm) and 16 detectors. The source-detector pairs allow for a maximum of 44 channels. In a multichannel system, such as the NTS2, each source can be paired with several detectors, therefore it is important to correctly identify which source the detected light has come from. One possible approach would be to shine the light from one source at the time (*time multiplexing*), but this method is very slow and not feasible for functional task-related studies. An alternative approach, employed by the NTS2 system is *frequency multiplexing*, in which each source is modulated at a slightly different frequency but in the same

wavelength spectrum. By using the Fourier transformation on the detected signal, the specific frequency of each source can be calculated. The header file of the software provides information about the different frequencies at which the sources emit the light, and based on this, the possible source-detector pairs. Once the experimenter has created the array design, the optodes position is digitised in a 'SD file'. This file, which contains also the wavelengths used for data acquisition, is then used to acquire data with the NTS2 software and to convert the light attenuation into concentrations by the modified Beer-Lambert Law.

NTS near infrared spectroscopy system, Gower Labs
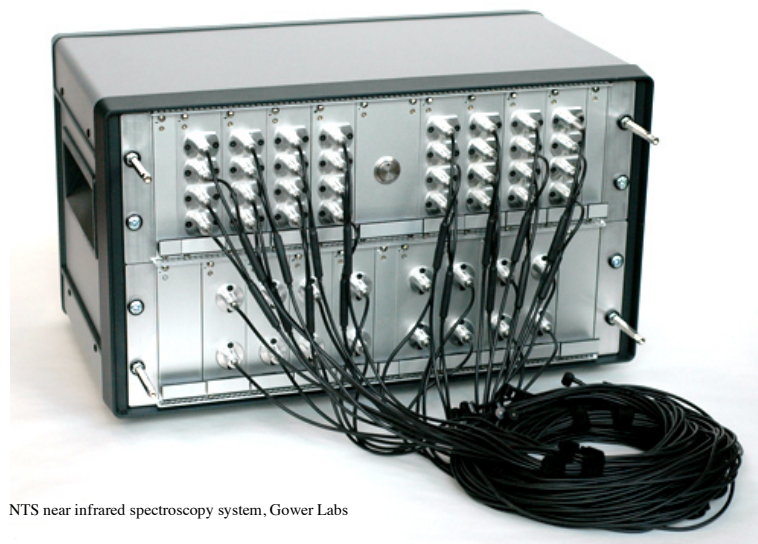
Figure 2.4. The NTS2 system used for acquiring fNIRS data in this PhD work (image reproduced with permission from www.gowerlabs.co.uk).

Light is delivered and detected by relatively light weight glass optical fibres, allowing the near-infrared light to travel from the system to the participant's head, with little signal loss. The tip of the glass fibres are 90 degrees bent to be positioned on the participant's head and different optode extremities can be designed depending on the subject's age. Adult fibers have

an extended fibre tip that can comb through the hair to increase the contact with the scalp and hereby the fNIRS signal quality. The absence of hair in young infants means that flat tipped fibers can be used, which are designed to minimise the pressure applied to the infants' scalp. In the studies reported in this PhD thesis, flat-tipped fibers were used with infants younger than 18-month-old, while adult fibers were employed with older ones, where hair could impede the contact between the fibre end and the scalp.

Optodes at the fiber end are embedded in arrays depending on the design of the channels, covering brain areas of interest. In infant studies, optodes are usually embedded in foam arrays and then placed on the subject's head with a custom-made silicon band. This method is widely used with young infants as the absence of hair allows the silicon band to be securely positioned on the infant's head without slipping during the experiment (S. Lloyd-Fox et al., 2010). However, this is more likely to happen when children have hair, thus using an EasyCap instead of a silicon band can be preferable when studying older children with more hair. EasyCaps come in different sizes allowing for the appropriate size to be selected for each participant's head size. The array design and the choice of the cap are dependent on several factors, such as number of channels available, brain regions of interest, age of participants and head size, stability on the head, and whether the participant will be awake or asleep during the experiment. The source-detector separation (S-D) is dependent on age and brain region, and studies based on anatomical features of an appropriate age brain template should be performed prior to every new design. Researchers often consider a 'rule of thumb' when defining the source-detector separation, estimating that the light path roughly travels as deep as half of the source-detector separation. However, this heuristic approach does not

overcome the need for relying on brain anatomy to estimate which areas the array measures.

After this general overview of the fNIRS technology, in the next sections I discuss specific features of the fNIRS arrays, experimental set-up and testing procedure used in the studies performed in this PhD project.

2.2.1 fNIRS cap and arrays in this thesis

fNIRS optodes were embedded in a flexible EasyCap. The cap was made of soft black fabric, with a chinstrap and cut outs for the ears on the side to allow a secure but comfortable positioning on the participant's head. In fact, the chinstrap and the ear cut outs guaranteed a fixed position of the cap on the head, preventing any lateral shifting encountered sometimes with the silicon band used with younger infants. A range of several cap sizes was available, in order to adjust the cap size to the participant's head circumference. Source-detector separation increased slightly due to the stretch of the cap on the head and also due to re-scaling based on the cap size. Adult fibers were clicked into black plastic holders that secured them to the cap. This headgear was used for all the participants tested within this PhD project, except for the 11-month-olds that were part of the study presented in next chapter, section 3.3. This sample was tested with a custom-made silicon band and with flat-tipped fibers because at this age most of the participants did not have too much hair yet.

Two array design were used during this PhD project. The first array design included 12 sources and 12 detectors to create a total of 30 channels. The second design included 16 sources and 16 detectors to create a total of 44 channels. The 44-channel configuration was an extension of the 30-channel configuration and included two additional rows of optodes that added 7

channels per hemisphere, in a superior location to the two existing lateral arrays (see Figure 2.5). This allowed us to improve detection of TPJ activation, a core region of interest for this thesis. Each study in this thesis specifies which design was used and if both were used, how many subjects were tested with each design.
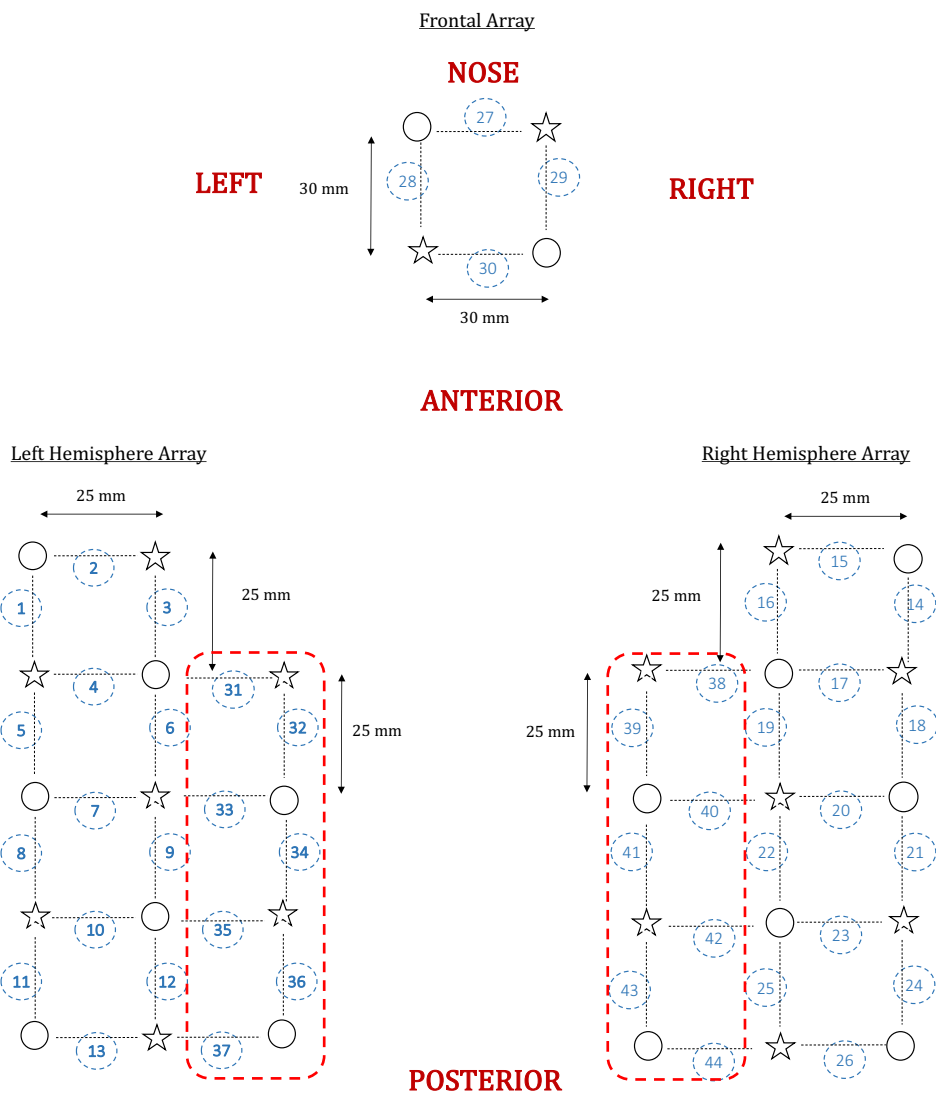
Figure 2.5 Representation of the fNIRS arrays. Sources are marked with stars, detectors are marked with circles, channels are marked with black dotted lines and numbered with blue circles. The red dotted lines highlight the additional rows of optodes that added 7 channels per hemisphere.

Figure 2.6 shows an example of infants wearing the two headgear configurations.

Configurations	Temporoparietal arrays	Frontal array
30-channel		
44-channel		
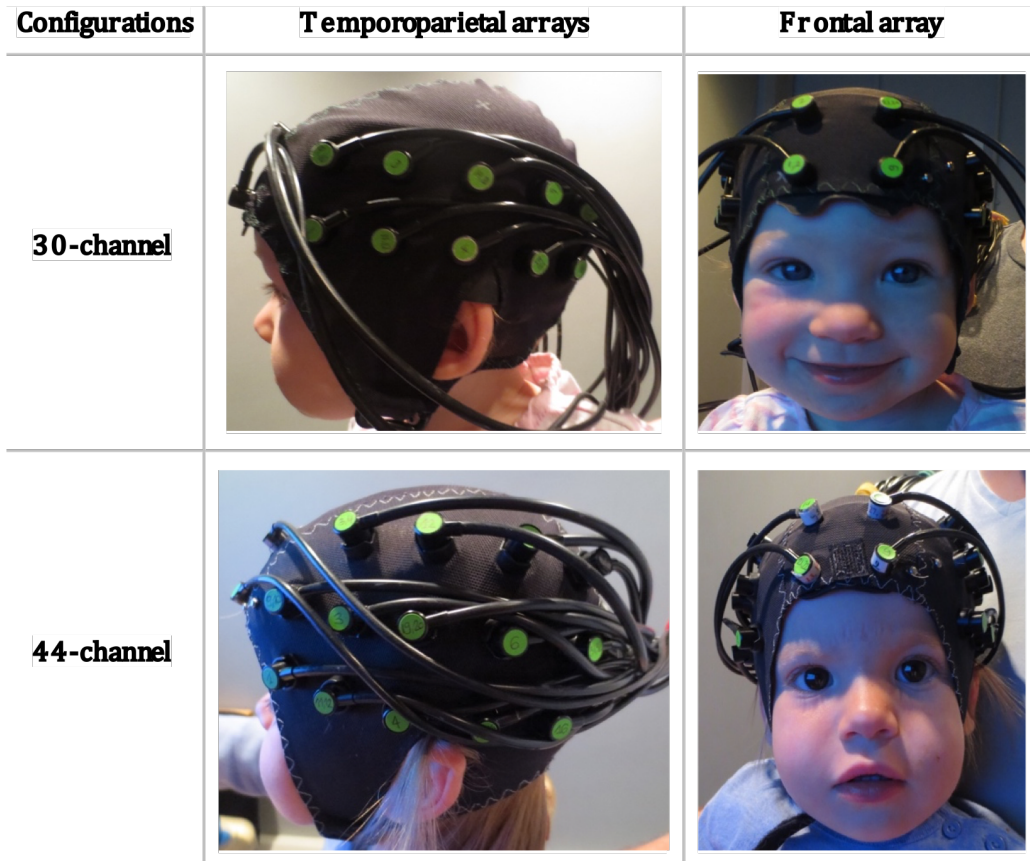
Figure 2.6 Infants wearing the two headgear configurations (Parents provided consent for these images to be used).

Source-detector separation was about 30 mm over the frontal lobe and 25 mm over the temporoparietal lobe. Given that the cortex is approximately 0.75 cm from the skin surface (Glenn, 2010) and based on studies on the transportation of near-infrared light through brain tissue, these selected source-detector separations were predicted to penetrate up to a depth of approximately 12.5-15 mm from the skin surface, allowing measurement of both the gyri and parts of the sulci near the surface of the cortex (S. Lloyd-Fox et al., 2010). As mentioned, considering that source-detector have been

rescaled based on the cap size, each study in this PhD thesis reports the correct source-detector separation in relation to the cap size used and the number of participants tested with each cap size.

2.2.2 Co-registration of the fNIRS arrays used in this PhD work on age-appropriate MRI scans

fNIRS has been described as a great tool to investigate brain activation in developmental populations, offering several strengths that other neuroimaging methods cannot provide. As mentioned before, although the spatial resolution of fNIRS is better than the one provided by EEG, it is not as accurate as the one provided by fMRI (S. Lloyd-Fox et al., 2010). For studies that aim to explore functional activations, this aspect is not trivial. Every participant's head shape and size are slightly different, and this can affect where the optodes are placed on the scalp. For this reason, the support of MRI images to co-register fNIRS data to structural templates is necessary to precisely infer the location of brain activations. This is even more important if the focus is on brain connectivity as in this PhD thesis, considering that poor spatial resolution may result in the incorrect inference that some brain regions belong to the same brain network (Satterthwaite et al., 2017). An ideal co-registration would be based on the infant's structural scan, but as an alternative it is possible to use high-resolution age-appropriate templates available (for example see Richards, Sanchez, Phillips-Meek, & Xie, 2016; Sanchez, Richards, & Almli, 2012a, 2012b).

Just a few developmental studies have localised fNIRS channels onto a MRI template (Emberson, Cannon, Palmeri, Richards, & Aslin, 2017; Emberson, Crosswhite, Richards, & Aslin, 2017; S. Lloyd-Fox, Richards, et al., 2014; S. Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2015). These studies used pictures

of the placement of the fNIRS array on the infant's head or digitised optodes location to log the position of the fNIRS arrays onto the infant's head. This allows an estimation of which areas of the brain the fNIRS arrays cover.

In the process of co-registering fNIRS data on MRI, it is important to make sure that the brain template that is used is based on an average of structural scans from infants within a relatively narrow age-range. The first two years of life are a period of fundamental growth of the brain during which the entire nervous system undergoes large changes (Johnson, 2001). Therefore, it would be inaccurate to infer which brain regions underlie the fNIRS arrays based on previous co-registration studies based on a different age range or using structural brain templates that are averaged using several different age points. Moreover, as the co-registration process is highly dependent on the array design used, co-registration studies tend to be quite specific and difficult to generalise to different array designs.

Given these peculiarities of the fNIRS co-registration process and given the lack of information on localisation in participants older than 1 year of age with the regions of interest I am interested in, I decided to co-register the fNIRS arrays used for the studies in this thesis on age-appropriate structural MRI scans. This allowed for conclusions on the localisation of the activity to be more precise throughout this PhD thesis. To achieve this, I collaborated with Dr. John Richards, Department of Psychology, at University of South Carolina, who provided a pool of high-quality MRI images of 24-month-olds.

In this thesis, the Polhemus Digitising System (http://polhemus.com/scanning-digitizing/digitizing-products/) was used to register i) five reference points (nasion, inion, right ear, left ear, Cz[6]) and ii)

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[6] Based on the International 10-20 EEG placement system.

optodes location of the fNIRS optodes used in this PhD work. This was done only if the participant was still compliant after the testing session. The in-house custom scripts for the acquisition of the reference points and the optodes location (written by my supervisor Professor Antonia Hamilton) took into account infant's movements during the recording, measured with a reference attached to the back of the participant's head. The Polhemus Digitising System comes with a transmitter box that, placed next to the participant, creates a magnetic field which allows the log of the selected points into a 3D space. During the recording, while one experimenter touched each point on the participant's head with the Polhemus stylus, making sure that the stylus is perpendicular to the point of interest, the other one logged each point location using the Matlab scripts. During this procedure, the infants watched an engaging video to minimise the movements. The outputs of the in-house scripts are two excel files, one with the location of the reference points and the other one with the optode locations in the 3D space related to the transmitter box, corrected for the participant's movements.

We selected the 10 best digitized recordings, based on the accuracy of the points marked in space compared to the optode locations in three pictures of the participant wearing the fNIRS cap (one from the front and two from the sides). For each of these recordings, Dr. Richards selected a structural MRI of an infant close in age, with a similar head shape and size, based on head measurements taken before the testing session. Despite the movement correction applied during the acquisition of the optode locations, for some of the recordings the two sets of points (reference points and fNIRS optode locations) were logged in a different space. However, within the set of points there was consistency and accuracy in the recording. Using *MriCron* toolbox, I

manually marked a third set of additional points (the two lower optodes belonging to the frontal array and the third lower optode belonging to the lateral arrays) on the structural MRI for each subject based on the three pictures of the participant. This third set of markers was used by Dr. Richards to re-register the two main sets of points, and thus to log the optode locations on the structural scan for each infant. Finally, the 10 fNIRS-MRI co-registrations were averaged together in order to estimate the location of the brain regions covered by the fNIRS arrays used in this PhD project. Table 2.1 lists the lobes and the anatomical labels based on the LPBA40 atlas associated with each channel referring to the array design described in the previous section.

Channel	Lobar Atlas	LPBA40 atlas
1	Frontal, Temporal	Inferior frontal gyrus, Superior temporal gyrus
2	Frontal	Inferior frontal gyrus
3	Frontal	Inferior frontal gyrus, Precentral gyrus
4	Frontal, Temporal	Inferior frontal gyrus, Superior temporal gyrus
5	Temporal	Middle temporal gyrus, Superior temporal gyrus
6	Parietal	Postcentral gyrus
7	Parietal, Temporal	Middle temporal gyrus, Superior temporal gyrus
8	Temporal	Inferior temporal gyrus, Middle temporal gyrus
9	Parietal, Temporal	Angular gyrus, Supramarginal gyrus
10	Parietal, Temporal	Middle temporal gyrus
11	Parietal, Temporal	Middle occipital gyrus
12	Parietal	Angular gyrus, Middle occipital gyrus
13	Parietal	Middle occipital gyrus
14	Frontal, Temporal	Inferior frontal gyrus, Superior temporal gyrus
15	Frontal	Inferior frontal gyrus
16	Frontal	Inferior frontal gyrus, Middle frontal gyrus
17	Frontal, Temporal	Precentral gyrus
18	Temporal	Middle temporal gyrus, Superior temporal gyrus
19	Frontal, Parietal	Postcentral gyrus, Precentral gyrus
20	Parietal, Temporal	Superior temporal gyrus
21	Temporal	Middle temporal gyrus
22	Parietal	Supramarginal gyrus
23	Parietal, Temporal	Middle temporal gyrus
24	Parietal, Temporal	Middle temporal gyrus
25	Parietal	Angular gyrus
26	Parietal	Angular gyrus, Middle occipital gyrus

27	Frontal	Middle frontal gyrus, Superior frontal gyrus
28	Frontal	Middle frontal gyrus
29	Frontal	Middle frontal gyrus, Superior frontal gyrus
30	Frontal	Superior frontal gyrus
31	Frontal, Parietal	Postcentral gyrus, Precentral gyrus
32	Frontal, Parietal	Postcentral gyrus, Precentral gyrus, Supramarginal gyrus
33	Parietal	Supramarginal gyrus
34	Parietal	Angular gyrus, Supramarginal gyrus
35	Parietal	Angular gyrus
36	Parietal	Angular gyrus
37	Parietal	Angular gyrus, Middle occipital gyrus
38	Frontal	Middle frontal gyrus, Precentral gyrus
39	Frontal, Parietal	Precentral gyrus ,Postcentral gyrus
40	Parietal	Postcentral gyrus, Supramarginal gyrus
41	Parietal	Postcentral gyrus, Supramarginal gyrus
42	Parietal	Angular gyrus, Supramarginal gyrus
43	Parietal	Angular gyrus
44	Parietal	Angular gyrus

Table 2.1. Lobes and anatomical labels based on the LPBA40 atlas associated to each channel (work performed in collaboration with Dr. Richards, Department of Psychology, University of South Carolina).

Table 2.2 lists channels belonging to regions of interest (ROI) as some of the analyses presented in the following chapters focus on these regions of interest. Figure 2.7 provides a graphical representation of the brain areas covered by the channels of the fNIRS array.

ROI	channels
mPFC	27, 28, 29, 30
Left IFG	1,2,3,4
Right IFG	14, 15, 16, 17
Left STG	5, 6, 7
Right STG	18, 19, 20
Left middle/posterior temporal gyrus	8,10,11,13
Right middle/posterior temporal gyrus	21, 23, 24, 26
Left TPJ	9, 12, 34, 35, 36
Right TPJ	22, 25, 41, 42, 43

Table 2.2 Regions of interest and corresponding channels defined by the co-registration study.
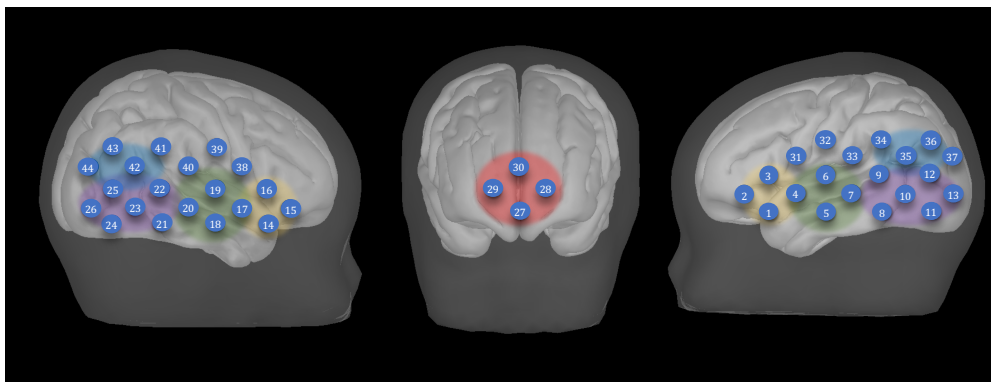
Figure 2.7 Representation of the channels on a 2-year-old structural template with regions of interest highlighted. Red represents mPFC, yellow represents IFG, green represents STG, purple represents middle/posterior temporal gyrus, blue represents TPJ.

2.2.3 Experimental set-up, fNIRS cap application, and testing procedure

In each testing session, after welcoming the family into the lab, the first minutes were dedicated to familiarise with the infant and to explain the aims of the studies and testing procedure to the parent. Before the beginning of the study, participant's head measurements (circumference, the distance between ears over the forehead, distance between nasion to inion, distance between ears measured over the top of the head) were taken to select the right cap size for the testing session and to align the fNIRS cap with the 10–20 coordinates (Klem, Luders, Jasper, & Elger, 1958).

All the fNIRS studies presented in this PhD thesis took place in a dimly lit and sound attenuated room, with the infant sitting on their parent's lap at approximately 90 cm from a 117 cm plasma screen. The only exception on this set-up is the study in Chapter 5, where participants sat on a high chair for experimental purposes. The parent was asked not to talk during the experiment to avoid eliciting brain activation not associated with the task. I excluded the trials where the parent or the experimenter talked to redirect the participant's attention on the screen (see paragraph 2.3.1 for more details on videocoding). Once the mother and infant had entered the testing room, the experimenters took some time to ensure that the infant was in a quiet state, then the fNIRS cap was placed on the infant's head. While one experimenter blew bubbles and/or held a novel and attractive toy in front of the child for distraction, the other experimenter positioned the hat on the infant's head. While applying the hat on the participant's head, the experimenter made sure the frontal array was centred on top of the participant's nose. After the application of the cap, the chinstraps were adjusted underneath the participant's chin to keep the cap in

place and adjustments were made to the positioning of the cap so that the ears were comfortably fitted through the cut outs on the side. Hereafter, a silicon band was placed on top of the optodes to keep the fibres in place and to keep them 'safe' from the child's reach. The experiment did not start until the participant was calm and relaxed. The experimenter then started the presentation of the stimuli using Psych-Toolbox and custom-made Matlab scripts.

Experimental studies in the current thesis involved paradigms structured in block designs, with experimental trials presented in a random order, interspersed with baseline trials, with the only exception of the second experiment of Chapter 3 and the study presented in Chapter 4, which are resting-state studies. The length of trials and baseline differed among studies, as well as the type of baseline chosen, therefore this information is specified in each study. The experimenter triggered the presentation of brief attention-getting sounds at random intervals to attract or maintain the infants' attention to the screen if needed. The presentation of sounds was constant during baselines and experimental trials in order to not differently affect infants' brain responses. The experimental sessions lasted until the participant was no longer paying attention to the stimuli or the video, or until he/she was getting fussy. Participants' behaviour was monitored and recorded for offline-coding via a remote-controlled video camera below the monitor showing the stimuli to the infant.

2.2.4 fNIRS recording

Oxygenated and deoxygenated blood changes were recorded using the NTS system introduced above. This system is provided with two continuous

wavelengths of source light at 770 and 850 nm, and the recording sampling rate was 10 Hz. The system was directly connected to the data acquisition computer where the NTS-Gowerlabs software displayed and stored the data. During the recording, the software interface showed patterns of raw intensity for each channel (both wavelengths) and a schematic representation of the fNIRS channels. Here, each channel was marked in green, blue or red to advise the experimenter on the optical coupling between the fiber and the scalp during the acquisition.

2.3 fNIRS data analysis

Despite the recent increased use of fNIRS in studies exploring functional brain development, data analysis pipelines still vary considerably among laboratories and teams. While other neuroimaging methods benefit of some defined standard 'golden rules', consensus on signal processing methods is still lacking among fNIRS research groups. In the fNIRS data processing, particular attention needs to be dedicated to motion artefact detection, as this is likely to create false positives in the estimation of brain activation (Pfeifer, Scholkmann, & Labruyère, 2018). Motion artefacts are particularly influential in the estimation of brain connectivity, as they likely lead to false positive (Satterthwaite et al., 2017).

After each testing session, videos were first coded for looking behaviour and other possible factors unrelated to the task that could affect brain activation. Data were pre-processed, corrected for motion artefacts, and filtered using Homer2 (Huppert, Diamond, Franceschini, & Boas, 2009). Thereafter, data were analysed using a combination of custom Matlab scripts

and the SPM-NIRS toolbox (Ye, Tak, Jang, Jung, & Jang, 2009). The rest of this section provides a more detailed account of each of these steps. Moreover, as stated in the introduction of this thesis, one of the aims of this PhD project was to apply advanced connectivity techniques on infant fNIRS data. A description of different types of brain connectivity and advantages of fNIRS that make it a valid method to investigate brain connectivity is described in Chapter 3, followed by validations studies of two connectivity techniques in sections 3.3 and 3.4.

2.3.1 Videocoding and minimum number of trials

Throughout the testing sessions, participants' behaviour was recorded for offline coding. Trials in which participants were not paying attention were excluded from analyses. Additionally, because the studies in the present thesis work aimed to investigate the activation of brain regions notably engaged in social situations, trials in which the participants looked at the parent or anything social, or in which the experimenter or the parent talked were excluded.

As a practice employed by several infants fNIRS studies (S. Lloyd-Fox et al., 2010), only participants with at least three valid trials per condition were included in the analyses. As the hemodynamic response is likely to be highly variable in infancy (Issard & Gervain, 2018), the averaged haemodynamic response based on three trials made the estimation more accurate.

As the second experiment of Chapter 3 and the study presented in Chapter 4 are resting-state studies, a different method of videocoding and a specific requirement for a minimum amount of valid data to be included in the

analysis is considered (more details are described in the method sections of these studies).

2.3.2 Pre-processing and motion artefacts detection

The pre-processing was performed using Homer2 (MGH-Martinos Center for Biomedical Imaging, Boston, MA, USA) (Huppert et al., 2009), a Matlab based program widely used for the analysis of fNIRS data. This program required the conversion of the raw file from a .txt format to a .nirs format, which was performed with an in-house custom script written by my colleague Dr. Anna Blasi. The general pre-processing pipeline on each participant was composed of:

- conversion of the data from raw intensity to optical density, using the normalized changes of light incident on a detector (function *hmrIntensity2OD*);

- pruning of channels with a low intensity level or a low signal to noise ratio ($<10^{-03}$ µmol) (function *enPruneChannels*);

- corrected for motion, either with wavelet or with the combination of spline interpolation (function *hmrMotionCorrectionSpline*) and wavelet filtering (function *hmrMotionCorrect_Wavelet*) (see below for details);

- checked for motion artefacts still in the data channel by channel (defined by signal change greater than 1 micromolar deviating from the mean value of the optical density of each channel within 2 seconds) and consequent exclusion of the trials with motion (function *hmrMotionArtifactByChannels*);

- filtered with bandpass filter to remove physiological noise (0.010-0.80) (function *hmrBandpassFilt*);

- conversion of the data from optical density to concentration (function *hmrOD2Conc*).

During the pre-processing, I dedicated particular attention to the motion artefacts detection. In fact, although the fNIRS technique is relatively robust to motion compared to other methods like EEG, movements can still have a considerable effect on the NIRS signal, especially in developmental data (Brigadoi et al., 2014). A general advice for the detection of artefacts due to movement in the signal, is to pay attention to any change that is rapid and sudden, as the haemodynamic response usually is characterized by slow and smooth features. Several causes can be linked to motion, most commonly attributed to alteration in optical coupling between the fiber and the scalp (i.e. the cap shifted on the participant's head or the fiber no longer properly touches the scalp).

Chapter 5 describes a study where participants sat in a high-chair, not on the parent's lap. This led to a greater amount and more frequent movements of the infants, resulting in a greater amount of very spikey movement artefacts. These artefacts are usually corrected using interpolation, a channel-by-channel approach proposed by Scholkmann (2010). This method works only on the motion artefacts detected (with the mentioned function *hmrMotionArtifactByChannels*), leaving the rest of the signal unmodified. The motion artefact is modelled via a cubic spline interpolation and then subtracted from the original signal (Brigadoi et al., 2014). In all the other datasets in this PhD project motion artefacts were corrected using the wavelet filtering, proposed by Molavi and Dumont (2012). The wavelet transform is applied to every channel, decomposing each time series by the duration of the recording. The wavelet filtering technique assumes that the haemodynamic response is

slower and smoother than motion artefacts. Thus, for every level of decomposition, this technique estimates approximation coefficients of the signal assuming a normal distribution. In this Gaussian, the haemodynamic response is centred (with values around 0), while motion artefacts characterize the outliers of the distribution. Therefore, the coefficients accounting for the tails of the distribution are removed for the signal (Brigadoi et al., 2014). Figure 2.8 summarises the described pre-processing steps.
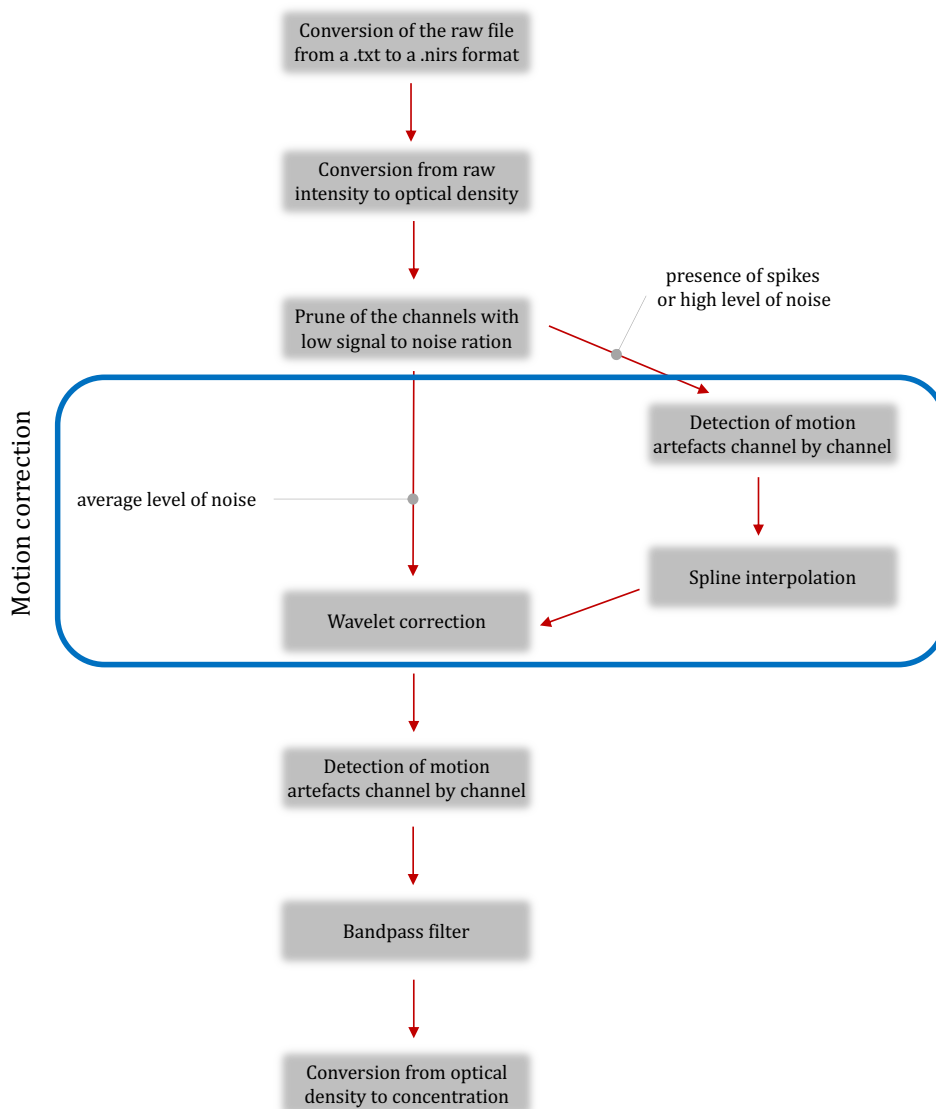
Figure 2.8 Diagram of the pre-processing steps.

2.3.3 SPM-NIRS toolbox

After the pre-processing, data were analysed using a combination of custom Matlab scripts and the SPM-NIRS toolbox (Ye et al., 2009). SPM, which stands for Statistical Parametric Mapping, is a tool widely used for fMRI analysis (Friston, 2007), and has been adapted for fNIRS (Ye et al., 2009). SPM takes as input the time series (i.e. the fNIRS signal in each channel over the time of the experiment – and models them within the General Linear Model (GLM) approach (Friston et al., 1995).

The GLM applied to neuroimaging data analysis is a valuable tool, as it allows the researcher to perform many different statistical analyses (e.g. one sample t-tests, two sample t-tests, paired t-tests, correlations, analysis of variance - ANOVA) (Poldrack & Nichols, 2011). The GLM estimates the likelihood that the haemodynamic response (or haemodynamic response function, HRF) fits the function provided by the model, which is a canonical Gaussian shape by default (Lindquist, Meng Loh, Atlas, & Wager, 2009). SPM offers also the possibility to expand the canonical HRF for two parameters, the temporal derivative (modelling small differences in latency) and the dispersion derivative (modelling small differences in duration). It is worth mentioning that several studies showed high variability in peak height, time to peak and width of the HRF. This might be due to difference in age of the population of interest, type of stimulation, brain areas (D'Esposito, Deouell, & Gazzaley, 2003; Handwerker, Ollinger, & D'Esposito, 2004; Kruggel & Von Cramon, 1999; Poldrack & Nichols, 2011).

The GLM for a dependent variable, i.e. the brain response, is:

$$y = G_1\beta_1 + G_2\beta_2 + \dots G_k\beta_k + \varepsilon$$

where i = 1,....,I indicates the observation, G is the design matrix (i.e. the experimental conditions, but it can also be covariates added to the model), while β are the unknown parameters (i.e. how much each factor contributes). ε are the errors, which the GLM assumes to be normally distributed. The GLM relates a single continuous dependent variable, i.e. the brain response, to one (or more) other variables (continuous or categorical predictor, covariates of interest and no interest). In the model, the dependent variable is described by the linear combination of a certain number of regressors, in a weighted sum up to the level of error. If the regressors accurately describe the brain response, it is more likely that the error presents a normal distribution. (Monti, 2011)

The estimation of the GLM is based on the *ordinary least square* (OSL) method, which minimizes the residuals (the distance between each data point and the predicted line by the model). The smaller the difference, the better the model fits the data. The outputs are beta parameters, representing how far the real data are from the predicted shape of the HRF, therefore the estimate of the amount of activation in a certain condition (Poldrack & Nichols, 2011). The simplest model proposed in the context of the GLM relies on the *simple linear regression*, where only one single independent variable is related to the brain response, written as:

$$y = \beta_0 + G_1\beta_1 + \varepsilon$$

More frequently, researchers build models based on *multiple linear regression*, considering the effect of multiple independent variables in the model, written as:

$$y = \beta_0 + G_1\beta_1 + G_2\beta_2 + G_3\beta_3 + G_4\beta_4 + \ldots + G_p\beta_p + \varepsilon$$

or as a design matrix as:

$$
\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ y_n \end{bmatrix} = \begin{bmatrix} x_{1,1} & x_{1,2} & x_{1,3} & \cdots & x_{1,p} \\ x_{2,1} & x_{2,2} & x_{2,3} & \cdots & x_{2,p} \\ x_{3,1} & x_{3,2} & x_{3,3} & \cdots & x_{3,p} \\ \cdot & \cdot & \cdot & \ddots & \cdot \\ \cdot & \cdot & \cdot & & \cdot \\ \cdot & \cdot & \cdot & \ddots & \cdot \\ \cdot & \cdot & \cdot & \ddots & \cdot \\ x_{n,1} & x_{n,2} & x_{n,3} & \cdots & x_{n,p} \end{bmatrix} \times \begin{bmatrix} \beta_p \\ \beta_p \\ \beta_p \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \beta_p \end{bmatrix} + \begin{bmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \\ \cdot \\ \cdot \\ \cdot \\ \cdot \\ \varepsilon_n \end{bmatrix}
$$

The GLM in SPM is represented as a matrix where every row is a time point in the observation and every column is an effect in the model (i.e. testing conditions of the experimental design or covariate). The last column is composed of the error estimated in the model (Monti, 2011). For each participant, a GLM design matrix is constructed, obtaining beta parameters for each condition modelled. The betas are then used to calculate a contrast, based on the condition of interest and on the effect hypothesised in the study (i.e. betas in condition 2 - betas in condition 1). The calculated contrast is then submitted to statistical tests analyses.

In this PhD work, the only exceptions to the GLM approach to analyse fNIRS data are the second study presented in Chapter 3 and the study in Chapter 4. These two studies measured spontaneous brain fluctuations during quiet waking, in the absence of any cognitive, sensory or social stimulation (Raichle, 2015).

One of the unique features of the SPM approach, is the possibility to use the GLM design matrix as a foundation for connectivity analyses, such as the Dynamic Causal Modelling and the Psychophysiological Interaction, used in this

PhD work as well. As I explained in the introduction of this thesis, the study of the developing brain can benefit from the use of network analyses, which provide a deeper understanding of and a more realistic approach to processes in the brain. The next chapter provides an overview of the use of fNIRS for connectivity analyses, and it shows two studies in which two connectivity techniques that are widely used in fMRI, have been adapted to be employed with infant fNIRS data.

2.3.3.1 Correction for multiple comparisons

The more statistical inferences are made, the more likely significant results may be obtained by chance (Field, Miles, & Field, 2013). Therefore, taking into account that the several comparisons are performed when considering a set of statistical tests simultaneously is necessary in order to avoid type I errors, i.e. incorrect rejections of the null hypothesis (Simmons, Nelson, & Simonsohn, 2011). To ensure statistical reliability, throughout this thesis, significant results are corrected for multiple comparisons using the False Discovery Rate (FDR) method (Benjamini & Hochberg, 1995). The FDR approach is a method widely used in functional neuroimaging (Chumbley, Worsley, Flandin, & Friston, 2010; Genovese, Lazar, & Nichols, 2002), and especially in multichannel NIRS analysis, defined as *the expected proportion of false detections among the declared active channels* (Singh & Dan, 2006). Compared with the FDR, the Bonferroni correction, which is the other method typically used in several neuroimaging studies, has been considered too conservative, reducing the power of the statistical tests and increasing the chance of type II errors, i.e. incorrect rejections of the experimental hypothesis (Bennett, Wolford, & Miller, 2009; Singh & Dan, 2006). While with the Bonferroni approach the power is

inversely proportional to the number of tests, therefore depending on the number of channels used to acquire data, the FDR approach estimates the proportion of false rejections among all the declared rejections, which should provide a more robust and consistent measure of the type I error (Singh & Dan, 2006). The FDR approach has been previously used by several infant fNIRS studies (for some examples see Blasi et al., 2015; Blasi, Lloyd-Fox, Johnson, & Elwell, 2014; Filippetti, Lloyd-Fox, Longo, Farroni, & Johnson, 2015; Lloyd-Fox, Papademetriou, et al., 2014; May, Byers-Heinlein, Gervain, & Werker, 2011; Watanabe, Homae, & Taga, 2010).

Chapter 3

A measure for the complexity of the brain:
connectivity analyses on infant fNIRS data

3.1 From functional segregation to functional integration

Exploring the patterns of neural connectivity associated with complex psychological domains, such as self-awareness, can provide a richer picture than the investigation of activation of single brain areas. The phrenology formulated by Gall in the 19th century can be considered the first attempt that defined brain regions as biological substrates to mental and psychological function (Gall & Spurzheim, 1835). This framework was later rejected for its aim to identify personality traits based on protrusion on individuals' head, but its merit was to acknowledge that different parts of the brain contribute to mental processes. In line with this view, decades later, clinical studies demonstrated that a specific mental ability or a psychological characteristic is represented by a particular brain region (Brodmann & Garey, 2006; Phillips, Zeki, & Barlow, 1984; Simpson, 2005). Consequently, the main aim of neuroscience has been to map the human brain and define the functions of each specific area (Friston, 2011). This approach has been extremely informative for our fundamental understanding of brain function. In particular, lesion studies have contributed to the understanding of brain area specialisation by highlighting how an injured brain region leads to a lack of or impaired behaviours (for example see the pioneering works by Broca, 1861). Ironically, it was the cortical reorganisation that can sometimes be observed in lesion patients that led researchers to start thinking about the brain in terms of *connectionism*, i.e. representing mental functions with brain networks, rather than *localisationism* and *specialisation*, i.e. representing mental functions with the activation of brain regions (Absher & Benson, 1993; Friston, 2011; Lee,

Harrison, & Mechelli, 2003). In 1991, Felleman and Van Essen created a connectional map of the macaque monkey brain (Felleman & Van Essen, 1991) and Crick, the famous molecular biologist, commented that, "it is intolerable that we do not have this information for the human brain. Without it, there is little hope of understanding how our brains work except in the crudest way" (Crick & Jones, 1993, p. 110).

The beginning of brain connectivity science in non-human species, the achievement of a good understanding of brain regions in terms of functional specialisation, and the improvement in techniques and tools for data analysis are some of the main factors that set the scene for a new significant stream in neuroscience, i.e. the functional integration of brain regions and the study of networks. The growing interest in brain connectivity has opened new avenues of research in several fields of neuroscience, such as basic cognitive science, brain diseases and lesions, psychopathology, neuroanatomy, and neurodevelopment. It is worth mentioning that *functional specialisation* and *functional integration* should not be considered mutually exclusive when studying the human brain. Instead, they are two fundamental principles that combine to contribute to the full picture of brain organisation. The concepts of integration and networks can be applied to several levels of the brain, from cells and neurons to circuits and more complex systems.

Recent neuroimaging research aims to define how brain areas are related within networks and has highlighted that it is necessary to think in terms of dynamic interactions between large populations of neurons to explain complicated cognitive processes and behaviours (Sporns, 2015). Embracing the concept of brain networks means conceiving neuronal activity as a whole, where one area is likely to affect or mediate the activity of another, and a pure

independence of neuronal events is barely observed (Friston, 1994). Network analyses are more likely to offer a realistic idea of the brain by describing the integration of different brain regions as the neural underpinnings supporting multifaceted psychological domains, such as the sense of self.

The next section provides an overview of the different types of brain connectivity that is necessary to correctly interpret the results in this PhD thesis. The following section describes why fNIRS, which is the neuroimaging technique used in this thesis, is a reliable tool for studying functional connectivity, as well as the validation of two connectivity techniques that allowed me to perform network analyses on infant fNIRS data.

3.1.2 Different types of brain connectivity

The term 'brain connectivity' refers to patterns of both anatomical and functional connections between brain regions (Sporns, 2013). *Structural connectivity* describes the anatomical connections between brain regions, e.g. synapses and axonal projections. These are edges that link together nodes, which are cortical and subcortical structures in the brain (Bullmore & Sporns, 2009; Laughlin & Sejnowski, 2003; Sporns, 2013). Structural connectivity is commonly considered to be state-independent, i.e. it cannot be manipulated by experimental conditions or stimulations. However, structural connections are relatively plastic, and go through significant changes over the course of development (Barnea-Goraly et al., 2005; Gunning-Dixon & Raz, 2000; Guttmann et al., 1998) and as a result of learning processes (Schlegel, Rudelson, & Tse, 2012; Zatorre, Fields, & Johansen-Berg, 2012). For example, it has been shown that children with Autism Spectrum Disorders (ASD) showed disruptions in white matter tracts (Barnea-Goraly et al., 2004). Markers of

impaired white matter projections have been found even in 6 month-old infants at high-risk of ASD (Wolff et al., 2012). Structural connectivity analyses are commonly performed using diffusion tensor imaging (DTI), which enables to map the diffusion process of water molecules in biological tissues in vivo and non-invasively (Le Bihan et al., 2001; Merboldt, Hanicke, & Frahm, 1985; D. G. Taylor & Bushell, 1985). As the water tends to diffuse along a preferential axis, the axonal tracts follow the orientation of the water molecules, enabling researchers to infer the integrity and direction of the tracts (Mori, Oishi, & Faria, 2009; Mori, Wakana, Nagae-Poetscher, & Van Zijl, 2005). Since the introduction of this technique in 1994, the research aiming to map the white matter projections in healthy adult brains and the brains of people with abnormal conditions has advanced (Catani & de Schotten, 2012). The relative stability of the tracts' structures makes the acquisition of this type of data feasible with no constraints. In fact, DTI analyses are performed on T_1-weighted MRI images of the participant's brain, which can be acquired while they are asleep, thus reducing any movement that can affect the quality of the data (Assaf & Pasternak, 2008; Hagmann et al., 2006). While studying structural connectivity is not the focus of this PhD thesis, its strong link with the functional connections (which is described afterwards) requires an overview on it.

Functional connectivity is defined as the statistical association or dependency between two or more anatomically distinct time series of brain activity (Friston, 1994). Functional connectivity is usually explored through pairwise interactions, using correlations or the corresponding measure in the frequency domain (i.e. coherence), which indicate which time series display similar fluctuation or activation patterns to another, even if they are not spatially close (McIntosh, 2010). The coupling between two brain regions is

described in terms of 'statistical dependencies', abstaining from any notion of causality or directionality (Friston, 2011). Functional connectivity can be estimated in the absence of any cognitive and social stimulation, so-called resting-state (Biswal, 2012). Resting-state functional connectivity estimates correlations among spontaneous fluctuations, therefore it is considered the intrinsic brain activity during quiet wakefulness (Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995; Damoiseaux et al., 2006; van den Heuvel & Pol, 2010). An estimation of functional connectivity during resting-state is the focus of section 3.4 and Chapter 4.

Functional connectivity can also be estimated during a task. As alternative to correlational approaches, Psychophysiological Interaction (PPI) is an advanced functional connectivity method that investigates how the relationship between areas changes during the task (Friston et al., 1997). Developed in the context of SPM for fMRI data, during this PhD project, I have adapted this method for infant fNIRS data with the support of one of my supervisors, Professor Antonia Hamilton. While classical functional connectivity methods only perform correlations among time series, PPI explores how connections between brain regions are modulated by the task. More specifically, PPI analysis allows the identification of brain regions whose activity depends on an interaction between psychological context (the task) and physiological state (brain activity time courses) of the seed region (O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012). PPI cannot infer any directionality or causality among the connections (Goldenberg & Galván, 2015). In this thesis, functional connectivity was estimated using PPI in Chapter 5 and Chapter 6.

Further investigation of the relationship between brain regions is provided by *effective connectivity*, which infers the "influence that one neuronal system exerts over another" and the possible causal relationship between hidden neuronal states (Friston, 1994, 2011). Researchers tend to agree that taking effective connectivity into consideration leads to a more advanced description of the relationships between brain regions and it provides more specific information than the one obtained by the correlational approach (Friston, 2011; Horwitz, 2003; Lee et al., 2003). One of the few limitations of the effective connectivity approach compared with the functional connectivity one is that effective connectivity methods handle fewer nodes than the functional connectivity ones (Smith, 2012). Therefore researchers are not advised to use effective connectivity analysis at an exploratory stage, but only when they have clear hypotheses of a limited number of brain regions integrated in a network (Friston, Harrison, & Penny, 2003; Garrido, Kilner, Kiebel, Stephan, & Friston, 2007). A validation study of the an effective connectivity technique on infant fNIRS data is the focus of section 3.3

Figure 3.1 shows a graphical representation of the three types of connectivity mentioned in this paragraph.
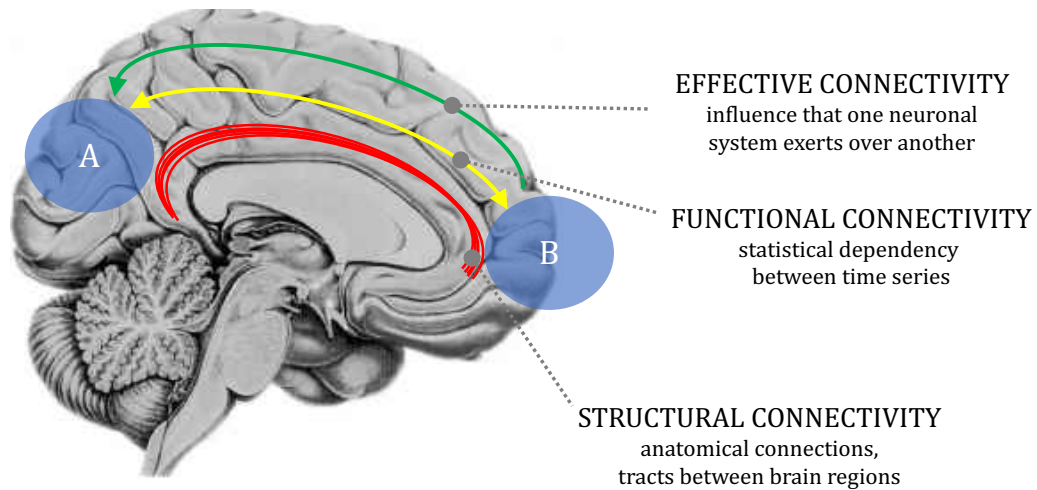
Figure 3.1 Graphical representation of the different types of brain connectivity. Structural connectivity is represented in red, functional connectivity in yellow, effective connectivity in green.

After reading this overview of the different types of brain connectivity, one may wonder about the relationship between structural and functional (and effective) connectivity. The first study to investigate the relationship between structural and functional connections was performed by Koch, Norris and Hund-Georgiadis in 2002. It was found that the areas that showed strong structural connections also had high functional connections. Interestingly, strong functional connections were also found in regions not necessarily linked by strong white matter tracts (Koch, Norris, & Hund-Georgiadis, 2002). This suggests that two brain areas can be activated together even in the absence of a direct anatomical link or even if they are physically connected by a long, indirect path (Honey et al., 2009; Sporns, 2015). This means that we can infer functional connectivity from structural connectivity, but not *vice versa* (Honey et al., 2009; Sporns, 2015). Knowledge of the structural-functional connectivity relationship has been increased by several other studies that have attempted to map the human connectome in typical adult brains (for some examples see Fjell et al., 2016; Fukushima et al., 2017; Greicius, Supekar, Menon, & Dougherty,

2009; Meier et al., 2016; Park & Friston, 2013; Stam et al., 2016), in developing brains (for some examples see Betzel et al., 2014; Marusak et al., 2017; Uddin, Supekar, Ryali, & Menon, 2011), and in psychopathological or diseased brains (for some examples see Damoiseaux & Greicius, 2009; Jalbrzikowski et al., 2017; Ray et al., 2014).

In this thesis, the focus was on estimating functional and effective connectivity in the developing brain. As I was interested in exploring the neural underpinnings of self-awareness, my interest was how brain regions which have been typically associated with self-processing, such as the mPFC and the TPJ, are activated together. For this purpose fNIRS was a suitable method, and the next section provides more details about the methodological advantages of fNIRS when exploring brain connectivity.

3.2 fNIRS as a suitable method to explore brain connectivity

Tracking functional connectivity of the developing brain is an area of increasing research interest, and fNIRS is a valid method for studying the infant brain. However, several other methods have also been used to explore connectivity in infancy and childhood. For example, some researchers have used EEG in awake infants (for some examples see Grieve et al., 2008; Meijer et al., 2016; Orekhova et al., 2014; Righi, Tierney, Tager-Flusberg, & Nelson, 2014; Tóth et al., 2017), while most of the fMRI studies focused on resting-state connectivity in sleeping infants (Damaraju, Caprihan, & Lowe, 2014; Emberson, Richards, & Aslin, 2015; Fransson, Åden, Blennow, & Lagercrantz, 2011; Gao, Lin, Grewen, & Gilmore, 2016; Kwon et al., 2016; Lin et al., 2008; Lu et al., 2010; Marrus et al., 2017).

These studies have started to shed light on how connectivity develops over the first years of life, although there still is a lot unknown about how different brain areas are functionally linked to each other, considering that the brain is constantly changing, maturing over the first years of life (Johnson, 2001; Knickmeyer et al., 2008).

Using fNIRS to investigate functional connectivity can provide some advantages that have the potential to further advance our understanding of the development of functional networks in the brain. Firstly, fMRI studies on sleeping participants should consider that connectivity measured during sleep does not display the same patterns of co-activation as connectivity during wakefulness. Additionally, sleep stages have been shown to affect functional networks (Tagliazucchi & Laufs, 2014). Secondly, fNIRS is quite robust to motion compared to fMRI (Friston, Williams, Howard, Frackowiak, & Turner, 1996). Head motion is a big limitation for fMRI-based connectivity studies, because even very small movements (smaller than 1 mm), that typically occur during natural sleep, will affect functional connectivity estimations. In particular, head movements decrease long-range connectivity and increase short-range connectivity (Deen & Pelphrey, 2012; Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; van Dijk, Sabuncu, & Buckner, 2012). Given this, it is obvious that acquiring reliable connectivity data from awake infants and toddlers in the MRI scanner is exceptionally difficult. Thirdly, as mentioned before, fNIRS has a higher temporal resolution compared to fMRI, which reaches only 1 hertz, allowing for rapid data acquisition up to 100 hertz[7] (Kim, Richter, & Uğurbil, 1997; Huettel; Song; Gregory McCarthy et al., 2004;

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[7] The sampling rate of acquisition of the fNIRS studies presented in this PhD thesis is 10 Hz, but this is still higher than the one provided by fMRI.

Weishaupt, Kochli, Marincek, & Kim, 2007). This enables researchers to obtain more time-accurate recordings of the hemodynamic fluctuations of the brain, therefore contributing with higher resolution information to studies using connectivity analyses, and those examining the correlations between the time-series and relations between brain areas (Lee, Zahneisen, Hugger, LeVan, & Hennig, 2013).

Connectivity methods for fNIRS are still underdeveloped compared to those available for fMRI. During this PhD project, I focused on validating some connectivity techniques - previously developed only for fMRI or for adult fNIRS data - for the use on infant fNIRS data. The aim was to enhance the fNIRS method for connectivity analyses on infant data, in order to open new avenues of studies for researchers interested in describing the developing brain with a focus on network analyses. Moreover, this could help to elucidate neural correlates of self-awareness in infancy, by providing a richer picture than simple analyses on brain activation.

The next section presents a validation study of Dynamic Causal Modelling (DCM) on infant fNIRS data (section 3.3). DCM is considered by many the most accurate technique that can estimate directionality of the connections, and how experimental conditions can affect them (Friston et al., 2003). By developing data analysis pipelines and guidance for their application, I am confident that this study will be a good reference for a new line of research. Section 3.4 presents a longitudinal investigation of the developmental trajectory of functional connectivity acquired in awake infants at rest. Intrinsic functional connectivity is thought to gradually increase during the first years of the development, but knowledge of this relies on fMRI studies with sleeping participants. Taken together, these two studies provide a validation of two

techniques to explore brain connectivity in the developing brain, enriching the

understanding of how neural networks changes over the first years of life.

3.3 Dynamic Causal Modelling on infant fNIRS data: a validation study on a simultaneously recorded fNIRS-fMRI dataset

Section 3.3 is based on the following article:

Bulgarelli, C., Blasi, A., Arridge, S.R., Powell, S., de Klerk, C. C. J. M., Southgate, V., Brigadoi, S., Penny, W., Tak, S., Hamilton, A. (2018). Dynamic causal modelling on infant fNIRS data: A validation study on a simultaneously recorded fNIRS-fMRI dataset. *NeuroImage.*

3.3.1 Abstract

DCM is an advanced connectivity technique developed for fMRI data, that aims to estimate the coupling between brain regions and how this might be modulated by changes in experimental conditions. DCM has recently been applied to adult fNIRS, but has never been applied to infant fNIRS data. The present study provides a proof-of-principle for the application of this method to infant fNIRS data and a demonstration of the robustness of this method using a simultaneously recorded fMRI-fNIRS single case study, thereby allowing the use of this technique in future infant studies. fMRI and fNIRS were simultaneously recorded from a 6-month-old sleeping infant, who was presented with auditory stimuli in a block design. Both fMRI and fNIRS data were pre-processed using SPM, and analysed using a general linear model approach. The main challenges that adapting DCM for fNIRS infant data posed included: (i) the import of the structural image of the participant for spatial pre-processing, (ii) the spatial registration of the optodes on the structural image of the infant, (iii) calculation of an accurate 3-layer segmentation of the

structural image, (iv) creation of a high-density mesh as well as (v) the estimation of the NIRS optical sensitivity functions. To assess our results, values obtained for variational Free Energy (F), Bayesian Model Selection (BMS) and Bayesian Model Average (BMA) with the same set of possible models were compared between the fMRI and fNIRS datasets. High correspondence in F, BMS, and BMA between fMRI and fNIRS data was found, therefore showing for the first time high reliability of DCM applied to infant fNIRS data. This work opens new avenues for future research on effective connectivity in infancy by contributing a data analysis pipeline and guidance for applying DCM to infant fNIRS data.

3.3.2 Introduction

DCM is an advanced connectivity technique developed for fMRI data, that aims to not only evaluates the couplings between brain regions, but also the directionality of the connections and how these are influenced by changes in the experimental context (Friston, 2011).

The alternative method to explore effective connectivity is Granger Causality (GC), which has been developed in the context of economic science and then applied to neuroscience (Granger, 1969; Seth, Barrett, & Barnett, 2015). This method uses linear regression modelling of stochastic processes to infer causality (Granger, 1969; Seth et al., 2015). However, GC is limited as it bases the inference of causality only on temporal precedence of one time series over another, inferring that earlier responses in a region predicts later responses in another one. This might reflect some imprecision in the estimation of causality if we consider data with low sampling rate (order of seconds) and at the convolution with the HRF process, which usually requires long delays between peaks. Moreover, GC hardly takes into account inter-region variability in the brain and it cannot inform us about the nature of the connections, i.e. whether they are excitatory or inhibitory (Anzellotti, Kliemann, Jacoby, & Saxe, 2017; Handwerker, Gonzalez-Castillo, D'Esposito, & Bandettini, 2012). On the contrary, the DCM approach proposes a more realistic and precise models of human brain networks, supporting the nonlinear and dynamic nature of interaction between neuronal populations. DCM provides a generative model of neuronal and biophysical states underlying specific brain networks, building up a model of the neural patterns in different brain regions and how they interact with each other. The novelty and the strength of this technique in the estimation of effective connectivity relies on the exploration of how

connections can be perturbed by experimental context, which goes beyond the evaluation of the couplings between brain regions (Friston, 2011). This makes this advanced method the first technique that can estimate changes in connectivity not only from endogenous noise, but also from external factors. Additionally, two different options in which experimental conditions can enter the model are considered by the DCM approach; either through direct influences on specific anatomical brain areas, or through a modulation of the coupling among brain areas, so on the functional connections between regions (Friston, Harrison, & Penny, 2003). Typically researchers build a family of models with slightly different connections or experimental contexts. Bayesian statistic is then used to determine which model gives the closest description of the data (Bayesian Model Selection, *inference on model space*) and to estimate the strength and the nature of the connections, excitatory or inhibitory (Bayesian Model Average *inference on parameter space*) (Penny, Stephan, Mechelli, & Friston, 2004). From the comparison detailed in the last paragraph with other connectivity techniques often used in neuroimaging research, it is understandable why DCM is so ground-breaking and innovative (Friston, 2011; Friston, Moran, & Seth, 2013; Stephan et al., 2010)

DCM has been developed and widely applied in the context of fMRI (Friston, Li, Daunizeau, & Stephan, 2011; Schuyler, Ollinger, Oakes, Johnstone, & Davidson, 2010), and it has been adapted for use on adult fNIRS data (Tak, Kempny, Friston, Leff, & Penny, 2015). The aim of the current study was to determine if DCM can be used on infant data as well. In order to validate the use of DCM on infant data, fMRI and fNIRS were simultaneously recorded from a 6-month-old sleeping infant, who was presented with auditory stimuli in a block design. MRI scans of the participant structural images were acquired as well to

allow for the coregistration of the fMRI and fNIRS data. The application of DCM on infant fNIRS data required several technical challenges to be solved. Firstly, the participant structural image had to be imported in the SPM-NIRS toolbox in order to get a precise spatial registration of the fNIRS optodes on the infant's brain. In order to correctly estimate the light path throughout the brain layers, the NIRS optical sensitivity functions was then evaluated on a high-density mesh based on the segmented structural image of the participant. Finally, the specification of DCM models had to be adapted for infant brain features.

This study aims to describe the solutions provided to the problems encountered when applying DCM to infant data, and therefore test if this analysis tool, initially developed for adult fNIRS only, can also be applied in the developmental context. The simultaneous fMRI-fNIRS recording allows the validation of this advanced connectivity technique, favouring its application to other fNIRS datasets, obviating the need for MRI. I hope that this project will provide a step toward better studies of functional connectivity with fNIRS, opening doors to new lines of research.

3.3.2 Material and Methods

Figure 3.2 displays the outline of the analysis conducted in this study for fNIRS, MRI and fMRI.
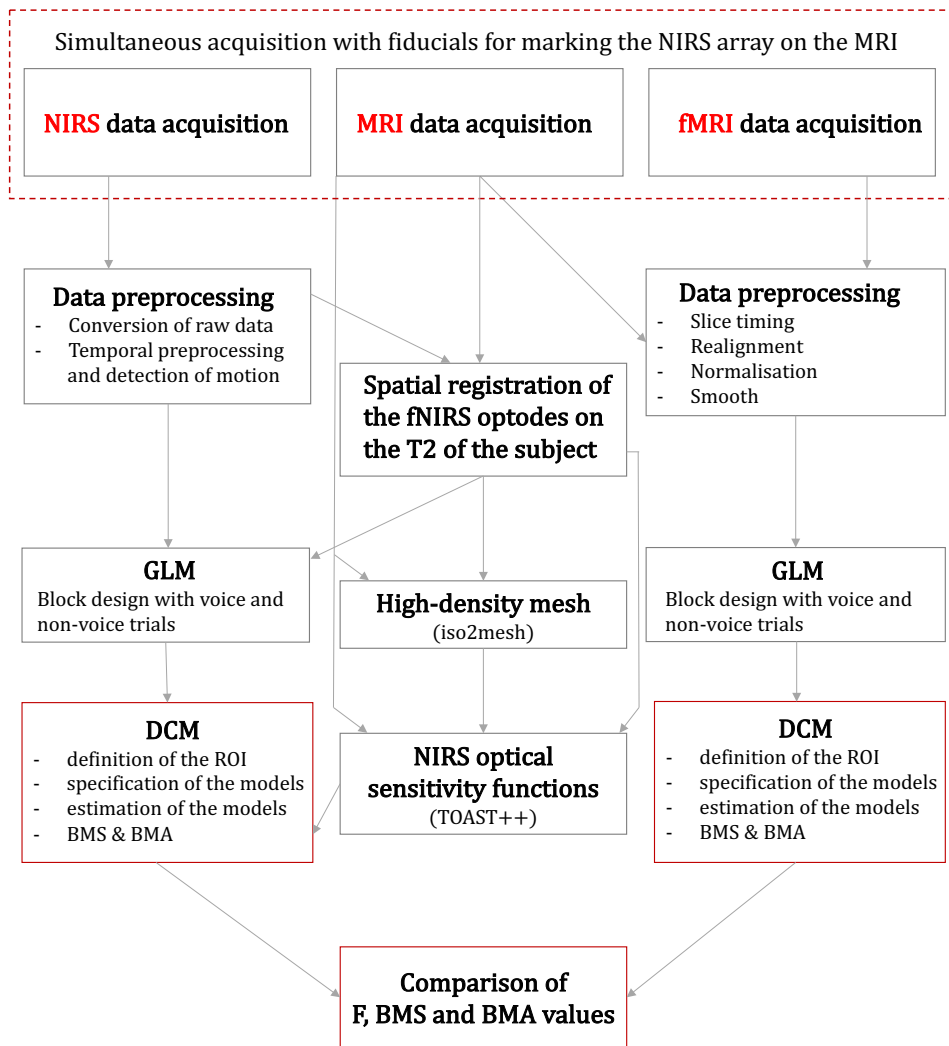
Figure 3.2 Outline of the analyses conducted in this study for fNIRS, MRI and fMRI.

3.3.2.1 Data acquisition

fMRI and fNIRS data were simultaneously acquired from a single participant (183 days-old) during natural sleep. The infant listened to vocal (e.g. coughing) and environmental (non-vocal) sounds (e.g. running water) interleaved with silence in a protocol previously tested with fNIRS and fMRI separately (Blasi et al., 2011, 2015; Lloyd-Fox, Blasi, Mercure, Elwell, & Johnson, 2012). The stimuli were organized in a block design, with a presentation time of 9 seconds and a rest period of at least 13 seconds between conditions. The recording session

lasted 11.5 minute, and we acquired 24 trials in total, 12 for the voices condition (V) and 12 for the non-voices condition (NV).

3.3.2.1.1 fMRI

MRI data were acquired using a GE 1.5 Tesla Twinspeed MRI scanner (General Electric, Milwaukee, WI, USA). 320 T2* weighted gradient echo planar multi-slice datasets depicting BOLD (Blood Oxygenation Level Dependent) contrast were acquired in each of 24 non-contiguous near-axial planes (4.0 mm thick with 1.0 mm spacing, 3.5 x 3.5mm in-plane resolution) parallel to the Anterior Commissure-Posterior Commissure line (TE 57 ms, TR 3000 ms, flip angle 90°, 16:04 minutes). At the same session, a T2 weighted fast spin echo (FSE) dataset was acquired (256x168 rectangular matrix, 2mm slice thickness, 0mm slice gap, field of view=18cm, TR=4500, TE=113ms, echo train length=17). Data quality assurance was carried out to ensure high signal to ghost ratio, high signal to noise ratio and excellent temporal stability using an automated quality control procedure. (Simmons, Moore, & Williams, 1999). The body coil was used for RF transmission and an 8-channel head coil for RF reception (a Simmons et al., 1999). The whole scanning procedure was stopped immediately if the infant awoke and/or expressed discomfort. An experimenter and the parent stood in the scanner room to observe the infant's behaviour at all times.

3.3.2.1.2 fNIRS

The fNIRS array (UCL Optical Imaging System (Everdell et al., 2005)) was placed over the right temporal lobe, and included 9 source-detector pairs (channels), defined by 4 sources and 4 detectors, with a 2 cm source-detector separation. The sources in the NIRS system provided light at 770 nm and 850

nm, and the sampling rate of acquisition was 10 Hz. MRI fiducial markers (vitamin E caplets) were attached to the inter-optode spaces of the NIRS array to guide the co-registration of the NIRS data onto the MRI image. Figure 3.3-A shows a design of the array.

Brain activations and connectivity analyses were restricted to the right hemisphere, because the fNIRS array was placed over the right hemisphere only, in order to optimise the number of sources and detectors available from the system, the difficulty of fitting the NIRS headgear within the restricted space in the MRI coil, and also considering the wide literature that suggests the main role of the right hemisphere in social auditory processing (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Blasi et al., 2011; Grossmann, Oberecker, Koch, & Friederici, 2010; Lloyd-Fox et al., 2012).

3.3.2.2 Data pre-processing

3.3.2.2.1 fMRI

All fMRI images were analysed using Statistical Parametric Mapping software (SPM12) (Friston & Ashburner, 1994). Scans were corrected for slice timing and realigned for head movements. Images were then normalized to the T2 image of the participant, and smoothed using a 7-mm full-width at half-maximum isotropic Gaussian kernel.

3.3.2.2.2 fNIRS

The fNIRS data were analysed using the SPM-fNIRS toolbox, a SPM12 based software for statistical analysis of fNIRS signal (Tak, Uga, Flandin, Dan, & Penny, 2016; Ye, Tak, Jang, Jung, & Jang, 2009). The raw intensity data were converted to haemoglobin changes using the modified Beer-Lambert Law (DPF = 5.13

(Duncan et al., 1995)). The spatial pre-processing registering the fNIRS channels over the native space of the participant was performed (see specific paragraph below). The temporal pre-processing included the removal of physiological noise (5th order Butterworth high-pass filter: 0.008 Hz; band-stop filter: 0.06-0.16 – 0.8-1.8 Hz), and the reduction of motion artefacts with spline interpolation. Artefacts were detected as changes in moving standard deviation larger than 3 μM using a 1 second sliding window (Scholkmann, Spichtig, Muehlemann, & Wolf, 2010). Our analysis of fNIRS data is based on changes in HbO_2, following the only study to date that has applied DCM to fNIRS data (Tak, Kempny, Friston, Leff, & Penny, 2015). Additionally, previous fNIRS studies with infants typically do not find any statistically significant HHb changes (for some examples see: Grossmann, Cross, Ticini, & Daum, 2013; Lloyd-Fox et al., 2010; Sarah Lloyd-Fox, Széplaki-Köllod, Yin, & Csibra, 2015; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014).

3.3.2.2.3 Spatial registration

A precise estimation of optode positions and reference points is crucial for calculating connectivity, therefore, particular attention needs to be dedicated to the fNIRS spatial registration to the MRI images. Location of the reference points and of the optode positions are required as an input of the fNIRS spatial processing to calculate the brain area covered by the NIRS channels. One option would be to use readily available adult MRI templates. However, this is not an ideal solution as the infant brain is not a reduced-size version of an adult brain (Sanchez et al., 2012b). Instead, we used the participant's own structural image for spatial co-registration of the NIRS data.

Optode positions on the head were manually estimated from the fiducial markers on the T2 structural image of the participant. In particular, we defined projection points from each fiducial onto the scalp as the location of each NIRS channel (Figure 3.3-B). We estimated the centre of the fiducial as the middle point between each source and detector, therefore they mark the centre of the channel. From here, we calculated the exact coordinates of each optodes on the infant's head.

The structural image of the infant was imported in the SPM-fNIRS toolbox, using custom modified code from the NFRI toolbox (Okamoto et al., 2004). On this structural image, the reference points and the optodes were plotted (see figure 3.3-C).

3.3.2.3 Segmentation and creation of the mesh

Two structural scans were recorded from the participant: one immediately before and another one immediately after functional data collection. Superimposition of both images revealed that the infant had barely moved between the two time points, therefore the two images were averaged and upsampled to improve their quality (Manjn et al., 2010). After that, the image was flattened to remove intensity level inhomogeneities caused by the magnetic field, and then, using in house scripts written in Matlab, its background was removed. The structural scan was skull stripped with FSL (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL) using the BET (Brain Extraction Tool) routine including the functions BET2 (to isolate the brain) and BETSURF (to separate the scalp and inner skull surfaces) (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012). The brain image was then further processed with SPM's SEGMENT option, using tissue probability maps from an age appropriate

segmented template (from the *Neurodevelopmental MRI Database* of the University of South Carolina), very light bias regularisation (0.0001), and FWHM Gaussian smoothness of bias with 30 mm cut-off. At the end of this process, the infant structural scan was segmented in 3 layers: skin and skull and extra-cerebral tissue, CSF, and brain (grey plus white matter). Using another set of Matlab scripts, the 3 layers were post-processed to fill in gaps and ensure that all voxels were assigned the correct labels. As explained in the previous section, the segmented images were then used to provide the necessary anatomical information to the fNIRS data reconstruction step (see Figure 3.3-D)

From the 3-layers segmentation image, a high-density volumetric tetrahedral mesh was created using *iso2mesh* toolbox (Fang & Boas, 2009) (see figure 3.3-E). Using in-house custom code, the optodes coordinates were converted from the MRI structural image context to mesh-based context. (For the estimation of the optode positions, the reader is referred back to the section on *Spatial registration* paragraph). The optode locations on the mesh and the mesh itself created from the structural scan were used as inputs for the estimation of the NIRS optical sensitivity functions.

3.3.2.4 NIRS optical sensitivity functions[8]

Application of the DCM technique requires estimates of the sensitivity of the optical measurements at different wavelengths to changes in the chromophore

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[8] This paragraph was jointly written with Professor Simon Arridge (Centre for Medical Image Computing, University College London, United Kingdom) and Dr. Samuel Powell from the Department of Medical Physics (Department of Medical Physics and Biomedical Engineering, University College London, United Kingdom), developers of the TOAST++ toolbox.

concentrations of interest. In the context of diffuse optical imaging, these sensitivity functions are referred to as photon measurement density functions (Arridge & Schweiger, 1995; Arridge, 1995). The requisite sensitivity functions are calculated from products of the forward field generated by a given optical source, and the adjoint field generated by placing an equivalent optical source at the location of a detector. To compute the forward and adjoint fields the diffusion equation was employed with a Robin boundary condition

$$(\nabla \cdot \kappa \nabla + \mu_a)\phi(r) = 0 \qquad (r \in \Omega),$$

$$\phi(r) + 2A\kappa n \cdot \nabla \phi(r) = q \quad (r \in \partial\Omega),$$

where 'r' is a point in space, Ω is the computational domain with boundary $\partial\Omega$, ϕ is the fluence rate resulting from application of the physical or adjoint source q, $\kappa = (3(\mu_a + \mu_s))^{-1}$ is the diffusion coefficient, μ_a and μ_s are the wavelength dependent baseline absorption and scattering coefficients, A is a term accounting for the index of refraction mismatch at the boundary, and n is the outward normal to the boundary (Arridge, Schweiger, Hiraoka, & Delpy, 1993).

The TOAST++ toolbox was used to solve the diffusion approximation numerically via the Finite Element Method (Schweiger & Arridge, 2014). In each case the properties of the source and detector were specified according to physical measurements, and the wavelength dependent baseline absorption and scattering coefficients were derived from a previous study performed on neonates (Singh et al., 2014).
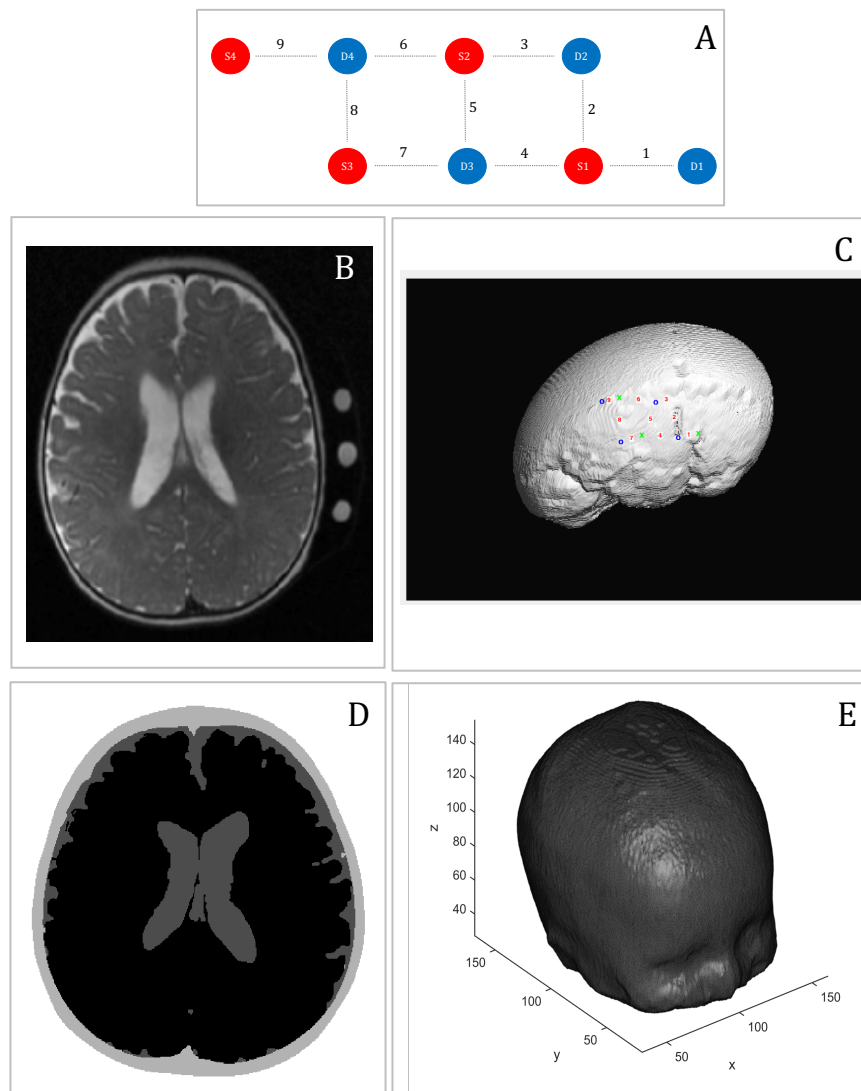
Figure 3.3 Representation of the main methodological steps. A, Representation of the array. Sources are marked in red, detectors are marked in blue. Channels are marked with grey dotted lines and the channel number is indicated. B, T2 structural image of the participant with fiducials for the fNIRS channels. C, Output from the NIRS-SPM toolbox, spatial registration of the optodes over the T2 of the infant imported with the NFRI toolbox. Green 'x' are the sources, blue 'o' are the detectors and channels are labelled with red numbers. D, 3-layers segmentation from the T2 structural image of the infant. E, High-density volumetric tetrahedral mesh created with *iso2mesh* toolbox from the segmented structural image of the infant.

3.3.2.5 General Linear Model for fMRI and fNIRS

For both fMRI and fNIRS data, the evoked hemodynamic responses were

modelled as a delta function convolved with a hemodynamic response and its

spatial and temporal derivatives within the context of the GLM. Onsets of voice (V) and non-voice (NV) trials were specified in seconds.

3.2.2.6 Selection of ROIs/cortical source regions and definition of the DCM models

In order to estimate effective connectivity with DCM, we selected a priori volumes of interest in IFG, STS and TPJ. The selection of the fMRI ROIs was based on maximum activation peaks showed from GLMs and considering previous literature on auditory processing (Belin et al., 2000; Blasi et al., 2011; Grossmann et al., 2010; Lloyd-Fox, Blasi, Mercure, Elwell, & Johnson, 2012). The fNIRS cortical source regions were defined based on previous coregistration works (S. Lloyd-Fox, Richards, et al., 2014), considering the coordinates of the closest channel to the region of interest (fNIRS source regions need to be specified on the surface of the participant's head). Both in the fMRI and in the fNIRS contexts, principal eigenvariates in 4 mm spheres centred in ROIs/cortical source regions were extracted. See the specific coordinates for both fMRI and fNIRS in figure 3.4.

IFG	STS	TPJ
fMRI: 49.5, 16.21, 0.4	fMRI: 53.23, -6.8, -2.4	fMRI: 45.64, -37.94, -0.01
fNIRS: 65.8, 10.7, 14.3	fNIRS: 67, -18.8, -7.3	fNIRS: 66, -31.2, 17.7
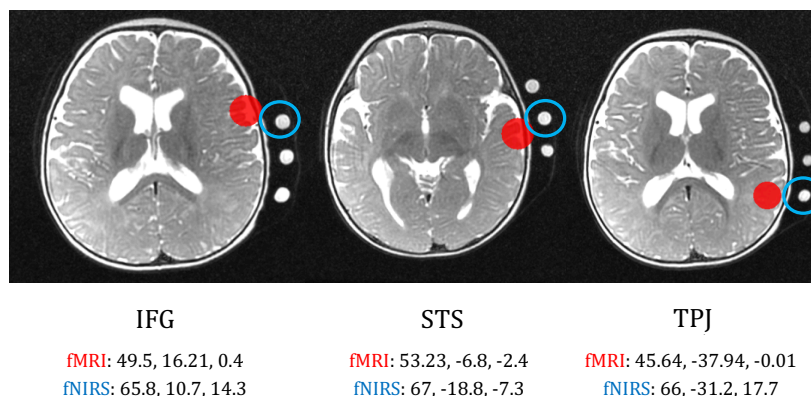
Figure 3.4 Coordinates and plots of fMRI ROIs and fNIRS cortical source regions on the T2 structural image. The red sphere corresponds to the fMRI ROIs and the blue circle to the fNIRS cortical source regions.

DCM analyses were restricted to the right hemisphere, to the volume covered by our fNIRS array layout. We modelled the differential state equations on different seed regions of interest (IFG, STS, TPJ in the right hemisphere), with fMRI and fNIRS. Each DCM model was defined by (i) a set of *intrinsic connections* (A) that specify the present state of one neuronal population, (ii) a set of *modulatory connections* (B) that indicate which intrinsic connections are dependent on experimental manipulations, (iii) *driving inputs* (C), considered as direct influences of the stimuli on the neural activity of involved regions of input connections (Friston et al., 2003).

Thirteen alternative models with different modulatory effects of V and NV were constructed with DCM-SPM toolbox for the fMRI data (Friston et al., 2003) and with DCM-fNIRS toolbox for the fNIRS data (Tak et al., 2015). All models were defined as bilinear and deterministic. Auditory input for both V and NV entered the network by directly activating STS across all models. In all the hypothesized models, we fixed bidirectional intrinsic connection between STS and TPJ and STS and IFG. The models varied for the presence or absence of modulatory effects of auditory processing of V and NV on the connections. See all the possible models in figure 3.5.
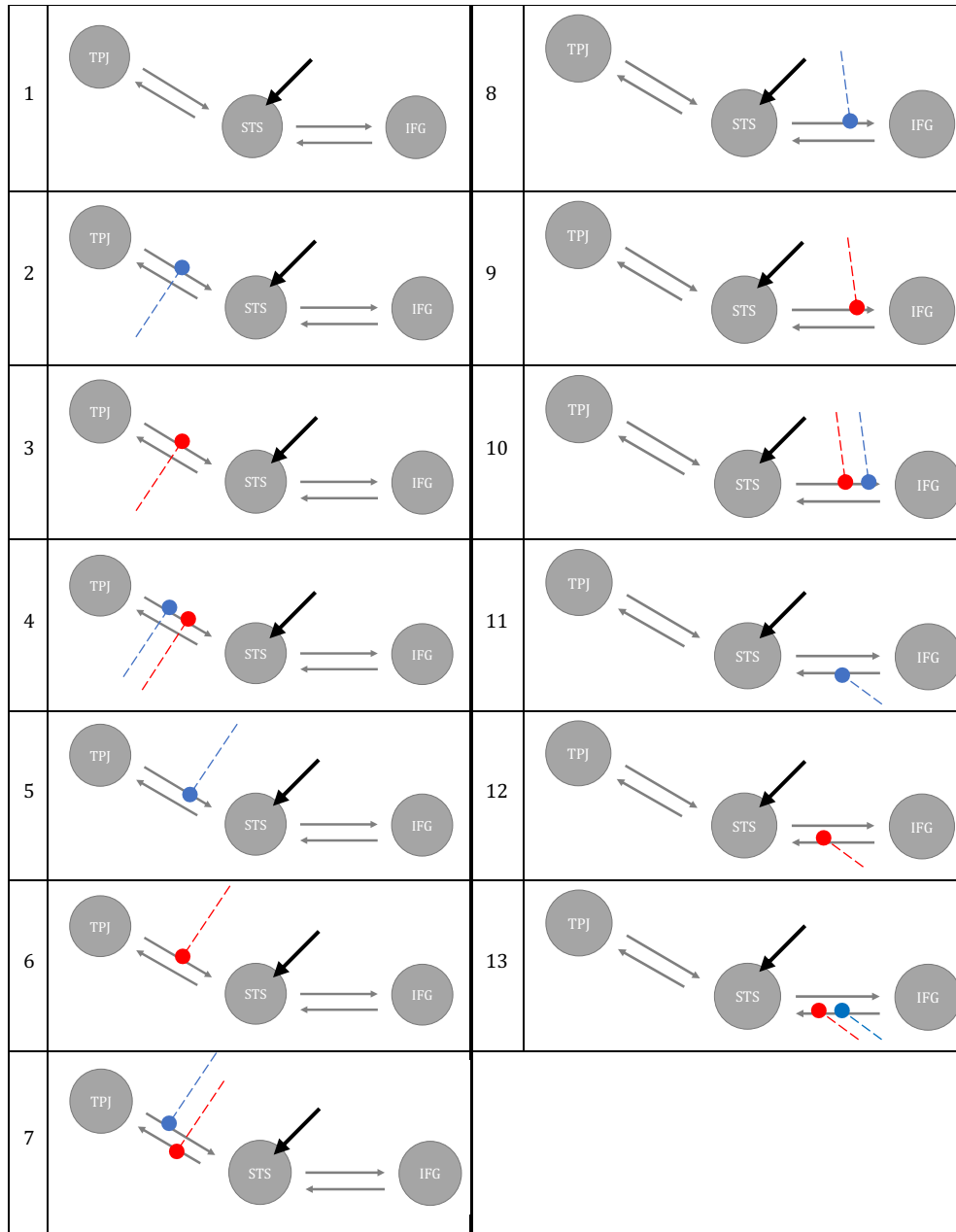
Figure 3.5 Models representation of the 13 hypotheses. Grey arrows represent the fixed intrinsic connections between the IFG, STS and TPJ; black arrows pointing at STS represent the input; blue lines represent the modulatory effect of NV and red lines the modulatory effect of V.

3.3.2.7 Specification and estimation of the DCM models [9]

The DCM models were fitted to the optical density signal averaged across trials.

Specifically, the generative model of fNIRS data was created by linking the

optics equation to the hemodynamic and neurodynamic equations (Arridge,

1999; Buxton et al., 2004; Cui et al., 2010; Delpy, Cope, van der Zee, et al., 1988;

Friston et al., 2003). The DCM parameters were then estimated from fNIRS data

using an established Bayesian framework (variational Laplace), which enabled

inference about changes in directed connectivity at the neuronal level (K. J.

Friston, Mattout, Trujillo-Barreto, Ashburner, & Penny, 2007; Penny, 2012). In

this study, we augmented the optics model used for DCM-fNIRS analysis (Tak

et al., 2015) by adding a scaling factor to a sensitivity matrix:

$$\begin{bmatrix} y(\lambda_1) \\ y(\lambda_2) \end{bmatrix} = \begin{bmatrix} \epsilon_H(\lambda_1)W_H S(\lambda_1) & \epsilon_Q(\lambda_1)W_Q S(\lambda_1) \\ \epsilon_H(\lambda_2)W_H S(\lambda_2) & \epsilon_Q(\lambda_2)W_Q S(\lambda_2) \end{bmatrix} \begin{bmatrix} \Delta H_c \\ \Delta Q_c \end{bmatrix},$$

where y is measurements of optical density changes; ϵ_H and ϵ_Q are extinction

coefficients for oxy-Hb and deoxy-Hb; W_H and W_Q are factors for correcting pial

vein contamination of fNIRS measurements; ΔH_c and ΔQ_c are oxy-Hb and

deoxy-Hb in the cortical source regions of interest; and $S = k \cdot S_0$ where S_0 is

the sensitivity function calculated from products of the forward field and the

adjoint field, and k is a scaling term. We treated this scaling term k as free

parameters with informed priors, to accommodate a variation in source

strength (and detection efficiency). This enabled us to calculate a matrix of the

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[9] This paragraph was jointly written with Dr. Sungho Tak (Bioimaging Research Team, Korea Basic Science Institute, South Korea), developer of the DCM-fNIRS version for adult data.

sensitivity, *S*, to the absorption coefficient changes, using outputs of the Toast software (Schweiger & Arridge, 2014).

3.3.2.8 fMRI-fNIRS DCM model comparisons

After the statistical estimation of each model for both fMRI and fNIRS data, comparisons of the DCM models estimated with fNIRS and fMRI were performed to evaluate effective connectivity correspondence between the two methodologies. The comparison of the DCM models was mainly based on the variational Free Energy (F), which is thought to have the best model selection ability and is highly recommended for comparisons, mostly in high signal-to-noise ratio conditions, as with infant data (Penny, 2012). Bayesian model selection (BMS) was applied in order to estimate the best model on the fMRI and fNIRS data (Friston et al., 2016; Stephan, Weiskopf, Drysdale, Robinson, & Friston, 2007). The aim in this study was not to investigate why a specific model wins in the BMS comparison, but to see whether there is any convergence between fMRI and fNIRS data, thus answering a methodological rather than a cognitive question. I then estimated the strength of connections for each model (Bayesian Model Average, BMA) for both fMRI and fNIRS to investigate whether there is any correspondence between the two methodologies.

3.3.3 Results

3.3.3.1 Activation Results

Prior to DCM analyses, brain regions activated by the two experimental conditions with fMRI and fNIRS were explored. As previously shown, IFG, STS, and TPJ were involved in the auditory processing in both fMRI and fNIRS (Blasi et al., 2011, 2015; Lloyd-Fox et al., 2012). The detailed comparison between

fMRI and fNIRS activations simultaneously recorded is object of another study in preparation (Blasi, A., Manini, B., Brigadoi, S., Cooper, R., Barker, T., Wastling, S., Lloyd-Fox, S., Johnson M.H., Elwell, C.E. Simultaneous fMRI and fNIRS analysis in young infants, Poster presentation at 2016 Biennial Meeting of the Society of functional near-infrared spectroscopy, Paris).

3.3.3.2 DCM results

Figure 3.6 shows the correspondence of F values and the BMS comparison between fMRI and fNIRS, and the correlation between BMA values estimated with fMRI and fNIRS.
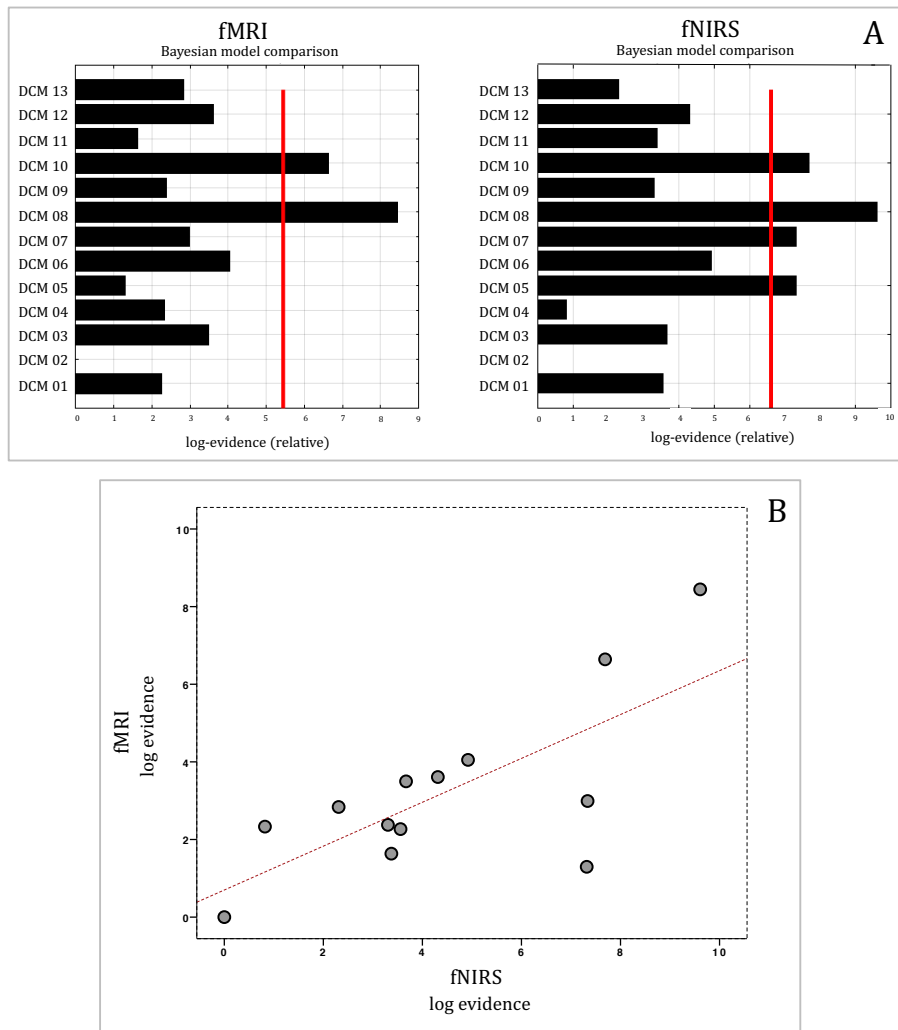
Figure 3.6 A, Bayesian Model Selection estimated with fMRI and fNIRS. B, Pearson correlation plot between fMRI and fNIRS log evidence of the 13 DCM models.

High correspondence between fMRI and fNIRS DCM models was found (Figure 3.6-A). Moreover, BMS showed model 8 as the best model for both fMRI and fNIRS, which presented modulatory effect of NV in the STS→IFG connection. Pearson correlation confirmed a strong relationship between fMRI and fNIRS BMS log evidence, r=0.718, $p = 0.006$ (Figure 3.6-B).

To assess the strength of the correspondence between the fMRI-DCM and the fNIRS-DCM results, a robust-regression method to compare the

parameters estimates obtained for all of the models across the two datasets was used. The strength of the connections (BMA values) estimated for the 13 models with the two methodologies are highly related for the endogenous connections (Figure 3.7-A), $F(1,89)=$ 5.55, $p=0.020$, $R^2 =0.058$, the inputs (Figure 3. 7-B), $F(1,24)=$ 4.35, $p=0.047$, $R^2 =0.153$, and the modulatory effects (Figure 3. 7-C and 3. 7-D) on V, $F(1,6)=$ 16.4, $p =0.006$, $R^2 =0.732$, and on NV, $F(1,6)=$ 6.65, $p =0.041$, $R^2 =0.526$.
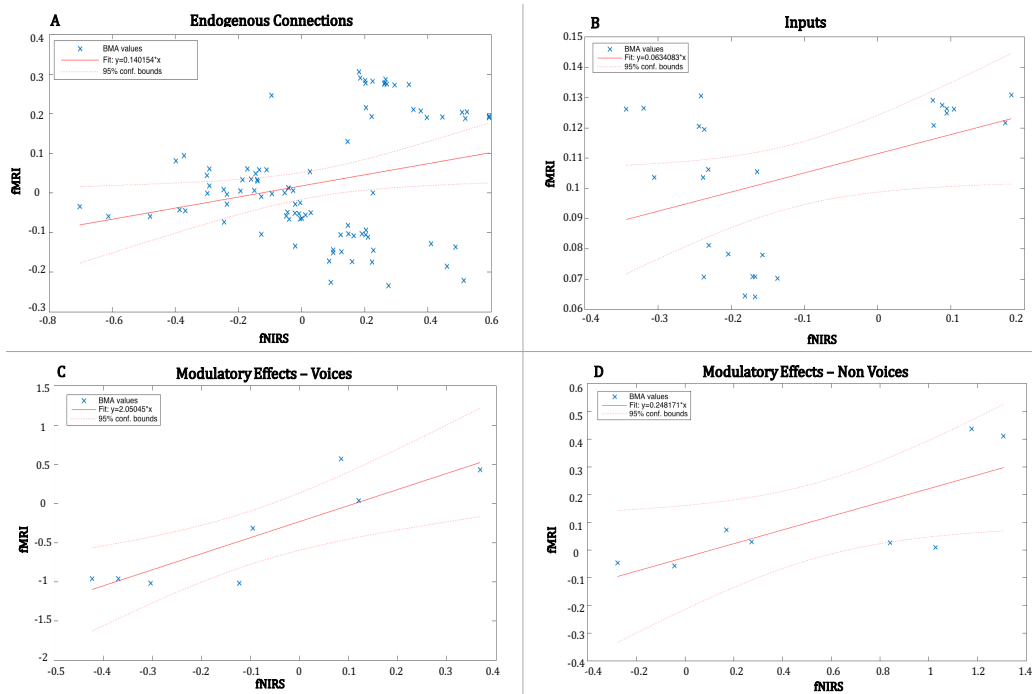
Figure 3.7 Robust regressions between BMA values estimated with fMRI and fNIRS. A, Scatterplot of the robust regression on the 91 endogenous connections BMA values (4 fixed connections + 3 connections within the area for each model). B, Scatterplot of the robust regression on the 26 inputs (one input for each model for the two conditions). C, Scatterplot of the robust regression on the 8 modulatory effects on V. D, Scatterplot of the robust regression on the 8 modulatory effects on NV.

In addition, I repeated the regression analysis with a bootstrap method for the endogenous connections (Figure 3.8-A), $F(1,89)=$ 5.63, $p =0.019$, $R^2 =0.059$, C.I.=0.114, 0.855, the Inputs (Figure 3.8-B), $F(1,24)=$ 4.67, $p =0.040$,

R² =0.163, C.I.= -1.712, -0.353), the modulatory effects (Figure 3.8-C and 3.8-D) on V, F(1,6)= 20.2, p =0.004, R2 =0.771, C.I = 0.17, 0.43, and on NV, F(1,6)= 7.6, p =0.033, R2 =0.559, C.I = 2.67, 3.7.
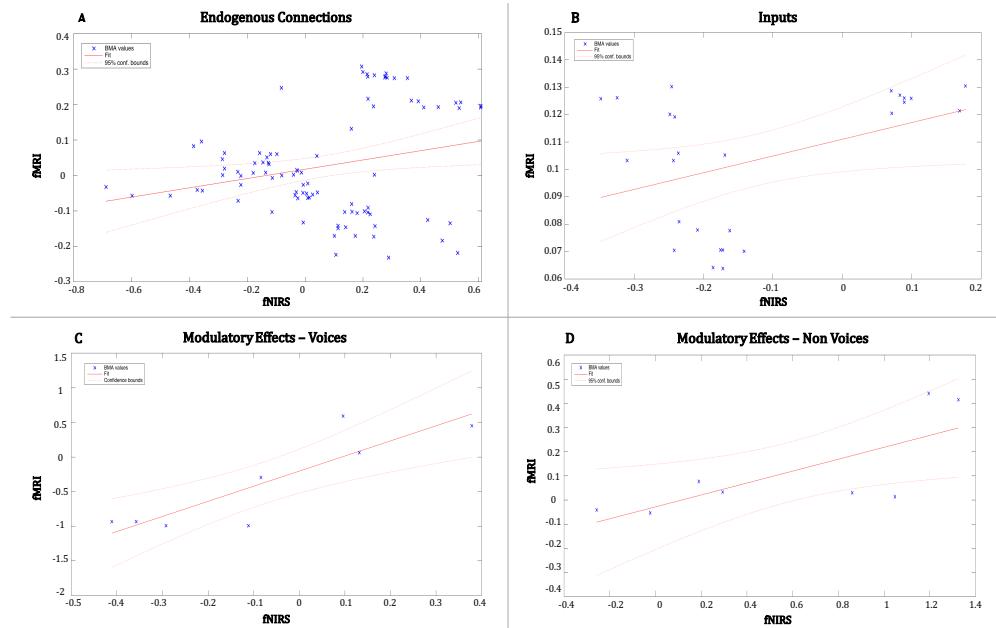
Figure 3.8 Regressions with bootstrap method between BMA values estimated with fMRI and fNIRS. A, Scatterplot of the robust regression on the 91 endogenous connections BMA values (4 fixed connections + 3 connections within the area for each model). B, Scatterplot of the robust regression on the 26 inputs (one input for each model for the two conditions). C, Scatterplot of the robust regression on the 8 modulatory effects on V. D, Scatterplot of the robust regression on the 8 modulatory effects on NV.

3.3.4 Discussion

fNIRS is a valuable method to study the developing brain and network analyses can potentially advance the understanding of how the emergence of complex psychological functions is supported by neural underpinnings. However, connectivity analyses for fNIRS are still underdeveloped and applying appropriate analysis methods for the study of neural connectivity in infant data is a complex technical challenge. In this study, a proof-of-principle for the

application of DCM to infant fNIRS data has been provided. I had the chance to work on unique dataset, comprising a simultaneous fMRI-fNIRS recording on a single infant listening to different sounds during sleep. The same GLM approach followed by the same DCM analyses was applied to both fMRI and fNIRS data, overcoming a number of challenges in the development of the fNIRS-DCM analysis stream. Converging results between the fMRI and fNIRS methods demonstrated the validity of applying DCM to infant fNIRS data. Although our results refer to a single case study, this study shows that DCM for fNIRS is a reliable method to explore effective connectivity in infant data.

This methodological study focused on the technical challenges encountered and then overcome in applying DCM on fNIRS infant data, here discussed:

- the T2 of the participant in the NIRS toolbox was successfully implemented in order to obtain an accurate estimation of the connectivity results;

- segmentation of the T2 of the participant, the creation of a high-density mesh and the estimation of the optodes location;

- in collaboration with the Department of Medical Physics at UCL, the NIRS optical sensitivity functions was estimated.

Solving these technical challenges will allow the use DCM on fNIRS data without the need for MRI in the future.

DCM is a complete and detailed technique for the exploration of human brain networks, allowing the inference of causality between temporal events, the inference of the nature of the connection (i.e. excitatory or inhibitory) and information about how experimental perturbation can modify the network (Friston, 1994). For this reason, DCM is unique and goes beyond most of the other functional connectivity techniques, which ask 'does signal A correlate

with signal B' without enquiring about where the signals come from. In contrast, DCM builds a full model of the neural origins of the signals and models connectivity at the neural level. For this reason, DCM requires detailed information as inputs about the origin of the signals. Thus, estimating the NIRS optical sensitivity function and a precise spatial localisation was necessary. However, the use of an age-specific template for both spatial registration and for the estimation of the NIRS optical sensitivity functions will allow future researchers to apply DCM to every infant dataset and follow our pipeline, avoiding the need for the acquisition of the MRI for each participant tested.

3.3.4.1 Advice for future studies and limitations of this work

Starting from this validation work of DCM in infants, future studies may benefit from some advice, to foster the application of this technique with infant fNIRS data. Here there are summarised some fundamental suggestions for future studies and possible limitations of this validation work, which should be taken into account for future research.

1. Although in this study an anatomical MRI scan of the participant was used, this is not essential if high-resolution age-appropriate templates are available. As mentioned in paragraph 2.2.2, in this PhD project I have already taken advantage of the '*Neurodevelopmental MRI Database*' in collaboration with Dr. Richards for a co-registration of the fNIRS arrays. Future researchers interested in applying DCM on infant fNIRS data are advised to use this database as this is the most accurate MRI database available in the developmental neuroscience field, both for quality of images and precision of the age range (Richards et al., 2016; Sanchez et al., 2012b, 2012a). The NIRS optical sensitivity functions can be estimated on the same age-range

specific structural template as used for the spatial registration, instead of using the T2 scan of the participant as in this study. It is worth to point out that in this specific study, both the spatial registration and the NIRS optical function estimation were performed on the structural scan of the participant, while for future studies the support of a template of the appropriate age was suggested. However, while it is established for adults that template-based methods work more precisely than registration performed on a single structural scan, there is no evidence that is still the case in the developmental field. Considering that, in this study, the same processing and connectivity analyses was not performed on an age-range specific structural template as suggested for the future, whether connectivity results could benefit from the choice of one or another method cannot be inferred.

2. For the accurate location of the optodes required in fNIRS data analysis, most of the researchers use pictures of the fNIRS hat on the participant's head to mark reference points and optodes location on an MRI template. This method might result in location inaccuracies, due for example to warping of the pictures - which might lead to erroneous estimation of the distance between points - or human mistakes in positioning the marks on the MRI template. Alternatively, researchers can register optode locations with a digitizer, such as Polhemus Digitising System (http://polhemus.com/scanning-digitizing/digitizing-products/), with the possibility to take into account infants' movement during the recording. However, the use of a digitizer is not always possible and realistic with restless and fidgety infants, so the support of pictures for spatial registration is still currently used in the developmental research practice. However, with

both these methods mentioned, optode locations and reference points can then be plotted on an MRI template, and then used as input for the spatial processing in both SPM-NIRS and *dcm_fnirs* toolboxes.

3. As already highlighted, motion artefacts are recognized as one of the major methodological challenge for functional connectivity studies (Satterthwaite et al., 2017), which is not a trivial aspect for researchers testing awake infants and interested in network analysis. In order to avoid false positives, data need to be as clean as possible, which is not always the case for data collected with awake and moving infants, even after the appropriate pre-processing. I acknowledge that that the present validation of DCM has been performed on a sleeping participant, thus any conclusion on how this method deals with more noisy infant data cannot be drawn. Given this limitation of this work, and considering that the avoidance of false positive in connectivity analysis is highly dependent on the pre-processing steps, future studies focusing on the application of different pre-processing streams and cleaning methods should elucidate how accurate DCM is with noisy infant data.

3.3.4.2 Future directions

Overcoming the various challenges mentioned above took significantly longer than initially anticipated. Therefore, I have not been able to apply DCM in any of the studies which are presented in this thesis. However, I will be engaged in this in the near future, to better explore how variables related to the development of self-awareness can interplay with changes in brain connectivity. Moreover, with the rest of the team, I will be involved in integrating the scripts modified for the specification of the DCM models in the

main *dcm_fnirs* package, in order to facilitate and promote the application of this technique by other research teams. I hope that this study can aid developmental neuroscientists who are interested in exploring brain connectivity in infancy and early childhood, encouraging the study of effective connectivity using DCM in the developing brain.

3.4 The developmental trajectory of the fronto-temporoparietal connectivity: a longitudinal fNIRS investigation

3.4.1 Abstract

The DMN is a network of brain regions activated while we are not engaged in any particular task. While there is a huge volume of adult works documenting functional connectivity within the DMN, knowledge of its development is still limited. There is some evidence of a gradual increase of the functional connections within the DMN during the first two years of life, in contrast to other primary resting-state networks, supporting basic functions, which are online from birth. This is consistent with the fact that functions have been related to the DMN, such as emerging self-awareness and other social functions, gradually develop over the first two years of life. Previous studies focusing on the development of the DMN acquired data using fMRI from sleeping infants, but sleep stages are known to affect functional connectivity. In this study, for the first time, fNIRS was used to acquire spontaneous fluctuations within the fronto-temporoparietal areas – as a proxy for the DMN – in awake participants longitudinally every six months at five time points, from 11 months to 36 months. A gradual development of the fronto-temporoparietal connectivity was found, supporting the idea that the DMN is shaping over the first years of life. The functional connectivity reached its maximum peak at about 24 months, which seems consistent with previous findings showing that by 2 years of age DMN connectivity is similar to that observed in adults. This study validated a method for recording resting-state data from awake infants, and a data analyses pipeline that allows the investigation of the functional connections with fNIRS. Therefore, a new line of research could benefit from the technique applied here.

3.4.2 Introduction

Many studies have shown that our brain displays a level of baseline activity characterised by correlations among spontaneous fluctuations in the low-frequency range (<0.1 Hz) (for a recent review see Raichle, 2015). Resting-state recording refers to the acquisition of this intrinsic brain activity during quiet wakefulness, in the absence of any cognitive, sensory or social stimulation (Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995; Damoiseaux et al., 2006; van den Heuvel & Pol, 2010). The DMN is the most studied resting-state functional network in adults, with evidence of structural connections to support the temporal correlations (Raichle, 2015; Sporns, 2010). The importance of the DMN is underlined by several recent studies that found changes in the connectivity strength in this network to be a marker of psychopathologies (Broyd et al., 2009), such as autism (Lynch et al., 2013; Padmanabhan, Lynch, Schaer, & Menon, 2017), depression (Mulders, van Eijndhoven, Schene, Beckmann, & Tendolkar, 2015; Sheline et al., 2009), schizophrenia (Garrity et al., 2007; Woodward, Rogers, & Heckers, 2011), Alzheimer disease (Greicius, Srivastava, Reiss, & Menon, 2004), and attention-deficit hyperactivity disorder (Fair et al., 2010). Moreover, as discussed in the introduction of this thesis, adult studies on the DMN consider this network to be an 'intrinsic system' that deals with self-related signal and self-processing (Golland et al., 2008). In fact, the DMN activity is remarkably similar to that one shown in self-processing tasks (Buckner & Carroll, 2007), and neuroimaging studies showed that the DMN activity is positively correlated with participant reports of mind wandering and self-related thoughts (Mason et al., 2007; McKiernan et al., 2006). Given the crucial role of the DMN in relation to self-processing, it has been suggested that that the gradual development of this functional network

can also support the emergence of self-awareness in the first years of life (Gao et al., 2016). However, despite the importance associated to this network, the research focusing on the development of the DMN is limited, and has some methodological constrains.

The first study that aimed to explore resting-state networks in the infant brain is dated to 2007 (Fransson et al., 2007). This study showed evidence of the presence of visual and primary sensorimotor networks from birth, which have been further replicated (Gao, Alcauter, Smith, Gilmore, & Lin, 2015; Lin et al., 2008; Liu, Flax, Guise, Sukul, & Benasich, 2008). However, Fransson and colleagues were unable to identify traces of a temporal synchronisation in core regions of the DMN before the first year of life (Fransson et al., 2007, 2009, 2011). Interestingly, while the early maturation of the primary sensory networks is thought to indicate the fact that primary sensory functions are in place from very early in life, the gradual development of the DMN might be consistent with the gradual emergence of self-awareness (Gao et al., 2016). More recent studies have been able to discover precursors of the DMN even before the first year of life. For example, functional correlations of core regions of the DMN were found in 4-months-old infants, but with posterior and anterior components still not connected yet (Damaraju, Caprihan, Lowe, et al., 2014). This anterior-posterior separation decreases over the development, suggesting a gradual long-range integration of the DMN (Damaraju, Caprihan, Lowe, et al., 2014). Gao and colleagues showed traces of a primitive DMN even at two weeks of life, and they demonstrated that at 2 years of age the DMN is similar to the one observed in adults (Gao et al., 2009). Moreover, a moderate individual variability of the DMN during the first 2 years

of life has been demonstrated (Gao et al., 2014), which is consistent with adult results (Mueller et al., 2013).

All the studies mentioned above acquired resting-state with fMRI in sleeping participants. However, as highlighted throughout this chapter, connectivity estimated during sleep does not display the same patterns of co-activation as connectivity measured during wakefulness. Moreover, sleep stages affect functional networks (Tagliazucchi & Laufs, 2014). Consistent with this, a recent study demonstrated that resting-state networks in sleeping infants resemble more closely the networks observed during sleep than during wakefulness in adults (Mitra et al., 2017). Therefore, knowledge of the development of the DMN collected so far might be possibly unprecise, and to compare the infant and adult findings, resting-state data need to be collected in awake infants. The study presented in this Chapter aims to fill this gap, exploring the developmental trajectory of the DMN in awake infants using fNIRS. This neuroimaging technique enables resting-state acquisitions under similar conditions to studies performed in adults.

To my knowledge, only a few infant investigated resting-state spontaneous fluctuations without any experimental conditions using fNIRS, but on sleeping participants (Homae et al., 2010; Konishi, Taga, Yamada, & Hirasawa, 2002; Taga et al., 2000). In particular, Homae et al. (2010) recorded resting-state in a longitudinal sample of sleeping neonates, at 3 months and 6 months. An increase in functional connectivity was shown over the frontal, temporal, parietal, and occipital regions. Moreover, a bilateral organization of spontaneous networks emerged around 3rd month of life, when clusters of connections started to form across the midline. Beforehand, in the neonates, connections were detected mainly within the same hemisphere (Homae et al.,

2010). Previous adult studies have used fNIRS to assess resting-state functional connectivity, suggesting it as a promising tool for this purpose (Lu et al., 2010; Mesquita, Franceschini, & Boas, 2010; Sasai et al., 2012). However, due to the inherent properties of fNIRS, its use is limited to the outer layers of the cortex. Therefore, in this chapter the fronto-temporoparietal connectivity was investigated as a component of the DMN. The approach of studying some portions of the DMN as a proxy for this network has been recently adopted by adult works, focusing in particular on the mPFC (Durantin, Dehais, & Delorme, 2015; Liang, Chen, Shewokis, & Getchell, 2016; Sasai et al., 2012) and on the parietal lobes (Rosenbaum et al., 2017; Sasai et al., 2012).

In this study, in order to assess the developmental trajectory of the fronto-temporoparietal connectivity, resting-state data were acquired with fNIRS in a longitudinal study with 5 time points. Participants were tested with the same resting-state procedure every six months, from 11 months to 36 months. As neural changes happen rapidly through the first years of life (Johnson, 2001; Yamada et al., 1997), the fact that data were acquired every 6 months should allow a precise description of the developmental trajectory of the functional connectivity. I hypothesized a gradual increase of the fronto-temporoparietal connectivity over the first years of life, which would be consistent with the gradual development of self-related processes.

3.4.3 Methods

3.4.3.1 Participants

fNIRS resting-state data were acquired longitudinally at five time-points, every six months at: i) 11 months; ii) 18 months; iii) 24 months; iv) 30 months; v) 36 months. All included infants were born full- term, healthy and with normal birth

weight. Written informed consent was obtained from the infant's caregiver prior to the start of the experiment. Hereafter follow details of the sample at each time point.

3.4.3.1.1 1st time point: 11 months

Resting state data were acquired from 11 11-month-olds (6 males, age mean $\pm$ SD = 342.72 $\pm$ 8.10 days). An additional 35 infants were excluded because: (i) their dataset did not reach the minimum length of 100 seconds of recording after behavioural coding was not reached (see section 3.3.3.3 for more details) (21 infants); (ii) they refused to wear the fNIRS hat or poor positioning of the fNIRS headgear/hat (9 infants); (iii) more than 30% of the channels had to be excluded due to poor light intensity readings (5 infants). For more details about behavioural coding and mean intensity of the channels, see paragraph 3.3.3.3. The mean $\pm$ SD of the resting state recording considered for the analysis was 134.25$\pm$57.15 seconds.

3.4.3.1.2 2nd time point: 18 months

Resting state data were acquired from 21 18-month-olds (10 males, age mean $\pm$ SD = 554.73 $\pm$ 9.19 days). An additional 28 infants were excluded because: (i) their dataset did not reach the minimum length of 100 seconds of recording after behavioural coding was not reached (see section 3.3.3.3 for more details) (7 infants); (ii) they refused to wear the fNIRS hat or poor positioning of the fNIRS headgear/hat (15 infants); (iii) more than 30% of the channels had to be excluded due to poor light intensity readings (5 infants). For more details about behavioural coding and mean intensity of the channels, see paragraph 3.3.3.3.

The mean $\pm$ SD of the resting state recording considered for the analysis was 196.64$\pm$60.69 seconds.

3.4.3.1.3 3rd time point: 24 months

Resting state data were acquired from 25 24-month-olds (11 males, age mean $\pm$ SD = 737.61 $\pm$ 14.10 days). An additional 24 infants were excluded because: (i) their dataset did not reach the minimum length of 100 seconds of recording after behavioural coding was not reached (see section 3.3.3.3 for more details) (6 infants); (ii) they refused to wear the fNIRS hat or poor positioning of the fNIRS headgear/hat (6 infants); (iii) more than 30% of the channels had to be excluded due to poor light intensity readings (6 infants). For more details about behavioural coding and mean intensity of the channels, see paragraph 3.3.3.3. The mean $\pm$ SD of the resting state recording considered for the analysis was 183.75$\pm$58.60 seconds.

3.4.3.1.4 4th time point: 30 months

Resting state data were acquired from 28 30-month-olds (18 males, age mean $\pm$ SD = 918.75 $\pm$ 8.68 days). An additional 20 infants were excluded because: (i) their dataset did not reach the minimum length of 100 seconds of recording after behavioural coding was not reached (see section 3.3.3.3 for more details) (3 infants); (ii) they refused to wear the fNIRS hat or poor positioning of the fNIRS headgear/hat (6 infants); (iii) more than 30% of the channels had to be excluded due to poor light intensity readings (9 infants). For more details about behavioural coding and mean intensity of the channels, see paragraph 3.3.3.3. The mean $\pm$ SD of the resting state recording considered for the analysis was 200.44$\pm$47.95 seconds.

3.4.3.1.5 5ᵗʰ time point: 36 months

Resting state data were acquired from 32 36-month-olds (23 males, age mean $\pm$ SD = 1101.13 $\pm$ 16.03 days). An additional 25 infants were excluded because: (i) their dataset did not reach the minimum length of 100 seconds of recording after behavioural coding was not reached (see section 3.3.3.3 for more details) (8 infants); (ii) more than 30% of the channels had to be excluded due to poor light intensity readings (8 infants). For more details about behavioural coding and mean intensity of the channels, see paragraph 3.3.3.3. The mean $\pm$ SD of the resting state recording considered for the analysis was 177.02$\pm$45.49 seconds.

3.4.3.2 Resting-state data acquisition

See section 2.2.3 for information about the experimental set-up and fNIRS cap application. See section 2.2.4 for information about the fNIRS recording. 11-month-olds wore a custom-built headgear with a total of 26 channels with a source-detector separation of 25 mm over the temporal areas, and 4 channels with a source-detector separation of 30 mm over the frontal area. The headgear was placed so that the third optode was centred above the pre-auricular point. Data acquired at the other time points were collected using the Easy cap described in the Chapter 2, as this provided a better fit on the participant's head, considering the increasing presence of hair. The 18-month-olds were tested with the 30-channel configuration with the Easy Cap. From the visit at 24 months participants were tested with the 44-channel configuration with the Easy Cap. Table 3.1 summarises information about the array design used at each visit, number of participants tested with each cap size, and S-D separation for each cap size.

Time point	Age	Silicon Band or Easy Cap	Array Design	Cap sizes and S-D separation
1	11 months	Silicon band	30-channel	25 mm temporal lobe 30 mm frontal lobe
2	18 months	Easy Cap	30-channel	48 cm, 17/21 participants, 25 mm temporal lobe 30 mm frontal lobe
				50 cm, 4/21 participants, 26 mm temporal lobe 31 mm frontal lobe
3	24 months	Easy Cap	44-channel	48 cm, 5/25 participants, 25 mm temporal lobe 30 mm frontal lobe
				50 cm, 18/25 participants, 26 mm temporal lobe 31 mm frontal lobe
				52 cm, 2/25 participants, 27 mm temporal lobe 32 mm frontal lobe
4	30 months	Easy Cap	44-channel	48 cm, 5/28 participants, 25 mm temporal lobe 30 mm frontal lobe
				50 cm, 16/28 participants, 26 mm temporal lobe 31 mm frontal lobe
				52 cm, 7/28 participants, 27 mm temporal lobe 32 mm frontal lobe
5	36 months	Easy Cap	44-channel	48 cm, 3/32 participants, 25 mm temporal lobe 30 mm frontal lobe
				50 cm, 18/32 participants,

				26 mm temporal lobe
				31 mm frontal lobe
				52 cm, 11/32 participants, 27 mm temporal lobe 32 mm frontal lobe

Table 3.1. Summary of the array design used at each visit, number of participants tested with each cap size, and S-D separation.

During the resting-state acquisition, to keep participants awake and as quiet as possible, a screensaver-like video with coloured bubbles accompanied by relaxing music was shown (Figure 3.9). The parent was asked not to talk during the experiment to avoid brain activation in areas of interest not associated with the spontaneous fluctuations commonly found during rest. If the parent talked to get the infant's attention on the screen or in case of fussiness or distraction, this chunk of data were excluded from the recording (see section 3.3.3.3 for more details).
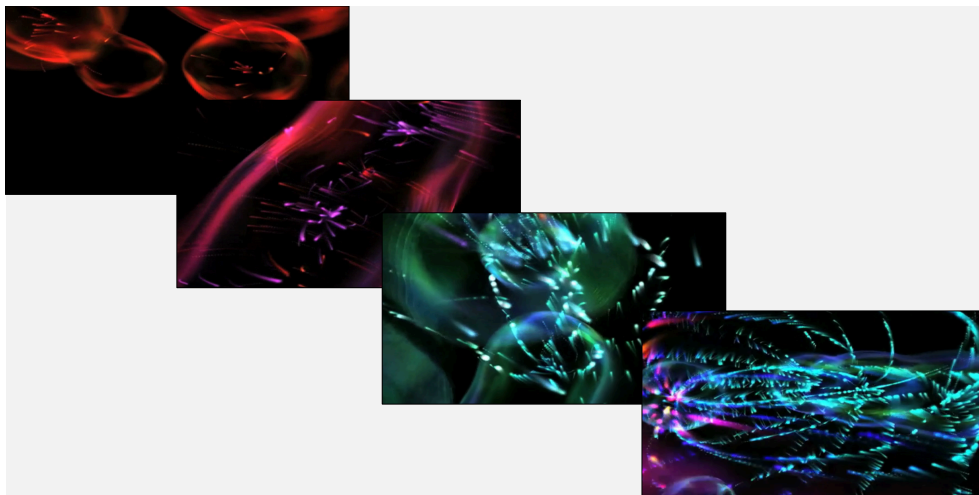
Figure 3.9 Fragments of the screensaver-like video shown during the resting-state acquisition.

In fMRI resting-state studies, adult participants are typically asked to think about nothing in particular. However, recent studies have shown that the use of non-social movies or videos helps to keep participants awake, increases compliance, and helps prevent social or emotional thoughts during mind-wandering[10] (Anderson, Ferguson, Lopez-Larson, & Yurgelun-Todd, 2011; Cantlon & Li, 2013; Conroy, Singer, Guntupalli, Ramadge, & Haxby, 2013; Sabuncu et al., 2010). Likewise, previous studies used non-social videos to acquire resting-state with fMRI in awake children (Müller, Kühn-Popp, Meinhardt, Sodian, & Paulus, 2015; Vanderwal, Kelly, Eilbott, Mayes, & Castellanos, 2015; Xiao, Friederici, Margulies, & Brauer, 2016). In adults, consistency within participants has been found between resting-state data acquired in a stimulus-free context and data acquired during observation of non-social videos (Finn et al., 2017; Vanderwal et al., 2015).

3.4.3.3 Resting-state data pre-processing and analysis

Data analysis were carried out in MATLAB (Mathworks, USA). fNIRS data were extracted for each participant from all the channels for both HbO_2 and HHb and channels with mean intensity lower than 10^{-3} μmol were excluded (most likely due to bad optode-scalp coupling, based on the intrinsic characteristics of the UCL-NIRS topography system).

Videos of the testing session were coded offline and periods of time during which the infant moved, cried, or looked at something socially engaging (e.g. the mum or the experimenter) were marked as invalid, as well as periods of time during which the mum or experimenter was talking. Assuming 8

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[10] Mind-wandering can affect resting-state functional connectivity as shown by Chou and colleagues (Chou et al., 2017)

seconds to be the minimum time for the infant HRF to return to baseline levels (Lloyd-Fox et al., 2010; Taga, Watanabe, & Homae, 2011), 8 seconds of data across all the channels were excluded after each invalid section, to ensure that we were only including periods of resting state. Sections of good data were included only if they were at least 5 consecutive seconds long. After the behavioural coding, time series for each fNIRS channel free from movement artefacts were extracted for each participant and only participants who had at least 100 seconds of clean data[11] in total, and less than 30% of the channels excluded were considered for further analysis. The light attenuation values were band-pass filtered (0.01-0.08) and converted to relative concentrations of haemoglobin using the modified Beer-Lambert law (Villringer & Chance, 1997).

For each participant, the correlation matrix between all the channels that remained after the previous pre-processing steps was calculated for both HbO_2 and HHb and the fisher Z-scores transformation was applied on the correlation matrix, to allow the comparison of the matrices and perform statistical analyses. Results are corrected for multiple comparisons using the False Discovery Rate (FDR). Pairs of functional connections were included in the analysis only if at least half of the sample contributed to the statistical tests.

Throughout this study, the connections between the frontal region and the temporoparietal region are defined as the connections between channels belonging to the mPFC (channel 27, 28, 29, 30) and the left STG (channel 5, 6, 7), the right STG (channel 18, 19, 20), the left middle/posterior temporal gyrus (channel 8, 10, 11, 13), the right middle/posterior temporal gyrus (channel 21,

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[11] A recent study on children showed that as little as 1 minute of resting-state fNIRS recording is sufficient to obtain accurate functional connectivity estimation (J. Wang, Dong, & Niu, 2017).

23, 24, 26), the left TPJ (channel 9, 12, 34, 35, 36), the right TPJ (channel 22, 25, 41, 42, 43) as specified in Chapter 2, section 2.2.2.

3.4.4 Results

3.4.4.1 Functional connectivity in the fronto-temporoparietal areas and in the whole set of channels per age group

Some previous research with adults explored the relationship between HbO_2 and HHb in fNIRS resting-state data, and revealed a comparable pattern of spontaneous fluctuation of the two chromophores, suggesting a similar underlying neurophysiological mechanism during resting-state (Lu et al., 2010; Sasai, Homae, Watanabe, & Taga, 2011; White et al., 2009). However, the HHb map seemed to show fewer connections than the HbO_2 map within fronto-temporoparietal areas (Sasai et al., 2011). Therefore, prior to any further analyses, I investigated the consistency of the connectivity patterns between the HbO_2 and HHb signal, performing one sample t-tests on the Fisher-transformed correlation coefficients on both chromophores for each age group. Figure 3.10 shows the fronto-temporoparietal connections that were significant per age group, for both HbO_2 and HHb. Significant functional connections within the whole set of channels were also plotted to assess whether functional connections in the whole set of channels. Results are summarise in Table 3.2

Time point	N	Fronto-temporoparietal connectivity				Whole set of channels			
		HbO$_2$		HHb		HbO$_2$		HHb	
		p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected
11 months	11	4	1/4	3	/	30	20/30	27	11/27
18 months	21	5	3/5	7	4/7	52	33/52	47	39/47
24 months	25	19	12/29	15	6/15	130	106/130	86	43/86
30 months	28	6	4/6	2	1/2	103	71/103	87	37/87
36 months	32	7	6/7	2	/	123	86/123	80	58/80

Table 3.2 Number of functional connections that are significantly different from zero at each time point, within the fronto-temporoparietal regions and in the whole set of channels, in HbO$_2$ and in HHb. p-values are reported uncorrected and FDR corrected.

Age	N	Fronto-temporoparietal connectivity		Whole set of channels	
		HbO$_2$	HHb	HbO$_2$	HHb
11 months	11				
18 months	21				
24months	25				
30 months	28				
36 months	32				
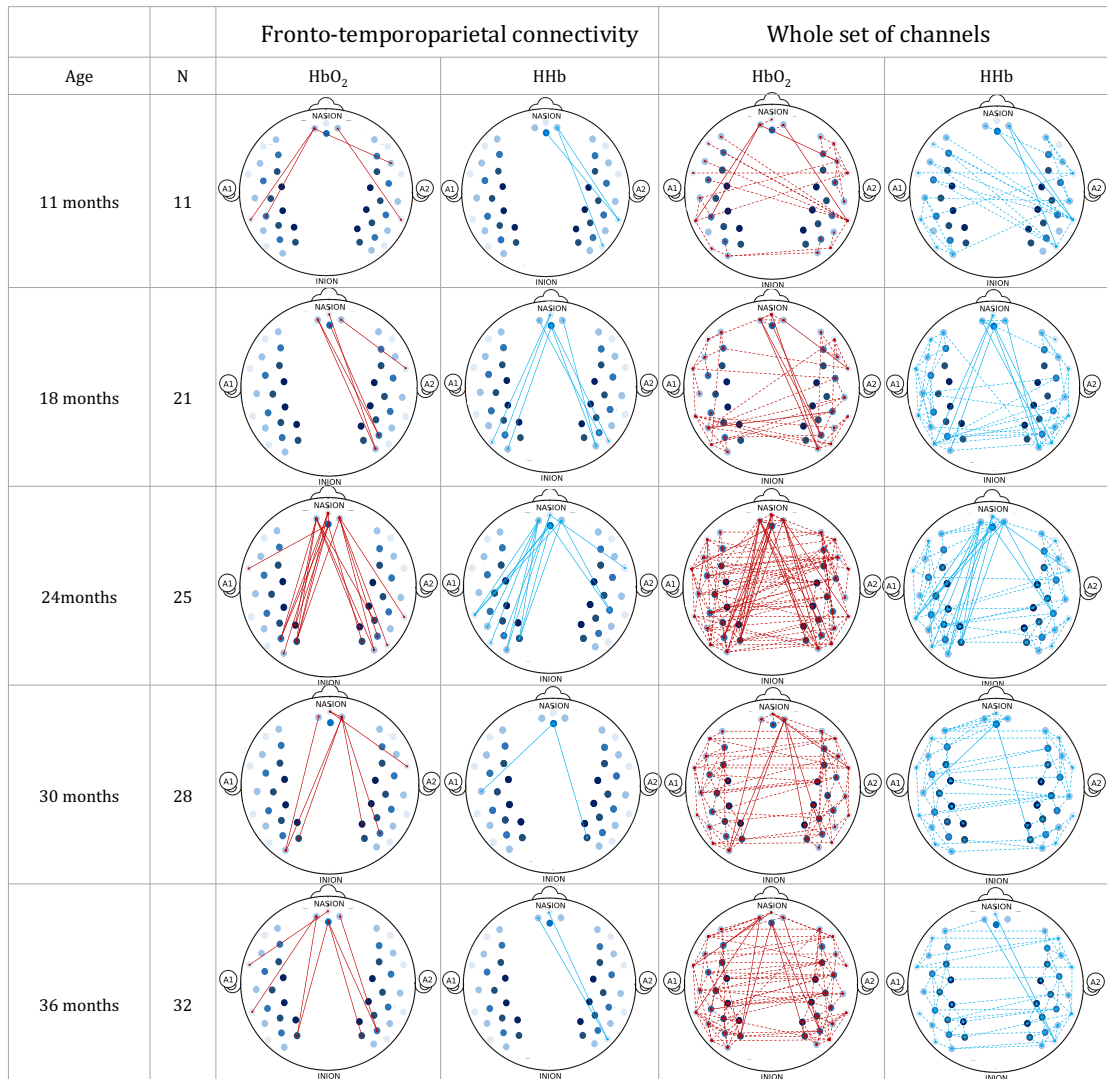
Figure 3.10 Graphical representations of the functional connections that are significantly different from zero, both in the fronto-temporoparietal regions (straight lines) and in the whole set of channels (dotted lines). HbO$_2$ is plotted in red, HHb is plotted in blue.

The table and the figure above highlighted that the number and the location of the connections that are significant different from zero in the HbO$_2$ and in the HHb maps are similar within each group.

3.4.4.2 Differences in fronto-temporoparietal connectivity

In order to test the hypothesis of an increased fronto-temporoparietal functional connectivity with age, the Fisher-transformed correlation coefficients were first compared with paired t-tests between the time points. Table 3.3 reports the number of the functional connections that are significantly different between the two time points, in the fronto-temporoparietal connections in HbO_2 and in HHb between two time points. Significant functional connections within the whole set of channels were also tested to assess whether changes in the connectivity are limited to the fronto-temporoparietal areas or whether they are affecting also connectivity between all the other channels. See Appendix A for degrees of freedom the t-tests between the two age points in each connection (Supplementary Table 1-10).

Time point 1	Time point 2	N	comparison	Fronto-temporoparietal connectivity				Whole set of channels			
				HbO$_2$		HHb		HbO$_2$		HHb	
				p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected
11 months	18 months	4	11 months>18 months	2/5	/	2/5	/	10/23	1/23	/	/
			18 months>11 months	3/5	/	3/5	/	8/23	5/23	9/27	13/27
11 months	24 months	6	11 months>24 months	2/7	/	1/6	/	11/28	1/28	4/15	/
			24 months>11 months	5/7	/	5/6	/	17/28	2/28	11/15	1/15
11 months	30 months	7	11 months>30 months	/	/	/	/	9/16	2/16	7/15	/
			30 months>11 months	4/4	/	3/3	/	7/16	1/16	8/15	1/15
11 months	36 months	8	11 months>36 months	1/6	1/6	7/10	1/10	9/22	/	23/35	/
			36 months>11 months	5/6	1/6	3/10	1/10	13/22	/	12/35	1/35
18 months	24 months	11	18 months>24 months	1/4	/	/	/	7/11	1/11	6/27	1/27
			24 months>18 months	3/4	1/4	11/11	3/11	5/11	/	21/27	1/27
18 months	30 months	10	18 months>30 months	/	/	/	/	13/40	1/40	11/19	1/19
			30 months>18 months	9/9	3/9	2/2	/	22/40	1/40	8/19	/
18 months	36 months	15	18 months>36 months	/	/	1/3	/	13/36	4/36	16/22	/
			36 months>18 months	4/4	2/4	2/3	/	23/36	5/36	6/22	/
24 months	30 months	15	24 months>30 months	3/6	/	4/5	/	20/30	/	29/43	3/43
			30 months>24 months	3/6	/	1/5	1/5	10/30	1/30	14/43	1/43
24 months	36 months	18	24 months>36 months	4/8	/	1/1	/	25/53	4/53	22/41	2/41
			36 months>24 months	4/8	/	/	/	28/53	2/53	19/41	4/41
30 months	36 months	22	30 months>36 months	3/6	/	1/4	/	12/35	/	21/25	1/25
			36 months>30 months	3/6	/	3/4	/	23/35	/	24/25	2/25

Table 3.3 Number of functional connections that are significantly different between the two time points, in the fronto-temporoparietal connections and in the whole set of channels in HbO$_2$ and in HHb. p-values are reported both uncorrected and FDR corrected.

Figure 3.11 shows graphical representations of the differences in the fronto-temporoparietal connections and in the whole set of channels in the HbO_2 and the HHb maps for each comparison.

11 months vs. 18 months
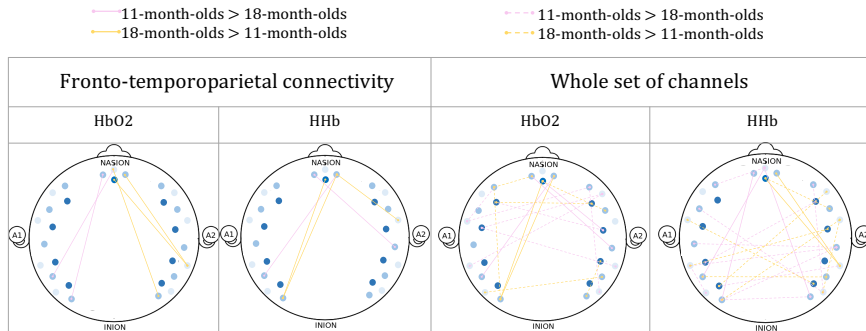
11 months vs. 24 months
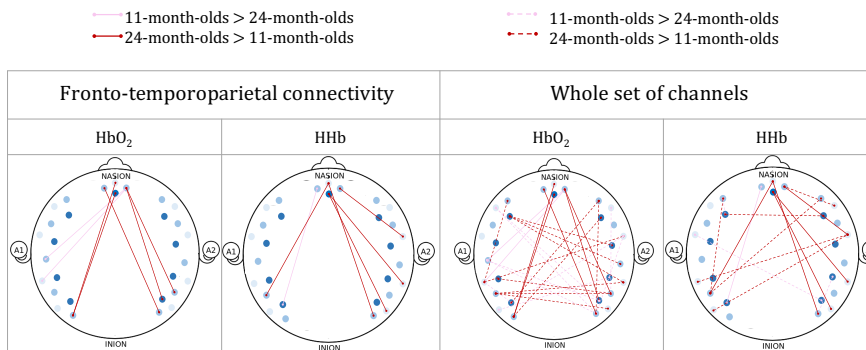
11 months vs. 30 months
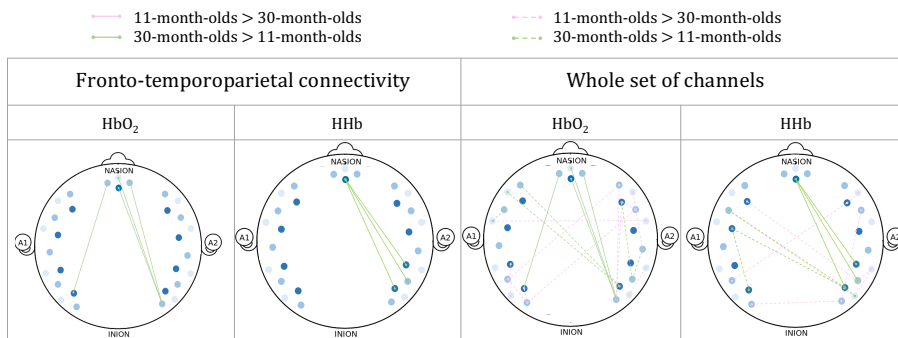
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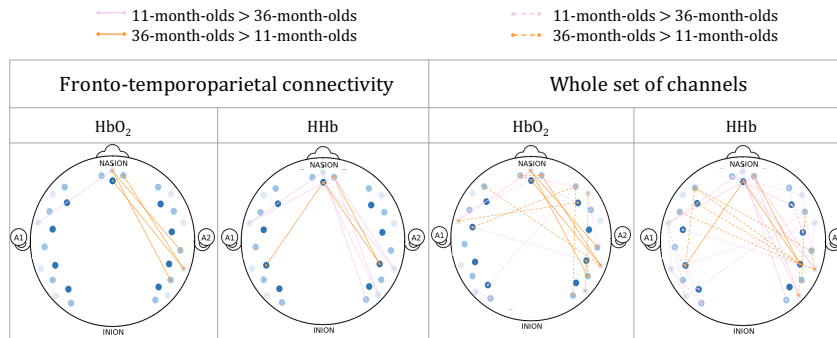
18 months vs. 24 months
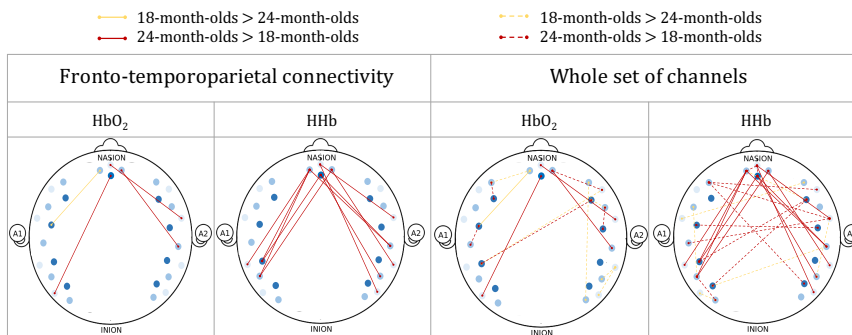
18 months vs. 30 months
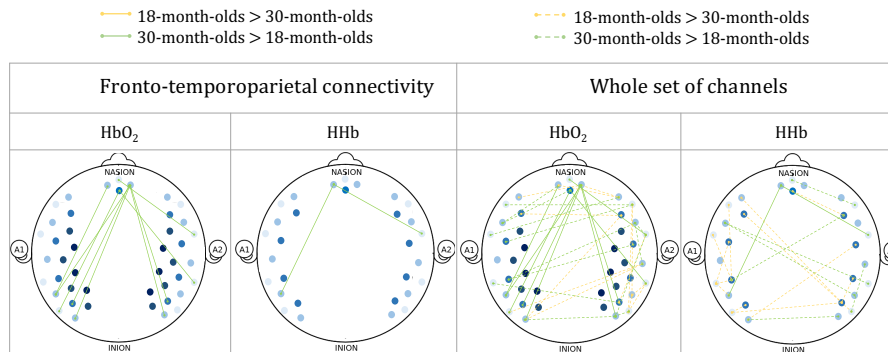
18 months vs. 36 months
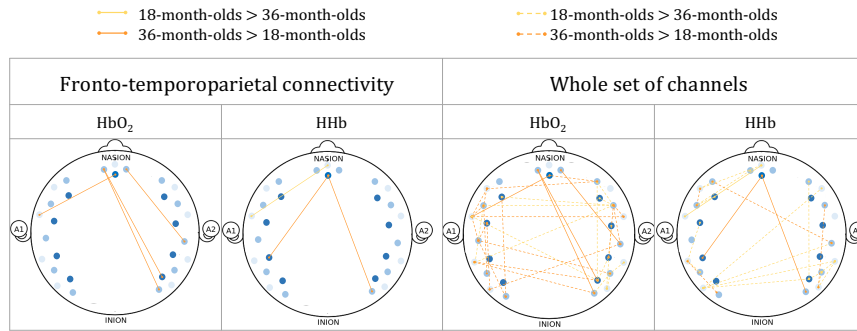
24 months vs. 30 months
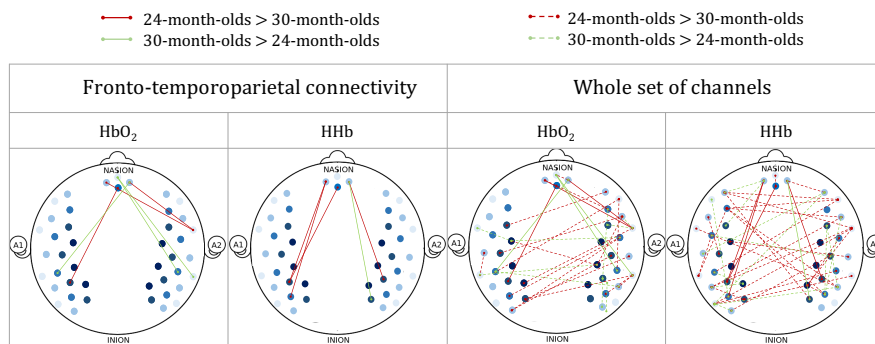
30 months vs. 36 months
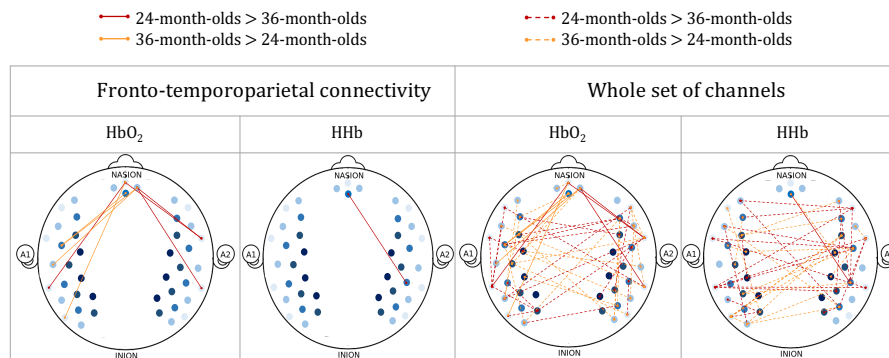
Figure 3.11 Graphical representations of the differences in the fronto-temporoparietal connections and in the whole set of channels in HbO$_2$ and HHb for each comparison.

3.4.4.3 Linear mixed model

A more appropriate estimation of the developmental trajectory of the fronto-temporoparietal functional connectivity is given by a repeated measures model that compares all the resting-state measures of the participants over time. To better characterise the developmental trajectory of the fronto-temporoparietal connectivity, each connection between channels belonging to the frontal region and the temporoparietal region was inserted as a dependent variable in a linear mixed model (Verbeke & Molenberghs, 2000). Compared to repeated measures ANOVA, mixed linear models account for within person dependence and allow for there to be missing data, using only information from the individual at the other time points (A. Field, Miles, & Field, 2012; Gad & Youssif, 2004). The linear mixed model for a dependent variable 'y', of the participant 'pth', at a specific time point 't', is:

$$y_{pt} = \text{Intercept}_p = d_p + \beta \text{Age}_{pt} + \varepsilon_{pt}$$

where Age$_{pt}$ is the age of the pth participant at the tth time of the data acquisition. The dependent variable, i.e the functional connectivity, was modelled here as a function age (βAge) with a random person effect (d_p) and errors (ε_{pt}). Intercept and age were fixed effects, while within person dependence (d_p) was modelled as a random effect. This same procedure was used in other longitudinal studies that explored brain connectivity changes over time (for example see Wierenga et al., 2018).

The linear mixed model included the 32 participants who had valid data at least two time points. The type of covariance between the observations was specified as Autoregression (AR) as two measures close in time of the same participant are likely to be correlated (Selig & Little, 2012).

Table 3.4 shows statistically significant changes of the connections within the fronto-temporoparietal channels over time, showing whether the model better fits changes in functional connectivity when the five time points are considered into the model (left part of the table). Betas at 11 months represent the connectivity values estimated at 11 months by the random effects and the p-value at 11 months tested the significant difference with zero. Betas at the following time points describe changes in connectivity compared with 11 months (right part of the table).

Temporo parietal channels	mPFC channels	F	p	11 months Beta(SE) p	18 months Beta(SE) p	24 months Beta(SE) p	30 months Beta(SE) p	36 months Beta(SE) p
10	28	4.18	0.004**	-0.06(0.15) 0.672	-0.26(0.19) 0.180	0.29(0.18) 0.116	0.21(0.17) 0.220	0.01(0.17) 0.965
	29	2.74	0.035*	-0.05(0.14) 0.733	-0.28(0.17) 0.111	0.01(0.17) 0.052†	0.13(0.17) 0.451	-0.09(0.17) 0.593
12	28	3.24	0.016**	-0.12(0.14) 0.391	-0.07(0.18) 0.679	0.41(0.16) 0.018*	0.26(0.16) 0.124	0.18(0.16) 0.258
13	29	3.97	0.006**	-0.36(0.15) 0.024*	0.33(0.18) 0.083	0.37(0.18) 0.045*	0.60(0.18) 0.001*	0.23(0.17) 0.184
13	30	4.33	0.004**	-0.55(0.14) 0.001*	0.41(0.17) 0.020*	0.62(0.17) 0.001*	0.65(0.16) 0.001*	0.48(0.16) 0.004*
18	27	3.09	0.021*	0.15(0.13) 0.276	-0.21(0.17) 0.221	0.26(0.16) 0.119	0.09(0.16) 0.540	-0.01(0.15) 0.973
20	29	4.04	0.005**	-0.03(0.12) 0.788	-0.30(0.15) 0.052†	0.14(0.15) 0.363	0.13(0.15) 0.391	0.02(0.15) 0.873
22	29	3.46	0.012**	-0.50(0.12) 0.001*	0.46(0.15) 0.003*	0.55(0.15) 0.001*	0.48(0.15) 0.002*	0.43(0.14) 0.005*
25	28	2.98	0.023**	-0.31(0.13) 0.023*	0.15(0.17) 0.381	0.35(0.16) 0.028*	0.34(0.15) 0.029*	0.42(0.15) 0.007*
	29	5.50	0.004**	-0.46(0.14) 0.002*	0.51(0.16) 0.003*	0.71(0.16) 0.001*	0.74(0.16) 0.001*	0.64(0.16) 0.001*

Table 3.4 Changes of the connections within the fronto-temporoparietal channels over time. For each time point, results are displayed in terms of , standard errors (SE) and p-values. **, p<0.05 that survived the FDR correction for multiple comparisons; *, p<0.05; †, p<0.065.

Figure 3.12 shows betas estimated from the models, representing changes of the connections within the fronto-temporoparietal channels over time.
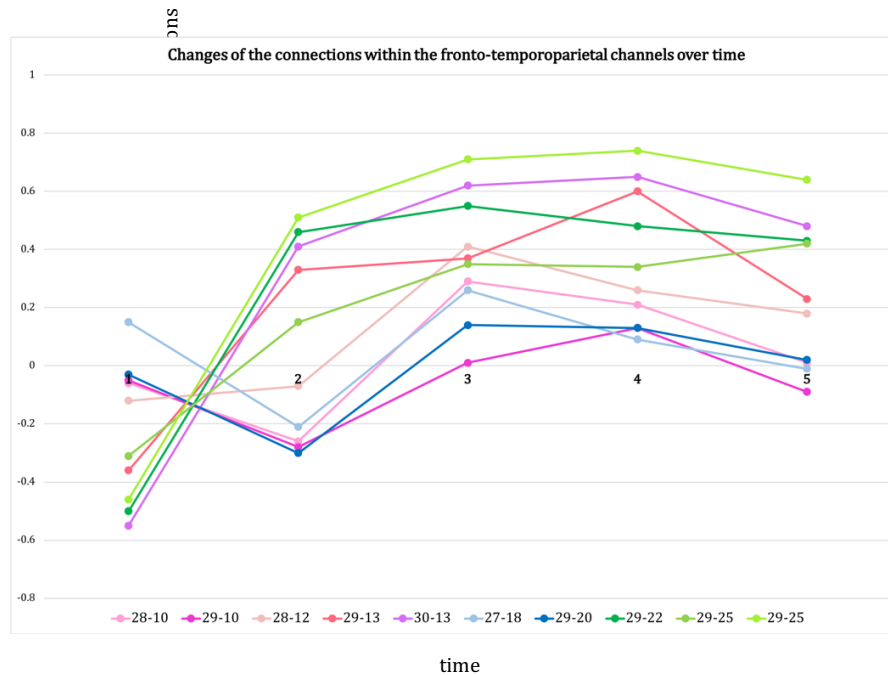
Figure 3.12 Graphical representation of the functional connections that showed a significant change over time within the fronto-temporoparietal channels. Functional connections with channels belonging to the left middle/posterior temporal gyrus are plotted in pink; functional connections with channels belonging to the right STG are plotted in blue; functional connections with channels belonging to the right TPJ are plotted in green.

As can be seen from the table, channels belonging to the temporoparietal regions that showed statistically significant functional connections with the frontal cortex can be clustered into two regions, the left middle/posterior temporal gyrus (channel 10, 12, 13) and the right STG/TPJ (channel 18, 20, 22, 25). Among the ten functional connections the showed a statistically significant change in time, only two did not survive the FDR correction for multiple comparisons (27-18 and 29-10). As can be seen from the values of the betas estimated, the peak in fronto-temporoparietal connectivity was at 24 months for 5 out of the 10 connections that significantly changed with time (28-10, 28-12, 27-18, 29-20, 29-22), at 30 months for 4 out of the 10 connections that significantly changed with time (29-10, 29-13, 30-13, 29-15), while only one

fronto-temporoparietal connection reached the maximum increase at 36 months (28-25).

In order to limit the number of the linear mixed models, the same mixed model analysis was repeated using the functional connections among the ROIs. To do this, Fisher-transformed correlation coefficients were averaged for the ROIs specified above in section 3.4.3.3. As the TPJ is covered by channels of the 44-channel configuration which were not used to acquire data from the 11-month-olds and the 18-month-olds, the estimation of the connectivity between the frontal cortex and the TPJ was performed considering two definitions of this region: i) the TPJ channels used at every time point (9 and 12 for the left TPJ and 22 and 25 for the right TPJ); ii) all the channels belonging to the TPJ region, but comparing only 24-month-olds, 30-month-olds and 36-month-olds. Table 3.5 shows the changes of the connections within the fronto-temporoparietal ROIs over time, where betas at 11 months showed the difference with zero, and betas and the following time points showed significant difference with 11 months.

Temporoparietal regions	F	p	11 months Beta(SE) p	18 months Beta(SE) p	24 months Beta(SE) p	30 months Beta(SE) p	36 months Beta(SE) p
Left STG	1.37	0.249	-0.12(0.079) 0.877	-0.04(0.10) 0.627	-0.09(0.09) 0.302	0.003 (0.09) 0.967	0.05(0.09) 0.571
Right STG	0.65	0.625	0.00(0.75) 0.990	-0.09(0.09) 0.358	0.02(0.08) 0.789	0.00(0.08) 0.016*	-0.03(0.08) 0.661
Left middle/posterior temporal gyrus	2.00	0.102	-0.08(0.08) 0.355	-0.04(0.13) 0.656	0.10(0.10) 0.321	0.14(0.09) 0.146	0.02(0.09) 0.808
Right middle/posterior temporal gyrus	0.91	0.458	0.16(0.08) 0.049	-0.17(0.09) 0.073	-0.14(0.09) 0.128	-0.14(0.09) 0.123	-0.16(0.09) 0.088
Left TPJ (channels 9, 12)	2.35	0.062†	-0.21(0.08) 0.015*	0.06(0.10) 0.538	0.26(0.10) 0.011*	0.13(0.10) 0.174	0.014(0.09) 0.137
Right TPJ (channels 22, 25)	4.33	0.03*	-0.27(0.07) 0.001*	0.27(0.09) 0.006*	0.24(0.09) 0.009*	0.29(0.09) 0.02*	0.23(0.08) 0.011*
Left TPJ	1.75	0.183	/	/	-0.02(0.03) 0.538	-0.09(0.05) 0.078	-0.02(0.04) 0.551
Right TPJ	1.31	0.278	/	/	0.01(0.04) 0.736	-0.04(0.05) 0.456	-0.08(0.05) 0.114

Table 3.5 Changes of the connections within the fronto-temporoparietal ROIs over time. For each time point, results are displayed in terms of estimated betas, standard errors (SE) and p-values. *, $p < 0.05$; †, $p < 0.065$.

Figure 3.13 shows betas estimated from the models , representing changes of the connections within the fronto-temporoparietal ROIs over time.
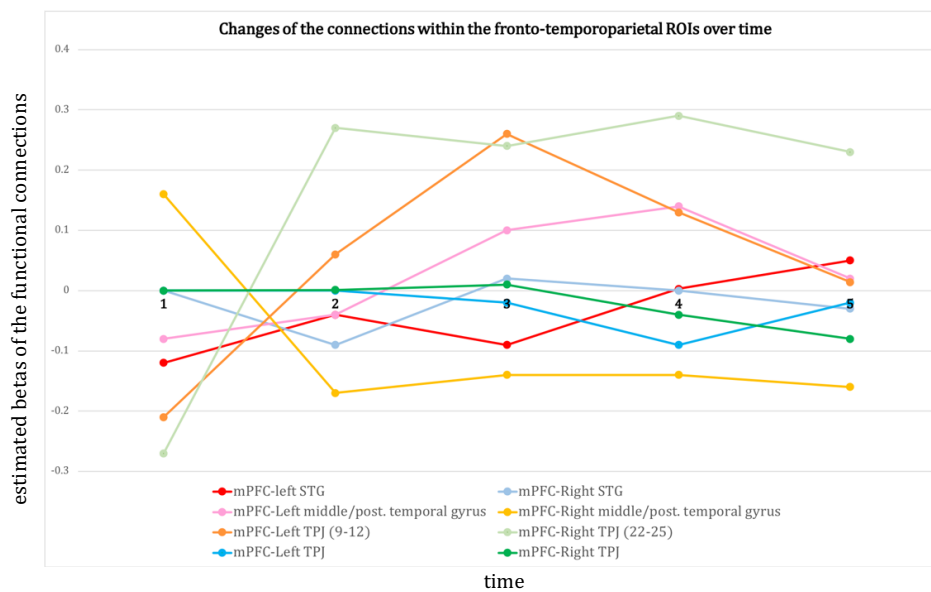
Figure 3.13 Graphical representation of the changes of the connections within the fronto-temporoparietal ROIs over time. Colours of the ROIs are the same as the ones used in the previous plot.

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As can be seen from the table, there was a statistically significant change in time in the functional connection between the frontal cortex and the right TPJ (only channels 22 and 25), with a maximum peak in the fronto-temporoparietal connections at 30 months, and a marginal significant change in time in the connection between the frontal cortex and the left TPJ (only channels 9 and 12), with a maximum peak in the fronto-temporoparietal connections at 24 months. However, these two statistically significant models did not survive the FDR correction for multiple comparisons.

3.4.5 Discussion

The DMN is a resting-state network that has been extensively studied in adults, but knowledge of its development is limited. In contrast to other primary sensory resting-state networks that are online at birth to support basic primary sensory functions, recent studies suggested that the DMN develops gradually over the first years of life. However, most of the data on the development of the DMN rely on studies performed with fMRI on sleeping infants. This might limit the understanding of the developmental trajectory of this network, as it has been shown that sleep stages can affect functional connectivity estimates (Mitra et al., 2017; Tagliazucchi & Laufs, 2014). Therefore, the use of fNIRS in awake infants might enrich this investigation. With the current study, I used this neuroimaging technique to explore the developmental trajectory of the fronto-temporoparietal connectivity – as a proxy of the DMN – in awake infants at 5 time points. The one sample t-test at each time point on the HbO_2 and the HHb maps showed consistency of the connectivity patterns, which is in line with HbO_2 and the HHb resting-state data acquired by previous studies,

suggesting reliability of the data acquired (Lu et al., 2010; Sasai, Homae, Watanabe, & Taga, 2011; White et al., 2009).

As hypothesized, the paired t-tests showed stronger fronto-temporoparietal connections at older ages compared to younger ages, up to 24 months. This is consistent with previous studies that have found a gradual increase of DMN connectivity over the first year of life (Damaraju, Caprihan, Lowe, et al., 2014; Gao et al., 2009). 24-month-olds showed the same number of fronto-temporoparietal connections as the 30-month-olds and 36-month-olds in the HbO_2 map, and a greater of connections in the HHb map (but none of these connections survived the FDR corrections for multiple comparison, which suggests that there may be no differences in the fronto-temporoparietal connections between 24-months-olds and older ages also in the HHb map). Results from the mixed model analysis between the fronto-temporoparietal channels and between fronto-temporoparietal ROIs are consistent with this finding, showing the maximum increase of the fronto-temporoparietal connections at 24 months or at 30 months. One may think that the maximum peak of the functional connection at 24 months could be related to methodological aspects, such as a higher level of noise in the data at this age. In fact, a high level of movement during the resting-state acquisition might have led to a spurious increase in functional connections (Deen & Pelphrey, 2012; Power et al., 2012; van Dijk et al., 2012). However, the noise in the data was limited to the chucks that were removed during the pre-processing. Among all the time points, the 11-month-olds provided the noisiest dataset, and the quality of the resting-state recordings increased with age. More likely, the maximum peak of the functional connection at 24 months indicates a stability in the strength of the connectivity in DMN regions, which is consistent with a

previous study from Gao and colleagues (2009), that showed that by 2 years, the DMN is similar to the one observed in adults (Gao et al., 2009; Gao, Lin, Grewen, & Gilmore, 2016). Therefore, in the current study, the absence of differences in the fronto-temporoparietal connections at 24 months and older ages might reveal a set of fronto-temporoparietal connections that are relatively stable from around 24 months of age.

Interestingly, while there were no differences between the 24 months and the older ages in the fronto-temporoparietal connections, the 24 months showed a greater number of connections within the whole set of channels compared with the older ages. This nonlinear growth of the functional connections can be related to pruning processes, i.e. the removal of redundant connections (Huttenlocher, Vasilyeva, & Shimpi, 2004), which is known to start at around 2 years and lasts for almost 20 years (Kolb & Gibb, 2011), with the aim of leaving a more efficient set of connections (Thompson et al., 2005) and enabling the reorganization of functional networks (Gao et al., 2016; Levitt, 2003). However, while the pruning process affects only connections outside the fronto-temporoparietal regions is unclear. It is worth mentioning that a limited number of the connections within the whole set of channels that were significantly stronger at 24 months than at older ages survived the FDR correction for multiple comparison, which might indicate that the actual differences in the functional connections within the whole set of channels between the 24-month-olds and older ages are very limited. Nonetheless, while most of the previous longitudinal studies acquired resting-state data up to 2 years, or with intervals not as frequent as 6 months (for example see Damaraju, Caprihan, & Lowe, 2014; Gao et al., 2009; Homae et al., 2010), this is the first study that explored the development of the fronto-temporoparietal

connections up to 3 years at frequent intervals. Further research needs to clarify the developmental trajectory of the fronto-temporoparietal connections after the 2nd year of life, to confirm the evidence of a maximum peak of the fronto-temporoparietal connections at 24 months.

Among the paired sample t-tests, the limited number of functional connections that survived the FDR correction for multiple comparisons represents the main limitation of this study. A post-hoc power analysis performed with G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that in order to detect a medium effect size as significant at the 5% level (d=0.5, Cohen, 1988), a sample of 54 participants would have been required for each paired sample t-test. This indicates that the comparisons between two time points are underpowered and results should be interpreted with caution. However, most of the linear mixed models survived the FDR correction for multiple comparison, which allows more confidence in interpreting the results.

It is interesting to notice that the main reason for exclusion from the analysis changed over time. While participants at younger ages were excluded mainly because their artefact-free resting-state data did not reach the minimum length or because they refused to wear the fNIRS cap, at older ages the main reason for exclusion was the high number of channels with poor light intensity. This informs fNIRS users on different challenges related to test infants at different ages with this technique, with younger infants being more fidgety and inattentive, and the older ones with inevitably more hair, which is known to affect the source-detector coupling. The difficulty for young infants to reach a quiet state reduced the 11-month-old sample, compared with the other time points, limited the degrees of freedom of the comparison with the 11 months. In addition to this methodological limitation, the fact that the participants at

different time points were tested with two different fNIRS array configurations did not allow the comparisons of some of the fronto-temporoparietal connections between all the time points. Although the 44-channel configuration was an extension of the 30-channel configuration, comparisons at 11 at 18 months were limited by the absence of the additional channels. As mentioned in Chapter 2, the rationale behind adding the additional channels to the 30-channel configuration was about the improvement of the detection of the TPJ activation, one of the core region of the investigation of the developmental changes in the fronto-temporoparietal connections.

Despite the mentioned limitations, this study seems to suggest a gradual increase of the fronto-temporoparietal connectivity, with a peak at 24 months which might indicate that the DMN is as shaped as in adults by this age. Moreover the gradual decrease of the functional connections within the whole set of channels may indicate an effect of pruning. As this is the first time that functional connectivity was estimated in awake infants with fNIRS, this work might be considered as a reference for other researchers who are interested in this technique. This study validated a method of resting-state data acquisition from awake infants, and provided a data analysis pipeline that allows the investigation of the functional connections. Therefore, a new line of research can benefit from this study in the future, and in this PhD work this technique is applied in the next chapter. In fact, it has been demonstrated in adults that the DMN supports self-referential processing (Gao et al., 2016; Golland et al., 2008), and researchers assumed that its gradual shaping between the first and the second year of life might reflect the emergence of self-awareness (Amsterdam, 1972). However, to date there is no scientific evidence supporting this hypothesis. The next chapter aims to fill this gap by exploring whether different

levels of self-awareness at 18 months might be associated with the strength in

the fronto-temporoparietal connectivity – as an index of the DMN – using the

technique validated in this current study.

Chapter 4

Fronto-temporoparietal connectivity as
a potential neural marker of
self-awareness in 18-month-olds:
a resting state fNIRS study

4.1 Abstract

How and when a concept of the 'self' emerges has been the topic of much interest in developmental psychology, yet there is still relatively little agreement on the validity of existing markers of self-awareness. Self-awareness is thought to develop at around 18 months, when infants begin to show evidence of mirror self-recognition. Understanding the neural underpinnings of self-awareness has been a focus interest, and adult research has shown that the DMN, a network that is activated when we are mind-wandering, is related to self-processing. Additionally, the TPJ and the mPFC, core regions of the DMN, are activated in self-processing tasks. However, we know very little about the neural mechanisms supporting self-processing at the age when the sense of self is still emerging. Taking advantage of fNIRS, I assessed whether infants who recognize themselves in the mirror – a behaviour that is thought to indicate emerging self-awareness - exhibit differences in the fronto-temporoparietal connectivity, – a possible proxy for the DMN - when compared with Non-Recognizers.

Resting state data were collected from 18 Recognizers and 22 Non-Recognizers at 18 months of age, and results showed significantly stronger fronto-temporoparietal connectivity in Recognizers compared to Non-Recognizers. This suggests that fronto-temporoparietal connectivity is associated not only with self-processing in adulthood, but also with the emergence of self-awareness in infancy.

4.2 Introduction

The emergence of an infant's sense of self is a topic of investigation which has progressed very little in developmental psychology over the last decades, as it is one that is difficult to investigate and operationalize empirically. There appears to be a consensus that we are born with some 'minimal' sense of self that allows us to interact with the environment (Zahavi, 2017), and empirical work suggests that young infants have some rudimentary bodily self-perception abilities (Filippetti et al., 2013). Nevertheless, there is also a consensus that there is a distinction between physical self-perception and psychological self-perception (Gillihan & Farah, 2005) and arguably, it is not clear to which extent the currently available measures assess physical or psychological self-perception (Bard, Todd, Bernier, Love, & Leavens, 2006; Gadlin & Ingle, 1975). The classic test to assess self-awareness in infancy is the MSR task (Amsterdam, 1972; Rochat, 2003), which has been used also in animals (Gallup, 1970; Marino, Reiss, & Gallup, 1994; Parker, Mitchell, & Boccia, 1995). While young infants placed in front of a mirror appear to perceive their specular image as an extension of the environment, from around 18 months, infants begin to systematically detect the link between seen and felt movements (Rochat, 2003), suggesting that at around this age, they start to understand that what they see in the mirror is themselves. Many have argued that this physical self-perception reflects a broader conceptualization of the self (Gallup et al., 2014; Suddendorf & Butler, 2013), including elements of psychological self-perception. Nevertheless, despite being the dominant measure of emerging self-awareness, there is to this day no general acceptance of the claim that the MSR test reflects a developing self-concept. Critics of this test argued that infants' self-recognition reflects a pure detection of matching visual and

kinaesthetic information (Heyes, 1996; Mitchell, 1993), or the understanding of the reflective proprieties of the mirror (Loveland, 1986).

While our current knowledge of early self-related processing is limited, much work in adult cognitive neuroscience has already made progress in identifying the neural underpinnings of self-related processing. Specifically, a network of brain regions engaged in passive rest in the low-frequency range (<0.1 Hz), appears to be recruited during self-related processing. This so-called DMN overlaps considerably with the social brain network (Davey et al., 2016; Greicius et al., 2003; Harrison et al., 2008; Mars et al., 2012; Molnar-Szakacs & Uddin, 2013; Raichle, 2015; Schilbach et al., 2008; Sporns, 2010), and is thought to play a pivotal role in several introspective and adaptive mental activities, such as autobiographical memory (Philippi, Tranel, Duff, & Rudrauf, 2014; Yang, Bossmann, Schiffhauer, Jordan, & Immordino-Yang, 2013), theory of mind and mentalizing (Li, Mai, & Liu, 2014; Mars et al., 2012), and planning and envisioning future events (Østby et al., 2012; Xu, Yuan, & Lei, 2016). Self-referential mental processing is the common feature of most of the processes which elicit DMN engagement, suggesting that this network is our 'intrinsic system' related to self-related signals and self-processing (Davey et al., 2016; Golland et al., 2008; Molnar-Szakacs & Uddin, 2013; Raichle, 2015; Sporns, 2010). The activity in the DMN has been shown to be remarkably similar to the one observed during self-processing tasks, suggesting that during quiet resting there might be a shift from perceiving the external world to internal modes of cognition (Buckner & Carroll, 2007). This is consistent with imaging studies that demonstrated that the DMN activity at rest was positively correlated with subjects reports of mind wandering and self-related thoughts (Mason et al., 2007; McKiernan et al., 2006). Crucially, the DMN appears to be primarily

involved in psychological self-processing and less so in physical self-recognition (Qin & Northoff, 2011).

To date we know very little about the neural underpinnings of self-awareness in the developing brain. However, given the debate surrounding the validity of the MSR task as an indicator of self-awareness beyond physical self-recognition (Suddendorf & Butler, 2013), investigating the relationship between the DMN and self-recognition in the mirror could inform this debate. Specifically, if a network of regions overlapping with those areas considered to comprise the DMN is associated with success on the MSR task in infants, it could suggest that MSR indexes a broader self-awareness than simple physical self-recognition, in line with those studies that have found relationships with empathy and personal pronoun use (Bischof-Köhler, 2012; Lewis & Ramsay, 2004). One of the few studies that investigated the neural substrates of the developing sense of self was found that the TPJ maturation was associated with self-recognition as early as 15 months of age, suggesting a role for TPJ during the emergence of self-awareness. However, while some research has begun exploring the maturation of the DMN during the first years of life (e.g. see Emberson, Richards, & Aslin, 2015; Fransson, Åden, Blennow, & Lagercrantz, 2011; Homae, Watanabe, Nakano, & Taga, 2011), and the experiment present in the previous chapter is consistent with this, to date, we have no knowledge of how spontaneous fluctuations in core regions for self-processing and part of the DMN might be related to the emergence of self-awareness.

fNIRS allows the acquisition of resting-state recordings under similar conditions to those in which data on the DMN involvement in self-related processing has been acquired in adults. Additionally, compared to other infant-friendly neuroimaging methods such as electroencephalography, fNIRS offers

clear advantages for assessing functional connectivity, as highlighted in Chapter 3. Previous adult studies have used fNIRS to assess resting-state functional connectivity (Lu et al., 2010; Mesquita et al., 2010; Sasai et al., 2012), but due to the inherent properties of fNIRS, its use is limited to the outer layers of the cortex. Therefore, the fronto-temporoparietal connectivity was investigated as a component of the DMN, as in the study presented in section 3.4.

In the current study, I employed fNIRS during awake rest to investigate the relationship between fronto-temporoparietal functional connectivity, as a putative index of DMN activity, and self-awareness as measured by the MSR task. Based on previous literature implicating the DMN in self-related processes, I hypothesized that infants who exhibited self-recognition would exhibit greater fronto-temporoparietal connectivity, as measured by resting-state fNIRS, compared to infants who did not yet exhibit self-recognition.

4.3 Methods

4.3.1 Participants

fNIRS resting state data were acquired from 43 18-month-olds (23 males, age mean $\pm$ SD = 553.11 $\pm$ 12.17 days). An additional 52 infants were excluded because: (i) their dataset did not reach a minimum of 100 seconds of recording after behavioural coding (28 infants); (ii) they refused to wear the fNIRS hat or poor positioning of the fNIRS headgear/hat (18 infants); (iii) more than 30% of the channels had to be excluded due to poor light intensity readings (6 infants). For more details about behavioural coding and mean intensity of the channels, see Chapter 3, section 3.4.3.3.

All included infants were born full- term, healthy and with normal birth weight. Written informed consent was obtained from the infant's caregiver prior to the start of the experiment.

4.3.2 MSR task and coding scheme

Prior to the fNIRS resting state-acquisition, self-awareness was assessed with the MSR task (Amsterdam, 1972). The task took place in a room with a mirror positioned against one of the walls. For 18 out of the 43 infants, one camera was used to record the task, while for the rest of the sample three cameras recording from different angles were used. One of the experimenters focused on adjusting the position of the cameras with the possibility to zoom in on the image, making sure the cameras captured a full view of the infant in front of the mirror (two cameras from the back and one from the side of the mirror). To avoid interfering with the testing session, the experimenter controlling the cameras entered the testing room first and hid behind the curtains covering the computer station. A second experimenter first engaged the infant in a warm-up play session in the room, and then redirected the infant's attention to the mirror. Once the infant had visually fixated the mirror image of his/her face at least three times, the experimenter covertly applied a red dot with lipstick on his/her cheek, while pretending to wipe the infant's nose. After this, the experimenter again engaged the infant in front of the mirror, making sure that the infant looked at him/herself at least three times. The experimenter prompted the child to look at the mirror by saying 'Look there' whenever necessary, but the only prompt for self-recognition that was used was the question "Who is that?", for a maximum of three times. This is the same procedure used by other infant studies (Asendorpf & Baudonnière, 1994;

Asendorpf et al., 1996; Kristen-Antonow, Sodian, Perst, & Licata, 2015; Lewis & Carmody, 2008; Nielsen, Dissanayake, & Kashima, 2003; Zmyj et al., 2013). The experimenter used bubbles to engage the child in playing, both before and after the red mark was placed (to avoid any differences between the two parts of the test). The caregiver was present in the room for the whole testing session, but asked not to alert the child to his/her image in the mirror and to stay outside of the visual field reflected in the mirror, preventing the infant from seeing his/her image reflected as a cue for self-recognition. The experimenter also remained outside the mirror field of view.

Two experimenters independently classified the infants as 'Recognisers', 'Ambiguous', or 'Non-Recognisers' based on their behaviours in front of the mirror after the red mark was placed, and they agreed in 96% of the cases. Discrepancies were discussed until agreement was reached. Participants were defined as 'Recognisers' if they touched the cheek with the red mark, the nose or the other cheek. They were classified as 'Ambiguous' if they said their name when looking at themselves in the mirror but did not touch their face. All other behaviours fell in the Non-Recognisers category.

4.3.3 Resting state data acquisition, pre-processing and analysis

See section 2.2.1 for information about the fNIRS cap and the arrays design. See section 2.2.3 for information about the NIRS system proprieties and the recording.

In this study, participants were tested with the two different fNIRS arrays described in Chapter 2, section 2.2.1[12]. The first array design, including

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[12] The 44-channel configuration was an extension of the 30-channel configuration and included two additional rows of optodes that added 7 channels per hemisphere, in a

30 channels, was used to test 20 out of the 43 participants; the second design, including 44 channels, was used to test 23 out of the 43 participants. Both configurations shared the design and the location of the channels covering frontal, inferior frontal and temporal regions (30 channels out of 44), therefore the data acquired with the two different configurations can be analysed together. As mentioned in Chapter 2, a range of several cap sizes was available, in order to adjust the cap size to the participant's head circumference. Table 4.1 lists information about source-detector separation and number of infants included in the analysis who were tested with each cap size.

Cap size	S-D temporoparietal lobe	S-D frontal lobe	Number of participants
48 cm	25 mm	30 mm	28/43
50 cm	26 mm	31 mm	15/43

Table 4.1 S-D separation and number of infants tested with each cap size.

The procedure for the resting-state data acquisition was the same as the one described in the second study in Chapter 3, section 3.3.3.2. fNIRS data pre-processing and analysis were the same as the one described in Chapter 3, section 3.3.3.3.

4.4 Results

Out of the 43 infants that contributed data to the resting-state analyses, 18 were classified as Recognisers and 22 as Non-Recognisers. Only 3 participants were classified as Ambiguous, and given the small size of this group, I focused the

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superior location to the two existing lateral arrays. This allowed to improve detection of TPJ activation, a core region of interest for this study.

analysis only on infants who clearly fell into the Recognisers and Non-Recognisers categories. The two groups did not show any significant difference in parameters that could potentially affect resting-state, such as age (mean $\pm$ SD Recognisers = 557.05 $\pm$ 9.29 days, mean $\pm$ SD Non- Recognisers = 550.54 $\pm$ 14.48 days), $t(38)$=1.18, p =0.24, and total length of the data sets after cleaning (mean $\pm$ SD Recognisers =164.65 $\pm$ 69.23 seconds, mean $\pm$ SD Non-Recognisers = 187.03 $\pm$ 61.61 seconds), $t(38)$=1.08, p=0.28.

As in the study presented in section 3.4, prior to any further analyses, I investigated the consistency of the connectivity patterns between the HbO_2 and HHb signal, performing one sample t-tests on the Fisher-transformed correlation coefficients on both chromophores in the whole sample. In fact, some previous adult studies explored the relationship between HbO_2 and HHb in fNIRS resting-state data, and revealed a comparable pattern of spontaneous fluctuation of the two chromophores, suggesting a similar underlying neurophysiological mechanism during resting-state (Lu et al., 2010; Sasai et al., 2011; White et al., 2009). Results are summarise in Table 4.2 and Figure 4.1 shows the fronto-temporoparietal connections that were significant per age group, for both HbO_2 and HHb. Significant functional connections within the whole set of channels were also plotted to assess whether functional connections in the whole set of channels.

Fronto- temporoparietal connectivity				Whole set of channels			
HbO_2		HHb		HbO_2		HHb	
p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected
5	2	2	/	112	77	89	63

Table 4.2 Number of functional connections that are significantly different from zero in the whole sample, within the fronto-temporoparietal regions and in the whole set of channels, in HbO_2 and in HHb. p-values are reported uncorrected and FDR corrected.
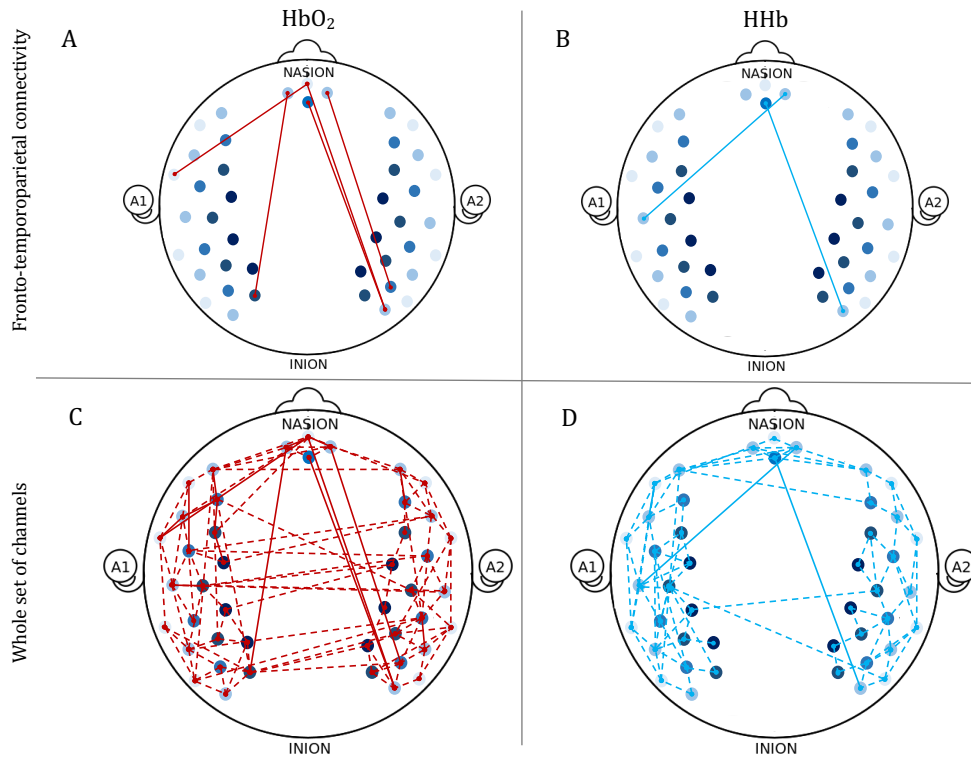
Figure 4.1. Graphical representation of the one sample t-tests in the whole sample within the fronto-temporoparietal regions and within the whole set of channels. HbO_2 is plotted in red, Hbb is plotted in blue. A, fronto-temporoparietal connections, HbO_2; B, fronto-temporoparietal connections, HHb; C, Whole set of channels, HbO_2; D, Whole set of channels, HHb. Solid lines show connections between frontal and temporoparietal regions, while dotted lines the connections within the whole brain.

In order to test the hypothesis of greater functional connectivity in fronto-temporoparietal areas in infants that exhibit self-recognition compared with those who did not, the Fisher-transformed correlation coefficients of Recognisers and Non-Recognisers were compared using independent sample t-tests. Driven by my hypothesis, the main interest was to compare Recognisers and Non-Recognisers on the fronto-temporoparietal connections – as a proxy for the DMN – but we report here also comparisons between connections within the whole set of channels for completeness. Results are summarise in Table 4.3 and Figure 4.2 shows connections that were significantly different between the two groups within both the HbO_2 and the Hbb maps ($p<0.05$). All the pairs of

functional connections were analysed, as more than half of the sample contributed to the statistical tests. See Appendix B for degrees of freedom of the t-test between the two groups in each connection (Supplementary Table 11).

comparison	Fronto- temporoparietal connectivity				Whole set of channels			
	HbO$_2$		HHb		HbO$_2$		HHb	
	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected
Recs> Non-Recs	13/14	3/14	7/8	3/8	48/57	6/57	19/27	9/27
Non-Recs> Recs	1/14	/	1/8	1/8	9/57	/	8/27	5/27

Table 4.3 Number of functional connections that are significantly different between Recognisers and Non-Recognisers in the 44-channel configuration, in the fronto-temporoparietal connections and in the whole set of channels in HbO$_2$ and in HHb. p-values are reported both uncorrected and FDR corrected.
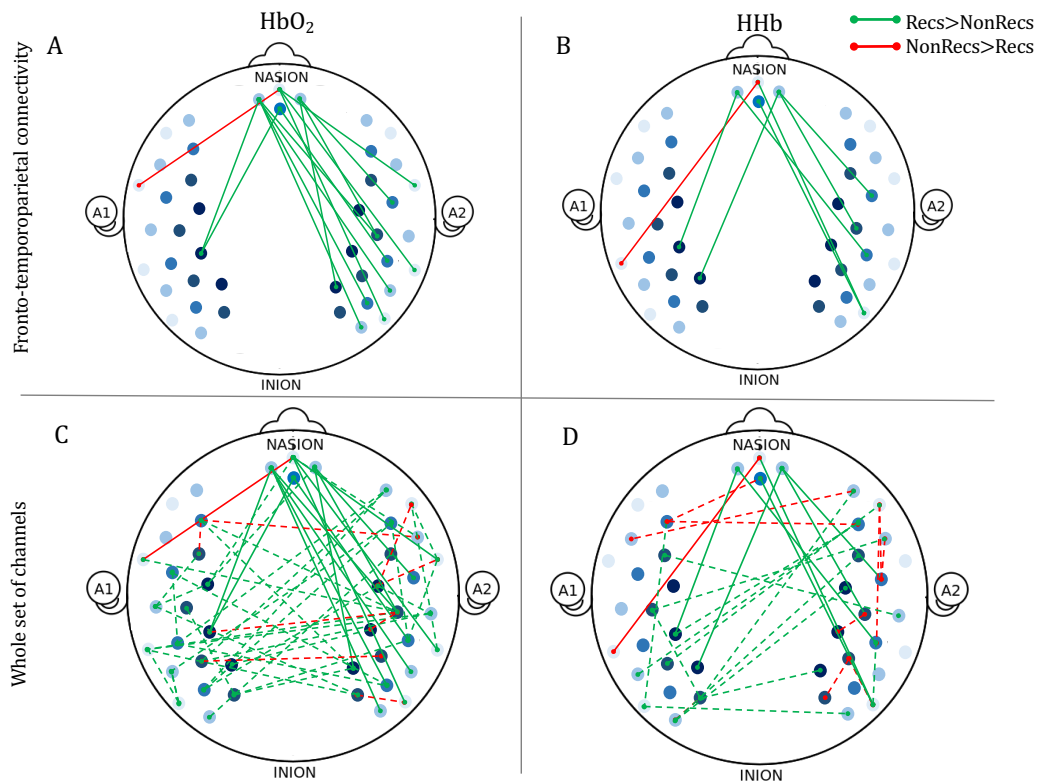
Figure 4.2. Graphical representation of the differences in fronto-temporoparietal connectivity between Recognisers and Non-Recognisers. A, fronto-temporoparietal connections, HbO$_2$; B, fronto-temporoparietal connections, HHb; C, Whole set of channels, HbO$_2$; D, Whole set of channels, HHb. Solid lines show connections between frontal and temporoparietal regions, while dotted lines the connections within the whole brain.

Table 4.4 reports difference in connectivity between Recognisers and Non-Recognisers only within the set of 30 channels in common to all the participants.

comparison	Fronto- temporoparietal connectivity				Whole set of channels			
	HbO$_2$		HHb		HbO$_2$		HHb	
	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected	p<0.05	FDR corrected
Recs> Non-Recs	8/9	2/9	4/5	2/5	28/28	7/57	7/13	4/13
Non-Recs> Recs	1/9	/	1/5	1/5	2/28	/	6/13	3/13

Table 4.4 Number of functional connections that are significantly different between Recognisers and Non-Recognisers in the 30-channel configuration, in the fronto-temporoparietal connections and in the whole set of channels in HbO$_2$ and in HHb. p-values are reported both uncorrected and FDR corrected.

Figure 4.3 shows difference in connectivity between Recognisers and Non-Recognisers only within the set of 30 channels in common to all the participants (p<0.05).
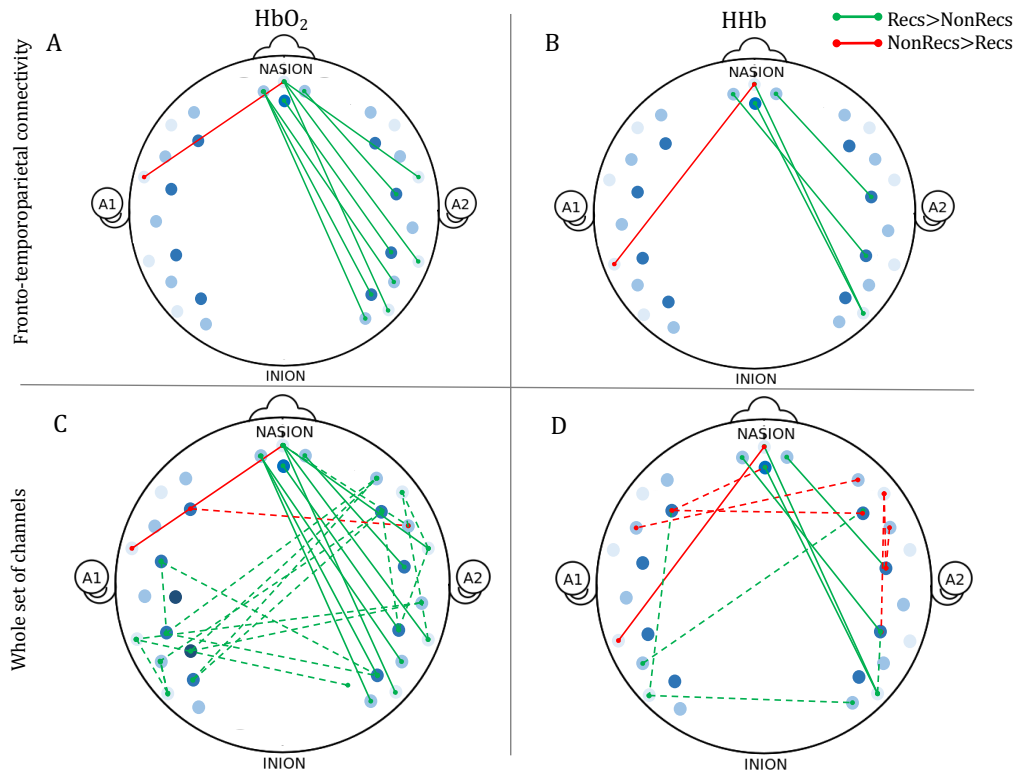
Figure 4.3 Graphical representation of the differences in the fronto-temporoparietal connectivity in the 30 channels in common to all the participants. A, fronto-temporoparietal connections, HbO_2; B, fronto-temporoparietal connections, HHb; C, Whole set of channels, HbO_2; D, Whole set of channels, HHb. Solid lines show connections between frontal and temporoparietal regions, while dotted lines the connections within the whole brain.

4.5 Discussion

Investigating the ontogeny of self-awareness remains challenging (Zahavi & Roepstorff, 2011), and one important way of moving this field of study forward is to develop measures which have a high degree of validity. While it has been claimed the MSR test indexes an emerging self-concept (Gallup, Platek, & Spaulding, 2016), there is still no general agreement that this is the case. To date, the confidence in the MSR test as a measure of emerging self-awareness is limited by: a) a lack of alternative age-appropriate self-related tasks against which performance on the MSR can be compared and b) alternative

explanations for success on the MSR test which do not involve any self-related processing (Heyes, 1994b). In the current study, I approached this question by asking whether a functional network of brain regions in adults – the DMN, which is commonly thought to be involved in psychological self-related processing – is associated with MSR in infancy. Specifically, I hypothesized that if the MSR task reflects self-related processing, and not merely recognition of the physical self, or a matching of seen and felt movements, then regions comprising the DMN could differentiate those infants who do and do not recognize themselves in the mirror. The results showed support this hypothesis, showing that the fronto-temporoparietal connectivity is associated with the emergence of infants' self-recognition, suggesting this as a possible neural marker for the development of the sense of self in early development.

While I cannot claim that this fronto-temporoparietal connectivity reflects the entire DMN, this increased connectivity in Recognizers is consistent with previous adult reports of a link between frontal and temporoparietal areas and the sense of self (Davey et al., 2016; Molnar-Szakacs & Uddin, 2013; Philippi, 2012). The pattern of long-range connectivity displayed by infants who have a more robust sense of self at 18 months of age might be supported by an advanced integration in a network of core areas for self-processing. The functional connections between these areas at rest displayed by those who recognised themselves in the mirror compared to those who did not may underlie an ongoing process of monitoring self-relevant internal signals and thoughts during the absence of any specific cognitive and social stimulation. It is worth mentioning that the connections stronger in the Recognisers than in the Non-Recognisers surviving the FDR correction for multiple comparisons are limited. A post-hoc power analysis performed with G*Power (Faul et al.,

2007) revealed that a power of only 0.46 is achieved for an effect size as significant at the 5% level (d=0.5, Cohen, 1988), given 18 and 22 participants in the two groups.

These findings of a possible role for the fronto-temporoparietal connections in the emergence of self-awareness are broadly consistent with the only previous study which has investigated the neural basis of MSR in infants. In that study, Lewis & Carmody (2008) found that infants who recognized themselves in the mirror showed greater maturation of the left temporoparietal junction, a region that is central to the DMN. In the current study, the vast majority of the fronto-temporoparietal connections that were stronger in Recognizers than in Non-Recognizers are observed in the right hemisphere, a tendency which has also been reported in previous adult studies (Keenan, Nelson, O'Connor, & Pascual-Leone, 2001; Kircher et al., 2001; Molnar-Szakacs & Uddin, 2013; Platek, Keenan, Gallup, & Mohamed, 2004; Platek et al., 2006; Sugiura et al., 2005). Moreover, a recent study aimed at identifying structural brain correlates of MSR in chimpanzees reported increased right hemisphere fronto-parietal white matter connectivity in chimpanzees who passed the MSR task (Hecht, Mahovetz, Preuss, & Hopkins, 2017). While these previous studies analysed structural connectivity, our study provides additional evidence for the importance of this network of brain regions by demonstrating a relationship between functional connectivity in these areas and MSR.

While the current study revealed only a few connections that were stronger in Non-Recognizers than Recognizers, most of those that were stronger tended to be short-range connections. Previous research suggests that increased short-range connectivity within frontal and temporal regions and decreased long-range connections between frontal and temporoparietal

regions can be observed in situations where self-awareness is impaired, such as in schizophrenia (Ebisch et al., 2014; Liemburg et al., 2012) or in autism (Lynch et al., 2013; Müller et al., 2011; Uddin & Menon, 2009; Uddin, Supekar, & Menon, 2010). While there were no predictions concerning short-range connectivity, our results are consistent with the idea that self-related processing may be associated not only with increasing long-range connectivity between frontal, temporal, and parietal cortex, but rather a gradual transition from short and localised connections to long-range connectivity.

It is important to note that these findings cannot exclude the possibility that the functional connectivity observed in the Recognisers reflects a generally more mature brain, which also gives rise to a more mature level of self-awareness (Fair et al., 2008; Gao et al., 2009, 2014; Nathan Spreng & Schacter, 2012). Relevant here might be that in the whole brain analysis, the Recognizers showed increased brain connectivity overall, so also outside the regions associated with the DMN. Assessing the brain maturation in each participant would allow us to investigate this possibility. However, this would require the acquisition of MRI images to assess structural connectivity and cortical thickness as an index of maturation of the brain.

Another limitation of this study is the fact that the investigation into the connectivity in the entire DMN was unachievable, as fNIRS allows to measure only from the surface of the cortex. However, I benefited from the excellent suitability of fNIRS for the acquisition of resting-state data from infants during quiet wakefulness, which most closely approximates the recording conditions under which resting-state data is typically acquired in adults. As a result, the data were likely less affected by motion artefacts than it would have been had we used fMRI. The high consistency between the HbO_2 and the HHb maps is in

line with fNIRS resting-state data acquired by previous studies, suggesting reliability of the data acquired (Lu et al., 2010; Sasai, Homae, Watanabe, & Taga, 2011; White et al., 2009).

With this study, it has been shown that the fronto-temporoparietal connectivity considered as a proxy of the DMN may plays a role in emerging self-awareness. However, how the developing brain responds during self-recognition, is something still unexplored. This investigation, which may provide a deeper insight on the mechanisms underlying the developing sense of self, is the focus of the next chapter.

Chapter 5

Neural underpinnings of

self-recognition in 18-month-olds

5.1 Abstract

The previous chapter showed that the fronto-temporoparietal connectivity measured at rest is associated with emerging self-awareness at 18 months. Adult studies suggest that these two brain regions are also engaged in self-processing and self-recognition tasks, but whether these areas are involved in self-processing also in the developing brain is something still unexplored. An important cue for self-recognition during the first years of life is thought to be the detection of temporal contingency between performed and observed movements. In this study, the temporal contingency of participants' movements was manipulated while 18-month-olds observed videos of themselves, either with matching observed and performed movements, or mismatching observed and performed movements. Additionally, participants were also observed an unfamiliar infant. Infants' brain responses were recorded using fNIRS and self-awareness was behaviourally assessed using the MSR task.

18-month-olds that exhibited self-recognition showed greater activation of the mPFC and the TPJ when they looked at themselves with matching rather than mismatching movements. They also showed greater mPFC activation when they looked at their own videos compared with those of an unfamiliar infant. Moreover, two behavioural measures used as indexes of self-recognition (looking time in the mirror during the MSR task and level of movements during the fNIRS task) were positively correlated with the mPFC activation. Consistent with findings from the previous chapter, these results suggest a role for the mPFC and the TPJ in self-related processes from early in life. Furthermore, these results are remarkably in line with the works in adult.

5.2 Introduction

As suggested by data discussed in the previous Chapter, functional connectivity between the mPFC and the TPJ – crucial areas of the DMN – is associated with emerging self-awareness at 18-months. This finding may represent one of the first neural markers of emerging self-awareness. Furthermore, it may suggest that self-recognition in the mirror is an index not only of physical self-awareness but also of the development of a broader sense of self, as indicated by the relationship between the DMN and psychological self-processing in adults. The positive association between fronto-temporoparietal connectivity and emerging self-awareness in 18-month-olds laid the foundation for a further question: are the mPFC and the TPJ also engaged in the process of self-recognition in infancy? Given the results from the previous chapter, one may hypothesize that these two brain regions would be functionally activated also during self-recognition.

The study of the neural correlates of self-awareness in adults has been a target of interest in recent neuroimaging research. The mPFC and the TPJ are defined by many as the 'self' brain regions (for reviews see Northoff et al., 2006; Northoff & Bermpohl, 2004; Ruby & Legrand, 2007). In fact, these regions were found to be remarkably engaged in several self-processing tasks (Davey et al., 2016; Kaplan et al., 2008; Kelley et al., 2002; Kircher et al., 2000; Uddin et al., 2005). Moreover, it has been shown that, when comparing self-faces with others', the frontal and parietal lobes are found to be engaged in self-face processing tasks when own faces are contrasted with familiar-faces, whereas the temporoparietal cortex is specifically activated when own faces are contrasted with unfamiliar faces (Kaplan et al., 2008; Platek, Keenan, Gallup, & Mohamed, 2004; Platek et al., 2006).

Most of our knowledge of the neural correlates of self-recognition come from adult studies, while infant research on this topic is still very limited. To summarise, the literature reviewed on the previous infants studies in Chapter 1 revealed that i) TPJ grey matter maturation is associated with self-representation between 18- and 30-month-old (Lewis & Carmody, 2008); ii) both TPJ and the STS are activated during self-body representation in 5-month-olds (Filippetti et al., 2015); iii) the N290 ERP component is a marker of self-image processing at 18-months when infants' own images are compared with familiar and unfamiliar ones (Stapel et al., 2016). However, brain regions functionally engaged in self-recognition in infancy are still unexplored.

During the first years of life the detection of temporal contingency between observed and performed movements has been suggested as an important cue for self-recognition (Rochat, 2003). A 'contingency detection module', aimed to analyse the temporal conditional probabilities of stimuli and responses, has been hypothesised as innate (Gergely & Watson, 1996, 1999) or present from very early in life (Reddy et al., 2007; Rochat & Striano, 1999; van der Meer et al., 1995). This module would enable infants to seek and explore contingent stimulations, serving the evolutionary function of developing a rudimentary representation of their bodily self (Gergely, 2004). However, the active exploration of temporal contingency in movements performed and observed in the light of emerging self-awareness will not be present until about 18-months (Rochat, 2003). Some behavioural works have already explored whether infants respond differently to delayed self-videos compared with live self-videos, showing that infants do not master self-recognition in delayed media before 2.5 years of age (Povinelli et al., 1996; Povinelli & Simon, 1998; Skouteris et al., 2009). In terms of neuroimaging studies, Sugiura et al. (2015)

showed that the adult brain responds differently to self-live and self-delayed videos, suggesting an important role for contingency. While the frontal and the occipital lobes were found sensitive to movements when comparing self-videos with self-static images, the cuneus was found significantly associated with the contingency of self-movements. These findings allude to a multicomponent brain network supporting self-recognition processes. Moreover, different patterns of brain responses to self-live and self-delayed videos seem to highlight the importance of the detection of temporal contingency for processing self-related information (Sugiura et al., 2015). Therefore, one may think that the developing brain could respond differently to self-videos with different level of temporal contingency in self-movements, when self-awareness has started to emerge.

In this study, I used fNIRS to test the neural underpinnings of self-recognition in 18-month-olds while they observed videos of themselves live (Self-Live condition) and videos of themselves previously recorded (Self-Recorded condition). At the beginning of the task, participants observed an additional condition with an unfamiliar infant wearing the same fNIRS cap in the same setting (Other condition). This allowed the investigation of the neural underpinnings of self-other differentiation. Participants were also tested for self-recognition in the mirror with the MSR task, to obtain a behavioural measurement of their level of self-awareness. I hypothesized a greater brain response in core regions for self-processing, i.e. mPFC and TPJ, in the Self-Live condition rather than in the Self-Recorded one, and that this would be mediated by whether or not the infants passed the MSR task. This would be consistent with the categorisation attributed by the MSR task, with adult studies and with the functional connectivity data previously presented in Chapter 4. If this

analysis reveals the hypothesized pattern of results, the Self-Live condition will be compared with the Other condition, in order to assess the neural substrates of Self vs. Other. Alternatively, if no differences in brain activation is identified when comparing the two Self conditions, these conditions will be collapsed and compared with the Other condition. Brain regions engaged in self-processing (Self-Live vs. Self-Recorded) are also expected to be activated in Self vs. Other - mainly in Recognisers at the MSR task - as a further marker of self-processing in infanthood. Additionally, functional connectivity analysis is employed to further investigate whether fronto-temporoparietal functional connections are associated with self-processing in the developing brain during a self-recognition task. Finally, behavioural measures related to self-related processing are acquired during the MSR task and the fNIRS task in order to provide a further description of emerging self-awareness. Looking time in the mirror after the red mark is placed during the MSR task and level of exploration of matching movements have been previously used as indexes of self-awareness (Keller, Kärtner, Borke, Yovsi, & Kleis, 2005; Rochat, 2003). Therefore, I hypothesize that a longer looking time at the mirror after the mark was placed than before characterizes only those participants exhibiting self-recognition. Moreover, I hypothesize that Recognisers at the MSR task will show a higher level of movements to explore matching behaviours during the fNIRS task. If these hypotheses are confirmed, the association between these two behavioural measures with brain response during the fNIRS task will be investigated.

5.3 Methods

5.3.1 Participants

24 18-month-old infants provided sufficient data to be included in the fNIRS analyses (14 males, age mean $\pm$ SD = 553.57 $\pm$ 14.05 days). An additional 57 infants were tested but excluded from the fNIRS analyses because: (i) they did not provide enough trials, either due to fussiness (14 participants) or to inattentiveness (24 participants); (ii) they refused to wear the fNIRS hat or poor positioning of the fNIRS hat (7 participants); (iii) they refused to sit on the high-chair (8 participants); (iv) they showed more than 30% of the channels excluded due to poor light intensity readings (3 participants); (v) technical error (1 participant). It is worth mentioning that the use of the high-chair constituted an additional stress factor for some infants. This contributed to a higher participants' exclusion rate compared to the other fNIRS studies presented in this thesis.

All included infants were born full- term, healthy and with normal birth weight. Written informed consent was obtained from the infant's caregiver prior to the start of the experiment.

5.3.2 MSR and coding scheme

Prior to the fNIRS task, self-awareness was assessed with the MSR task (Amsterdam, 1972). The task took place in an empty room with a mirror positioned against one of the walls. For all the participants tested in this study, three cameras from different angles were used to record the task. The MSR task procedure and the coding scheme used was the same as described in Chapter 4, section 4.3.2. Two experimenters independently classified the infants as

'Recognisers', 'Ambiguous', or 'Non-Recognisers' based on their behaviours in front of the mirror after the red mark was placed, and they agreed in 92% of the cases. Discrepancies were discussed until agreement was reached.

For each infant, looking time at his/her own image in the mirror before and after the red mark was placed on his/her cheek was coded. In particular, the percentage of looking time (%LT) in the mirror was calculated, considering the looking time in the mirror after/before the mark was placed over the length of the testing session after/before the mark was placed.

5.3.3 fNIRS task: stimuli and procedure

See section 2.2.3 for experimental set-up, fNIRS cap application and testing procedure.

In this task, infants sat on a high-chair positioned in front of the plasma screen, and the parent sat next to them. The set-up used in this study is different from the usual one discussed in Chapter 2 with participants attending the fNIRS session on the parent's lap. In fact, as in this task the self-videos of the participants are recorded and projected during the experiment, positioning the child by him/herself prevented the recording of any body-part of the parent. A Logitech-HD Pro Webcam was positioned on top of the plasma screen, allowing the recording of the participant's videos to be presented in the Self-Recorded condition.

Infants were presented with 3 conditions: i) an unfamiliar infant (Other condition); ii) their-selves in a live video (Self-Live condition); iii) their-selves recorded few minutes before (Self-Recorded condition). In order to avoid any brain activation not related to the task, the videos showed in the 3 conditions presented the same set-up, with the infants (either the participant or the

unfamiliar infant) sitting on the high-chair while wearing the fNIRS cap. Each experimental trial, which lasted 15 seconds, was alternated with Baseline trials which were screensaver-like videos of colourful swirly bubbles coloured shapes (Baseline), which lasted 10 seconds. The trials were structured in a block-design, divided into two parts. In the first part of the block design, infants were presented with a series of Other trials alternated with Baseline trials. While the participant attended at the Other trials, the experimenter recorded videos of the infant with the Logitech-HD Pro Webcam positioned on top of the plasma screen. These videos constituted the trials to be presented in the Self-Recorded condition in the later part of the task. For each participant, four videos were recorded, to provide some varieties of movements performed by the participants as in the Self-Live and Other conditions. After the acquisition of enough videos for the Self-Recorded condition and the presentation of at least 4 trials for the Other condition, the experimenter started the second part of the block design, composed of Self-Live and Self-Recorded trials, alternated with Baseline trials. The Self-Live and the Self-Recorded trails were pseudo-randomised to make sure that each condition was presented not more than twice in a row.

5.3.4 fNIRS data acquisition and processing

See section 2.2.1 for information about the fNIRS cap and the array design. All the participants of this study were tested with the 44-channel array design. Table 5.1 lists information concerning S-D separation and the number of infants included in the analysis who were tested with each cap size.

Cap size	S-D temporoparietal lobe	S-D frontal lobe	Number of participants
48 cm	25 mm	30 mm	14/24
50 cm	26 mm	31 mm	10/24

Table 5.1. S-D separation and number of participants tested with each cap size.

See section 2.2.4 for information about the NIRS system proprieties and the recording. As mentioned in section 2.3.1, infants were video-recorded throughout the testing session. In addition to the general exclusion criteria[13], trials where infants did not attend to the screen for more than 60% of the length of the trial were excluded. In order to observe any difference between the Self-Live and Self-Recorded trials, it was essential that i) in the Self-Live condition, the participant performed at least one movement visible by him/herself in the live-video; ii) in the Self-Recorded condition, the participant saw at least one movement performed by him/herself in the recorded video or the participant performed at least one movement not present in the recorded video. Therefore, Self-Live trials were included only if participants attended at least one gross movement matching the performed one, whereas Self-Recorded trials were included only if participants attended at least one gross mismatching movement (of at least 2 seconds). In order to assess the level of movements performed and observed during the task, Self-Live and Self-Recorded trials were coded for movements performed and seen with a value from 1 to 3 (1= small limbs or body movements, 3 = big limb or body movements).

As described in section 2.3.2, fNIRS data were pre-processed in Homer_2 (Huppert et al., 2009), and the spline interpolation (function

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[13] Trials were excluded if participant looked at the parent or anything social, if the experimenter or the parent talked.

hmrMotionCorrectionSpline) was added to the general pipeline as a further motion correction (Scholkmann et al., 2010), after the prune of the channels with a low signal to noise ratio. This additional correction was applied due to a high level of noise and several spikes presented in the fNIRS raw data by most of the participants, which is likely to be due to the greater chance that the infants were moving while seated in the high-chair in this task, compared to the classic set-up on the parent's lap. In fact, fNIRS data recorded from the same participants in the same testing session using the classical set-up did not present as many spikes and noise as this dataset[14].

After the pre-processing, data were analysed using a combination of custom Matlab scripts and the SPM-NIRS toolbox (Ye et al., 2009), as described in section 2.3.3. For each participant, a design matrix was built modelling the 3 experimental conditions and the baselines. Trials excluded due to the cleaning in the pre-processing or due to behavioural coding were removed from the analyses. Betas extracted from the design matrix were used to calculate contrasts of interest for each participant (Self-Live vs. Self-Recorded and Self-Live vs. Other), and then submitted to statistical tests. Statistical analyses were performed both on each channel and on the mPFC, the left TPJ and the right TPJ as ROI defined by the co-registration study presented in section 2.2.2, for their crucial role in self-processing (Northoff et al., 2006; Northoff & Bermpohl, 2004; Ruby & Legrand, 2007). Analysis of fNIRS data were based on changes in HbO_2, as previous fNIRS studies with infants typically do not find any statistically significant HHb changes (for some examples see: Grossmann, Cross,

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[14] After this task, if participants were still quiet and compliant, they were tested with the EMG-fNIRS task presented in Chapter 6 and with the resting-state protocol presented in Chapter 4.

Ticini, & Daum, 2013; Lloyd-Fox et al., 2010; Lloyd-Fox, Széplaki-Köllod, Yin, & Csibra, 2015; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014). However, the pattern of HHb will be plotted for completeness. fNIRS results are corrected for multiple comparisons using the FDR approach.

To further explore the relationship between areas engaged in the self-processing task, functional connectivity was estimated using PPI (see section 3.1.2 for more details) (Friston et al., 1997). Consistently with the functional activation analysis, PPI analysis is performed only on the HbO_2 signal. In order to ensure statistical reliability, PPI results are corrected for multiple comparisons with FDR.

5.4 Results

5.4.1 Characteristics of the sample and behavioural results

Out of the 24 infants that contributed data to the fNIRS analyses, 10 were classified as Recognisers and 11 as Non-Recognisers. Only 3 participants were classified as Ambiguous, and given the small size of this group, analyses are focused only on infants who clearly fell into the Recognisers and Non-Recognisers categories. The two groups did not show any significant difference in parameters that could potentially affect the haemodynamic response in this task, such as age (mean $\pm$ SD Recognisers = 550.55 $\pm$ 16.50 days, mean $\pm$ SD Non-Recognisers = 553.75 $\pm$ 12.44 days), $t(21)=0.52$, $p=0.603$, sex (Recognisers = 5 females, 5 males; Non-Recognisers =4 females, 7 males), $\chi^2(1,$ N=21)=0.39, $p=0.528$. A repeated measure ANOVA with number of trials included per type as within subject factor (Self-Live vs. Self-Recorded vs. Other) and MSR outcome as between subject factor (Recognisers vs Non-Recognisers)

did not show a significant interaction, $F(1, 19) = 1.04$, $p = 0.371$, $\eta_p^2 = 0.104$, suggesting no significant differences between Recognisers and Non-Recognisers in number of trials included per each condition.

A repeated measure ANOVA with % LT as within subject factor (before vs after) and MSR outcome (Recognisers vs Non-Recognisers) as between subject factor did not show any significant interaction, $F(1, 19)=1.96$, $p=0.177$, $\eta_p^2=0.094$. However, post-hoc paired t-tests revealed that Recognisers showed a significantly longer %LT in the mirror after the mark was placed in the MSR task compared to before the mark was placed (mean $\pm$ SD %LT after $= 21.53 \pm$ 17.04, mean $\pm$ SD %LT before $= 7.34 \pm 4.70$), $t(9)=2.36$, $p=0.042$. No significant difference in %LT either after or before the mark was placed was found in Non-Recognisers (mean $\pm$ SD %LT after $= 11.08 \pm 8.60$ trials, mean $\pm$ SD %LT before $= 6.78 \pm 11.60$ trials), $t(10)=1.08$, $p=0.30$. Among the Recognisers subset, one data point fell around two standard deviations from the mean in %LT in the mirror after the mark was placed. Although this was not an extreme outlier, to ensure that the comparison between %LT in the mirror before and after the infant's cheek was marked was not merely driven by this one data point, it was replaced with a value .01 greater than the highest non-outlier scores to normalise the distribution (Tabachnick & Fidell, 2007). Hereafter, the comparison between %LT in the mirror before and after the mark placed is still significant in the Recognisers group, $t(9)=2.62$, $p=0.028$.

A repeated measure ANOVA with level of performed movements as a within subjects factor (performed movements in the Self-Live condition vs performed movements in the Self-Recorded condition) and MSR outcome (Recognisers vs Non-Recognisers) as a between subjects factor demonstrated a main effect of condition, $F(1, 19)=7.21$, $p=0.015$, $\eta_p^2=0.275$, revealing a

significantly higher level of performed movement in the Self-Live rather than in the Self-Recorded condition in the whole sample. No significant interaction between level of performed movements and MSR was found, $F(1, 19)=0.02$, $p=0.885$, $\eta_p^2=0.001$. However, paired sample t-tests between Self-Live and Self-Recorded conditions in the two groups showed that Recognisers moved significantly more in the Self-Live rather in the Self-Recorded condition, $t(9),=2.53$, $p=0.032$, while Non-Recognisers did not, $t(10),=1.57$, $p=0.146$. Moreover, a repeated measure ANOVA with level of movements in the Self-Recorded condition as a within subjects factor (performed movements vs observed movements) and MSR outcome (Recognisers vs Non-Recognisers) as a between subject factor demonstrated a main effect of movement, $F(1, 19)=10.32$, $p=0.005$, $\eta_p^2=0.352$, revealing a significantly higher level of performed rather than observed movements in the Self-Recorded condition in the whole sample. No significant interaction between level of movements observed and performed in the Self-Recorded condition and MSR was found, $F(1, 19)=0.947$, $p=0.343$, $\eta_p^2 =0.047$. However, post-hoc independent t-tests within the Self-Recorded condition showed that Recognisers performed significantly more movement than the ones they observed in the Self-Recorded videos, $t(9),=3.54$, $p=0.006$. Non-Recognisers did not show a significant difference between observed and performed movements in the Self-Recorded condition, $t(10),=1.42$, $p=0.185$ (Figure 5.1).
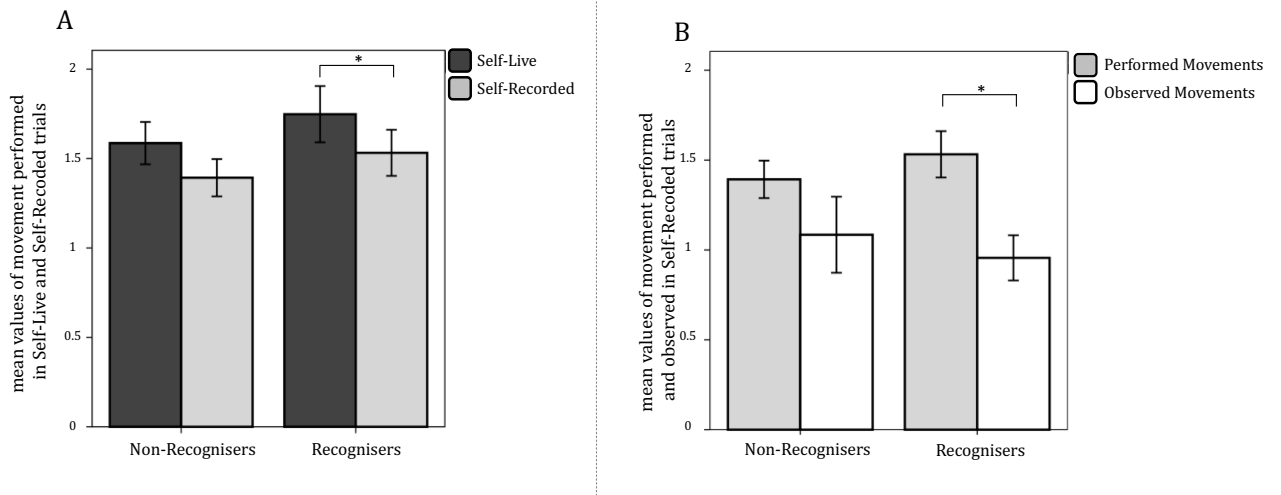
Figure 5.1 Mean values of movements during the Self conditions in the task. A, Graph bars represent mean values of movements performed in Self-Live and Self-Recorded trials in Non-Recognisers and Recognisers. B, Graph bars represent mean values of movements performed and observed in Self-Recorded trials in Non-Recognisers and Recognisers. Error bars indicate 1 SEM; *, $p < 0.05$.

5.4.2 fNIRS results

5.4.2.1 Self-Live>Baseline, Self-Recorded>Baseline, Other>Baseline contrasts

To explore which channels were activated by the task, the Self-Live, the Self-Recorded and the Other conditions were contrasted to the Baseline (see Table 5.2). Table 5.2 shows the channels that are statistically significant and marginally statistically significant activated by the task.

channel	brain region	t value	p value	df
Self-Live>Baseline				
26	Right posterior temporal gyrus	2.02	0.055†	17
30	mPFC	2.25	0.034*	22
40	Right supramarginal gyrus	2.10	0.046*	23
Self-Recorded>Baseline				
1	Left IFG	2.20	0.039*	20
Other>Baseline				
/	/	/	/	/

Table 5.2 Channels that showed greater activation for Self-Live>Baseline, Self-Recorded>Baseline, Other>Baseline. *, p<0.05; †, p<0.065.

As can be seen by the table, the Self-Live condition engaged one channel over the right posterior temporal gyrus (channel 26), one channel over the mPFC (channel 30) and one channel over the right supramarginal gyrus (channel 40), whereas the Self-Recorded condition engaged some channels only one channel over the left IFG (channel 1). However, none of these channels showed a significant activation after FDR correction. No channels were significantly activated by the Other condition.

Table 5.3 shows channels that are significantly and marginally significantly activated for Baseline>Other. No channels were significantly activated in the baseline trials when contrasted with Self-Live and Self-Recorded.

channel	brain region	t value	p value	df
Baseline>Other				
5	Left STG	2.29	0.034*	18
9	Left TPJ	1.95	0.064†	21
18	Right STG	2.04	0.055†	19
20	Right STG	1.99	0.06†	20
35	Left TPJ	2.29	0.033*	19

Table 5.3 Channels that showed greater activation for Baseline>Other. *, p<0.05; †, p<0.065.

As can be seen from the table, one channel over the left STG (channel 5) and one over the left TPJ (channel 35) were found to be significantly activated by the Baseline when compared with the Other condition.

5.4.2.2 Repeated measures ANOVA

A repeated measures ANOVA with the betas from the Self-Live and the Self-Recorded condition compared with Baseline as a within subjects factor (Self-Live>Baseline vs. Self-Recorded>Baseline) and the MSR outcome as a between subjects factor revealed a marginally significant main effect of condition in channel 28 (mPFC), $F(1, 20) = 3.85$, p=0.064, η_p^2=0.300, in channel 30 (mPFC), $F(1, 19) = 3.80$, p=0.065, η_p^2=0.395 and in the mPFC as ROI, $F(1, 20) = 4.28$, p=0.055, η_p^2=0.176, but no significant interaction with the MSR outcome. Post-hoc analysis revealed that channels 28 and the mPFC as ROI that showed a marginally significant effect main effect of condition were significantly more activated for the Self-Live than the Self-Recorded condition (channel 28: t(23)=2.24, p=0.035; mPFC: t(23)=2.15, p=0.042).

A repeated measures ANOVA with the betas from the Self and the Other condition compared with Baseline as a within subjects factor (Self>Baseline vs. Other>Baseline) and the MSR outcome as a between subjects factor revealed a significant main effect of condition in channel 30 (mPFC), $F(1, 17) = 7.38$, p=0.015, η_p^2=0.467 (not significant after FDR correction), but no significant interaction with the MSR outcome. Post-hoc analysis revealed that channel 30 was significantly more activated for the Self than the Other condition, $t(20)$=2.94, p=0.008.

5.4.2.3 One sample t-tests in the Recognisers and in the Non-Recognisers

5.4.2.3.1 Self-Live>Self-Recorded contrast

To explore whether there are any brain regions that showed any differences in activation in response to self-processing (Self-Live>Self-Recorded) in the two groups, one-sample t-tests on the HRF contrast were performed in the Recognisers and in the Non-Recognisers by using the split analysis. This analysis might elucidate different neural brain regions activated by the two conditions in the two groups which can be associated with the behavioural measures (%LT and level of performed movements). Table 5.4 shows the channels that showed greater activation for Self-Live>Self-Recorded and Self-Recorded>Self-Live in Recognisers and in Non-Recognisers (see figure 5.2 for the HRF plots).

Self-Live>Self-Recorded				
channel	brain region	*t* value	*p* value	df
Recognisers				
23	Right posterior temporal gyrus	1.94	0.078†	8
26	Right posterior temporal gyrus	1.95	0.082†	7
28	mPFC	2.89	0.018*	9
29	mPFC	3.67	0.005*	9
30	mPFC	2.12	0.052†	9
mPFC (ROI)		2.31	0.046*	9
Right TPJ (ROI)		3.64	0.007**	9
Non-Recognisers				
/	/	/	/	/
Self-Recorded>Self-Live				
Recognisers				
14	Right IFG	2.59	0.032*	8
Non-Recognisers				
37	Left TPJ/angular gyrus	2.36	0.056†	8

Table 5.4 Channels that showed greater activation for Self-Live>Self-Recorded and Self- Recorded>Self-Live, in the whole sample and in the subsets of Recognisers and Non-Recognisers at the MSR task. **, p<0.05 that survived the FDR correction for multiple comparisons; *, p<0.05; †, p<0.065.

A   Channels significantly activated for Self-Live>Self-Recorded in the Recognisers

B   Channels significantly activated for Self-Recorded>Self-Live in the Recognisers
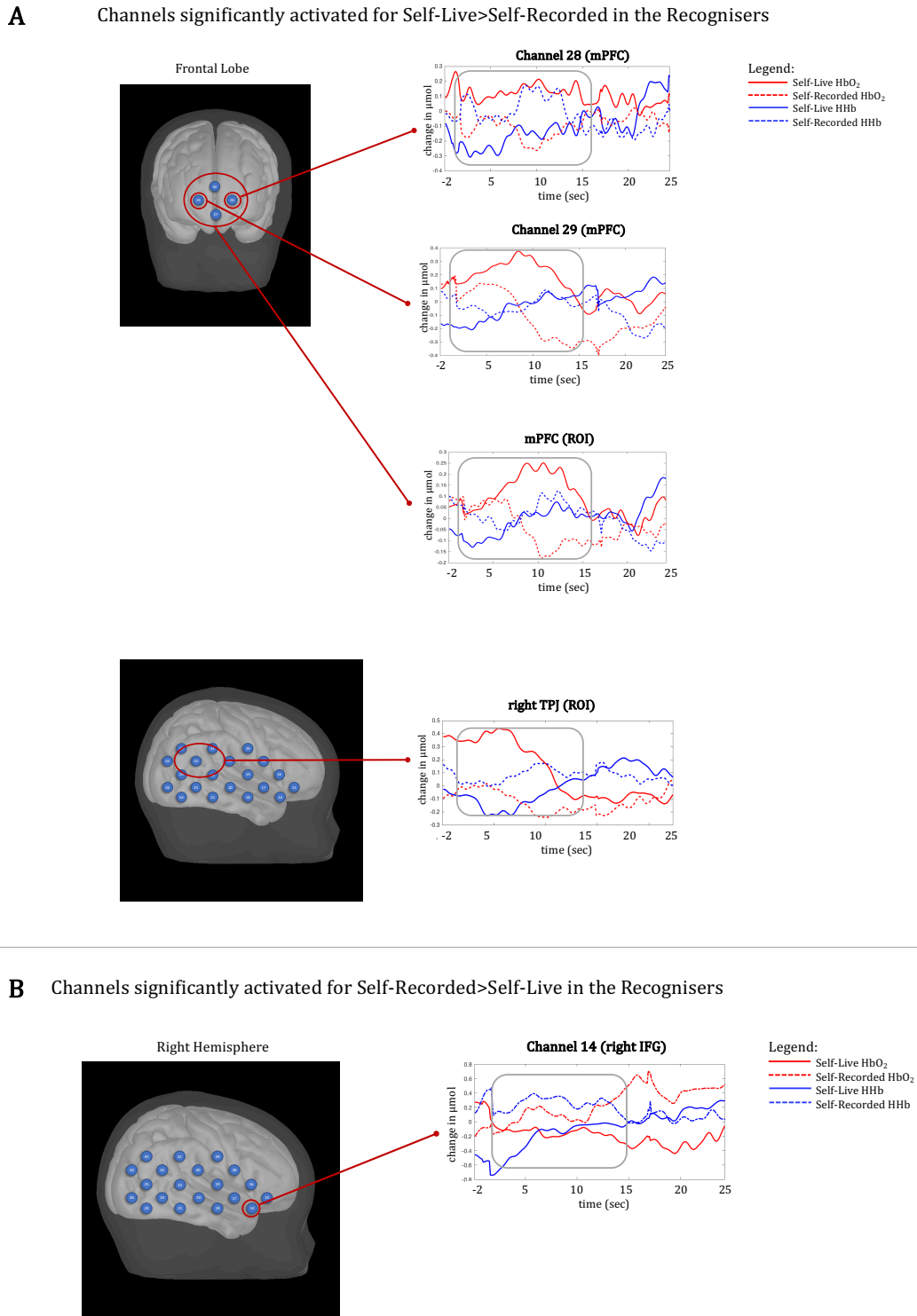
Figure 5.2 HRF plots of the channels that are significantly activated at the one-sample t-tests for the Self-Live>Self-Recorded contrast in the Recognisers and in the Non-Recognisers. A, channels significantly activated for Self-Live>Self-Recorded in the Recognisers; B, channels significantly activated for Self-Recorded>Self-Live in the Recognisers. The grey square indicates the length of the experimental trial.

As can be seen from the table, Recognisers showed activation in two channels over the mPFC (channel 28 and 29) for Self-Live>Self-Recorded. Moreover, Recognisers showed significant activation in the mPFC and the right TPJ as ROI showed significant activation for Self-Live>Self-Recorded, which also survived the FDR correction for multiple comparisons. The Non-Recognisers did not show any significant activation for Self-Live>Self-Recorded. While the Recognisers showed only one channel over the right IFG (channel 14) significantly activated for Self-Recorded>Self-Live, the Non-Recognisers showed marginally significant activation in only one channel over the Left TPJ/angular gyrus (channel 37) for Self-Recorded>Self-Live. However, none of these channels showed a significant activation after FDR correction.

As except for channel 6 and 19, all the channels exhibited a normal distribution, parametric independent t-tests were performed in order to explore whether Recognisers showed higher responses than Non-Recognisers in Self-Live>Self-Recorded contrast (see Table 5.5, Figure 5.3 and Figure 5.4).

Self-Live>Self-Recorded				
channel	brain region	*t* value	*p* value	df
Recognisers>Non-Recognisers				
25	Right TPJ	1.98	0.023*	13
28	mPFC	1.91	0.071†	17
29	mPFC	2.63	0.016*	17
37	Left TPJ/ angular gyrus	2.69	0.023*	11
42	Right TPJ	2.06	0.058†	14
	Right TPJ (ROI)	3.17	0.005**	16
Non-Recognisers>Recognisers				
/	/	/	/	/

Table 5.5 Channels where Recognisers showed greater activation for Self-Live>Self-Recorded than Non-Recognisers. **, p<0.05 that survived the FDR correction for multiple comparisons; *, p<0.05; †, p<0.065.
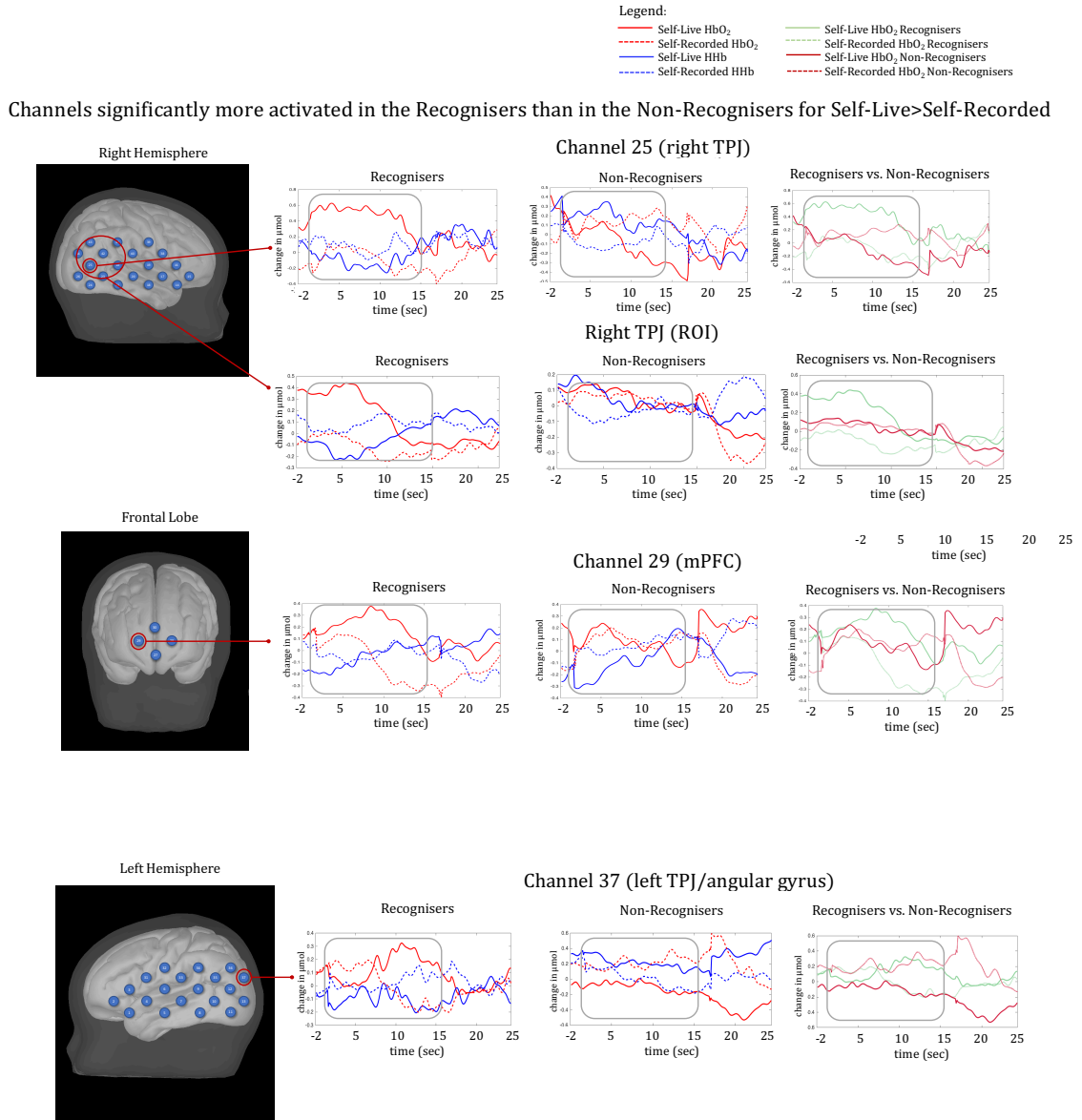
Figure 5.3 HRF plot of the channels that showed significantly greater activation the Recognisers and in the Non-Recognisers for Self-Live>Self-Recorded. The grey square indicates the length of the experimental trial.

As can be seen from the table, Recognisers showed stronger activation in two channels over the mPFC (channel 28 and 29), one channel over the left TPJ (channel 37), two spatially contiguous channels over the right TPJ (channel 25 and 42), and in the right TPJ as ROI in the Self-Live>Self-Recorded contrast, which also survived the FDR correction for multiple comparisons. However,

only channel 25 channel 37, channel 29 and the TPJ as ROI reached a significant difference, and none of these channels are contiguous. Non-Recognisers did not show any greater activation than Recognisers for Self-Live>Self-Recorded. Figure 5.4 shows the mean betas values for the channels that showed significant more activation in the Self-Live>Self-Recorded in the Recognisers rather than in the Non-Recognisers.
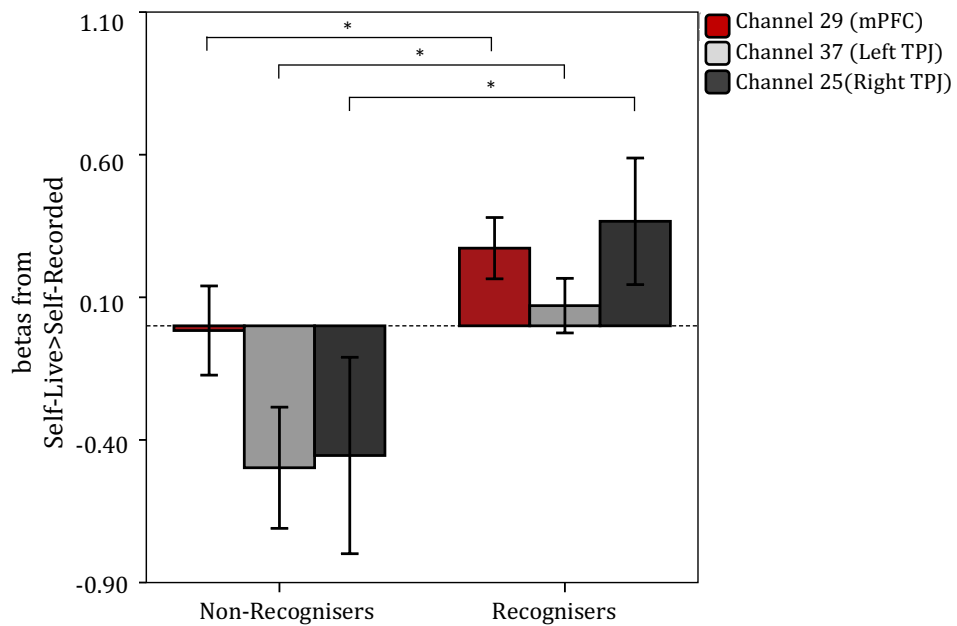
Figure 5.4 Mean betas values for Self-Live>Self-Recorded contrast in the Recognisers and in the Non-Recognisers. Error bars indicate 1 SEM; *, $p < 0.05$.

Although the right TPJ is the only ROI that is significantly more activated in the Recognisers than in the Non-recognisers in Self-Live>Self-Recorded, Figure 5.5 shows the mean betas values of three main ROIs (mPFC, the left TPJ and the right TPJ) and the HRF plots for both Recognisers and Non-Recognisers for the mPFC and the left TPJ for completeness (the HRF plot of the right TPJ can be observed in figure 5.3). As it has been previously shown, both the mPFC and the right TPJ are significantly activated in the Recognisers (see table 5.4

and figure 5.2), and the right TPJ is significantly more activated in the Recognisers than in the Non-Recognisers in Self-Live>Self-Recorded.
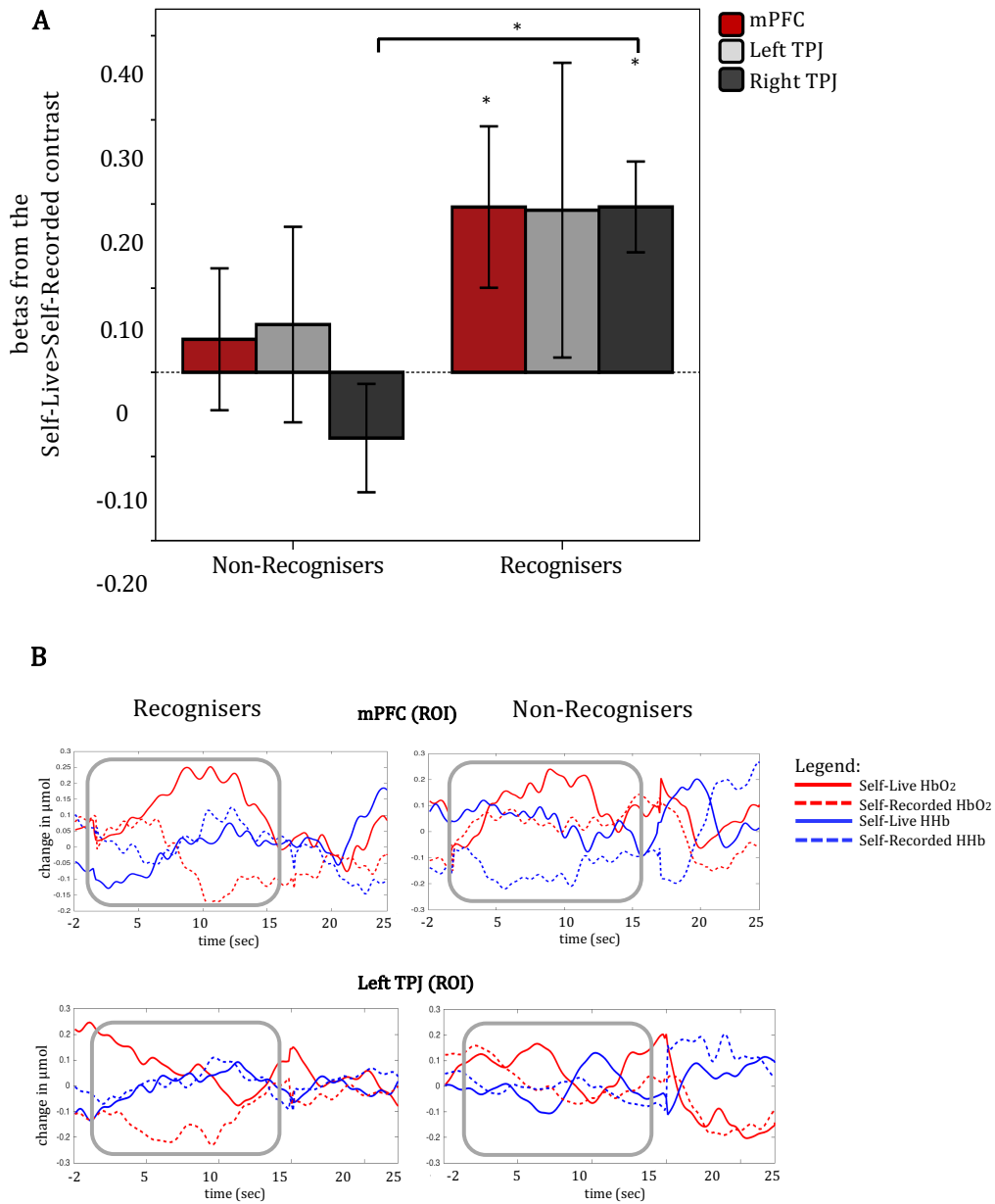
Figure 5.5 A, Mean betas values for Self-Live>Self-Recorded contrast in the Recognisers and in the Non-Recognisers. Error bars indicate 1 SEM; *, p<0.05. B, HRF plot of the mPFC and the left TPJ in the Recognisers and in the Non-Recognisers for Self-Live and Self-Recorded.

In addition, Chi-squared (χ) tests on the Self-Live>Self-Recorded betas in the ROIs were performed between Recognisers and Non-Recognisers to test whether the two subsets significantly showed a consistent pattern of brain regions engagement in the task. 8/10 Recognisers showed greater activation for Self-Live rather than Self-Recorded condition in the Right TPJ, while only 4/11 Non-Recognisers showed greater activation for Self-Live rather than Self-Recorded condition in the Right TPJ, χ^2(1, N=21)=6.07, p=0.014. No other significant differences were detected when considered other ROIs.

5.4.2.3.2 Self>Other contrast

As the previous section showed significant differences in the brain response to self-processing, engaging mPFC and TPJ significantly more in the Self-Live rather than in the Self-Recorded condition, the Self-Live condition was considered the most appropriate to be contrasted with the Other condition. To explore whether there were any brain regions that showed any differences in activation in response to Self>Other in the two groups, one-sample t-tests on the HRF contrast were performed in the Recognisers and in the Non-Recognisers by using the split analysis. Table 5.6 shows the channels that showed greater activation in Self-Live>Self-Recorded and Self-Recorded>Self-Live in Recognisers and in Non-Recognisers (see figure 5.6 for the HRF plots).

channel	brain region	t value	p value	df
Self >Other				
Recognisers				
28	mPFC	2.25	0.049*	8
30	mPFC	2.92	0.019*	8
Non-Recognisers				
/	/	/	/	/

Table 5.6 Channels that showed greater activation for Self>Other, in the whole sample and in the subsamples of Recognisers and Non-Recognisers at the MSR task. *, p<0.05.

Channels significantly activated for Self>Other in the Recognisers
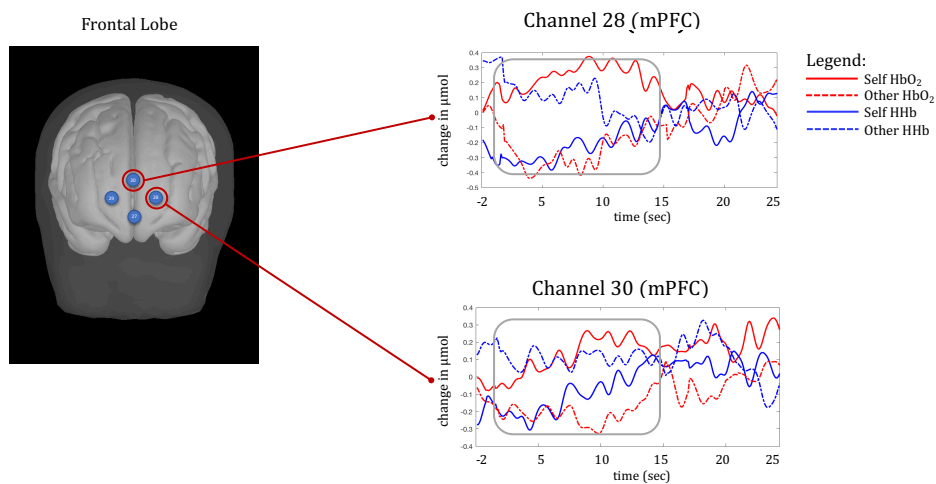
Figure 5.6 HRF plot of the channels that showed significantly greater activation the Recognisers for Self>Other. The grey square indicates the length of the experimental trial.

As can be seen from the table, the Recognisers showed grater activation in Self>Other in two spatially contiguous channels over the mPFC (channel 28 and 30, not significant after FDR correction).

5.4.2.4 Psychophysiological Interaction results

Analyses performed on brain activation revealed that the mPFC was a brain region highly engaged in self-processing, both when testing for Self-Live>Self-Recorded and Self>Other. Therefore, channels over mPFC were chosen as a region of interest for the PPI analyses. As PPI analysis estimates the coupling between two time series, in each participant both channels belonging to each connection must be included in the previous pre-processing steps. Therefore, due to the limited sample size of this study, degrees of freedom of each connection dropped considerably. For this reason, results presented hereafter in table 5.7 are related to the whole sample only, without exploring functional connectivity in the two subgroups of Recognisers and Non-Recognisers separately. None of these couples of channels survived the FDR correction for multiple comparisons.

channel	brain region	t value	p value	df
Self-Live>Self-Recorded				
27-20	mPFC – right STG	2.31	0.031*	21
27-43	mPFC – right TPJ	2.31	0.034*	16
30-36	mPFC – left TPJ	2.04	0.062†	13
Self >Other				
27-23	mPFC – right posterior temporal gyrus	2.27	0.034*	20
27-40	mPFC – right supramarginal gyrus	2.03	0.050*	21
29-15	mPFC – right IFG	1.02	0.063†	14
30-15	mPFC – right IFG	2.28	0.040*	13
30 - 39	mPFC – right precentral gyrus	2.42	0.028*	16

Table 5.7 Significant and marginally significant functional connections for Self-Live>Self-Recorded and for Self>Other in the whole sample. *, p<0.05; †, p<0.065.

As can be seen from the table, the mPFC presented greater functional connectivity with right STG (27-20), with the left TPJ (27-43), and with the right TPJ (30-36) in the Self-Live rather than in the Self-Recorded condition. Moreover, the mPFC presented greater functional connectivity with right posterior temporal gyrus (27-23), with the right supramarginal gyrus (27-40), and with the right IFG (29-15 and 30-15) and with the right precentral gyrus (30-39) in the Self-Live rather than in the Other condition.

5.4.3 Correlations between brain activation and behavioural measures

Hereafter I investigated the relationship between the haemodynamic response over the channels significantly activated for the Self-Live>Self-Recorded contrast in the Recognisers and in the Non-Recognisers (see previous table 5.5) and infants' behavioural measures. The level of performed movements in the Self-Live condition was significantly positively correlated with betas of Self-Live>Self-Recorded in channel 29, $r(22)=0.437$, $p=0.033$ (not significant after FDR correction), and almost significantly in channel 30, $r(22)=0.273$, $p=0.065$, which were both over the mPFC region (Figure 5.7). The level of performed movements in Self-Recorded condition did not show any significant correlation with channels significantly activated for the Self-Live>Self-Recorded contrast.
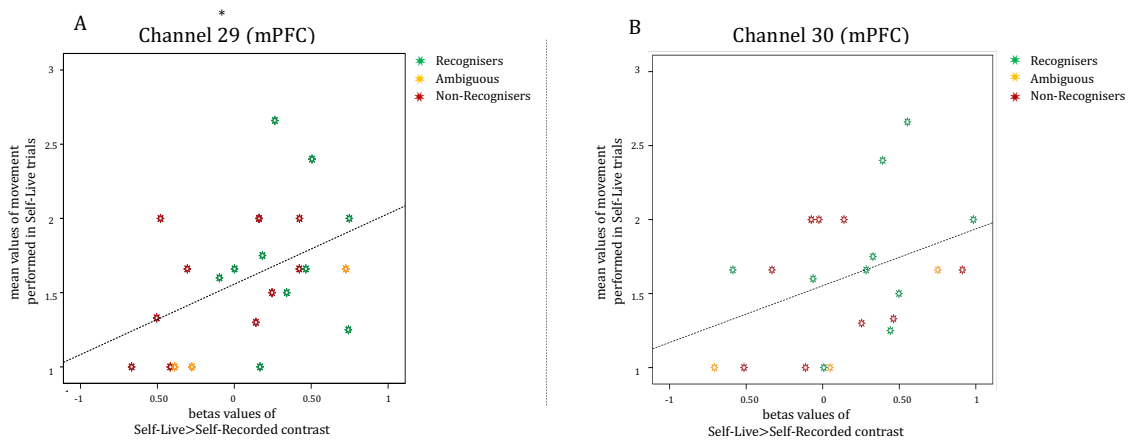
Figure 5.7 Scatterplots of the relationship between beta values of Self-Live>Self-Recorded in channel 29 (A) and channel 30 (B) and mean values of movement in Self-Live trials. *, p<0.05.

As %LT in the mirror post mark placement was higher than before only in Recognisers, suggesting this as an index of self-recognition, the relationship between betas of Self-Live>Self-Recorded in channels significantly engaged by this contrast and %LT in the mirror after the mark was placed was explored. %LT in the mirror after the mark was placed was significantly positively correlated with activity in Channel 29, $r(22)=0.403$, $p=0.050$ (not significant after FDR correction), and channel 30, $r(21)=0.430$, $p=0.041$ (not significant after FDR correction), both over the mPFC. After correcting for the outlier, the positive correlation between %LT in the mirror after the mark was placed and channel 30 was still significant, $r(23)=0.485$, N=23, $p=0.019$) (Figure 5.8).
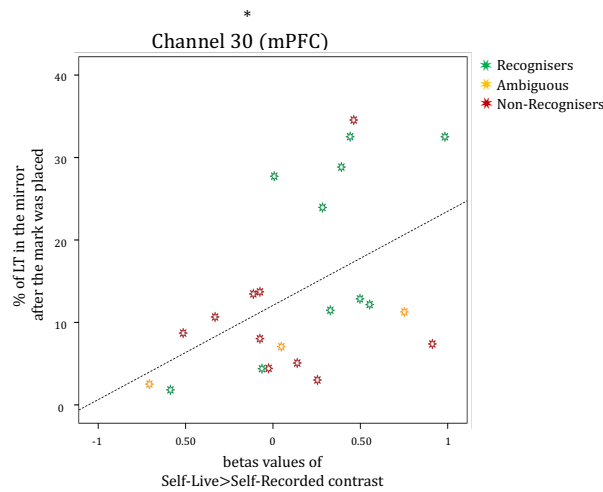
Figure 5.8 Scatterplot of the relationship between beta values of Self-Live>Self-Recorded in channel 30 and % LT in the mirror after the mark was placed (corrected for the outlier). *, p<0.05.

The relationship between the haemodynamic response over the channels significantly activated for the Self>Other contrast in the Recognisers and in the Non-Recognisers (see previous table 5.6) and infants' behavioural measures was investigated. A positive relationship between %LT in the mirror after the mark was placed was found with betas of Self>Other in channel 28, $r(20)=0.530$, $p=0.011$; corrected for the outlier: $r(20)=0.518$, $p=0.013$ (significant after FDR correction), and with channel 30, $r(19)=0.610$, $p=0.003$; corrected for the outlier: $r(19)=0.553$, N=21, $p=0.009$ (significant after FDR correction). (Figure 5.9)
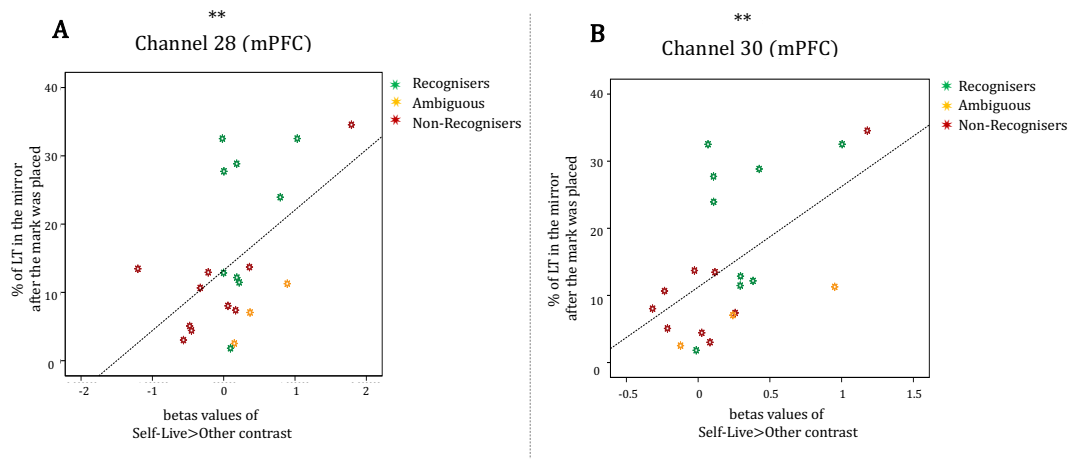
Figure 5.9 Scatterplots of the relation between beta values of Self>Other in channel 28 (A), channel 30 (B) and % LT in the mirror after the mark was placed (corrected for the outlier). **, p<0.05 that survived the FDR correction for multiple comparisons.

5.5 Discussion

The study presented in this Chapter sought to investigate the neural substrates of self-recognition in 18-month-old infants. A cohort of 18-month-olds was tested with fNIRS, manipulating the temporal contingency of their performed and observed movements while they observed videos of themselves (Self-Live and Self-Recorded conditions). Their brain activation was additionally recorded while they looked at videos of an unfamiliar infant (Other condition). Consistent with previous adult works, mPFC and TPJ were engaged by this self-recognition task. In particular, only infants with more developed self-awareness, as indexed by the MSR task, showed a significant engagement of the mPFC and the TPJ when looking at videos where they might have recognised themselves (Self-Live vs. Self-Recorded and Self vs. Other). Moreover, Recognisers showed a significantly greater activation than Non-Recognisers in Self-Live vs. Self-Recorded in channels over the mPFC and the right TPJ.

More than one finding in this study indicates that the mPFC may play a role in a component of self-processing, the detection of own movements, in the developing brain. In particular, results showed: i) a significantly greater activation of the mPFC only in Recognisers in the Self-Live vs. Self-Recorded and Self-Live vs. Other contrasts; ii) a positive relationship between the mPFC activation and two behavioural measurements collected during the MSR task and suggesting self-recognition, and the fNIRS task; iii) greater functional connections between mPFC and TPJ in the Self-Live compared to the Self-Recorded condition and in the Self rather than in the Other condition. The crucial role of the frontal cortex as a neural substrate of self-awareness was previously shown in adults (for some examples see Araujo, Kaplan, Damasio, & Damasio, 2015; Heatherton et al., 2006; Heatherton, Macrae, & Kelley, 2004; Jenkins & Mitchell, 2011; Platek, Wathne, Tierney, & Thomson, 2008), and here it has been implicated in the developing brain for the first time. Interestingly, animal studies showed that non-human primates that exhibited self-recognition in the mirror are those that have significantly more developed frontal lobes (Platek et al., 2008; Semendeferi, Damasio, Frank, & Van Hoesen, 1997). In human beings, the frontal lobes are rapidly developing between the first and third years of life (Bell & Fox, 1992; Fuster, 2003; Johnson, 2001), which is a fundamental period for developing capacities to represent self and other (Amsterdam, 1972). The essential role of the mPFC in social and cognitive abilities early in age has been demonstrated by several studies (for a review see Grossmann, 2013), and this work further supports its role in social domains, and in particular, in emerging self-processing. Studies on patients with damaged frontal lobes which showed impaired abilities to recognise their own faces, and deficits in self-evaluation, are consistent with the importance of the

frontal lobes in physical and mental self-related aspects (for a review see Feinberg & Keenan, 2005).

Functional connectivity analysis may have provided further evidence for the mPFC as a core region for self-processing, showing stronger connections between the mPFC and the right TPJ in the Self-Live compared with the Self-Recorded condition and in the Self compared with the Other condition. The limited sample sizes of the Recognisers and Non-Recognisers subsets did not allow for any functional connectivity investigation in the two groups separately. However, given the brain activation results and the positive relationship between the mPFC activation in the self-recognition task and the behavioural measures, a cautious prediction is that the mPFC-TPJ coupling related to self-recognition may be driven by the Recognisers. Future studies should build on this work by attempting to replicate these findings with larger samples of infants, so as to be able to perform more statistically meaningful functional connectivity analyses. This would allow the investigation of different brain connectivity pattern in Recognisers and Non-Recognisers, which will potentially provide support for the findings from the previous chapter on functional connectivity estimated at rest. While this work suggests that the mPFC and the TPJ work simultaneously when processing self-related stimuli, the analysis performed does not provide any further description of the relationship between these two brain regions. In the next future, I aim to apply the DCM technique validated for infant fNIRS data in Chapter 3 on this dataset, which will provide a more informative understanding of the mPFC-TPJ connections in this task, providing knowledge of directionality and causality. Platek et al. (2008) hypothesized a posterior–anterior stream of self-processing, whereby TPJ serves as a first level characterization of bodies and

faces. Later, the information might be sent to the frontal cortices to differentiate self from others at a higher level of processing, and perhaps at an abstract level of knowledge about the self (Platek et al., 2008). Further research should test this hypothesis, which will contribute to a better understanding of the brain mechanisms supporting emerging self-awareness.

Recognisers also showed stronger activation of the TPJ in Self-Live vs. Self-Recorded conditions. This is consistent with findings from adult studies which showed that this area responds to visual self-face processing stimuli (for a review see Ruby & Legrand, 2007). It has been shown that the right TPJ plays a role in maintaining a coherent sense of physical self, as disruptions in this brain region make the distinction between what is or is not part of one's body more ambiguous on the basis of multisensory evidence (Tsakiris et al., 2008). Moreover, bilateral activation of the TPJ was demonstrated to be a central hub of a complex network attributed to bodily self-awareness (Ionta, Martuzzi, Salomon, & Blanke, 2013). The role of the TPJ in self-other interaction is a focus of much interest of the recent developmental research, mostly in studies focused on theory of mind, i.e. predicting others' actions and beliefs. Recently, Hyde and colleagues found activation of the TPJ when 7-month-olds participated in a perspective taking task (Hyde, Simon, Ting, & Nikolaeva, 2018), which is consistent with adult research into the role of TPJ in mentalizing processes (for some examples see Aichhorn et al., 2009; Costa, Torriero, Oliveri, & Caltagirone, 2008; Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). The agreement on the strong link between emerging self-awareness and social cognitive abilities (Bradford, Jentzsch, & Gomez, 2015; Happe, 2003; Kyselo, 2016; Southgate, 2018; Vogeley et al., 2001; Zahavi, 2017) is consistent with empirical

research showing a shared activation of the TPJ in mentalizing and perspective taking tasks but also in self-processing tasks, when more abstract self-concepts are considered, such as self-judgments and self-evaluation (Decety & Sommerville, 2003). Future studies focusing on the relationship between the development of the sense of self and the development of theory of mind skills might better disentangle how these two psychological domains interact during the first years of life.

The different pattern of brain activation characterizing Self-Live vs. Self-Recorded conditions suggests the importance of the detection of temporal contingency in movements as a cue for self-recognition in the first years of life, which is in line with previous behavioural studies (Povinelli et al., 1996; Povinelli & Simon, 1998; Skouteris et al., 2009), and with a neuroimaging adult study (Sugiura et al., 2015). Additionally, it has been previously shown that the TPJ, the posterior temporal gyrus and the mPFC respond to the manipulation of sensory-feedback (Farrer, Franck, Paillard, & Jeannerod, 2003; Farrer & Frith, 2002; Hashimoto & Sakai, 2003; Yomogida et al., 2010), which is consistent with the brain activation showed in this task to the temporal contingency modulation.

The fact that different outcomes in the MSR task are associated with different patterns of brain activation during a different self-recognition task, might provide support for the validity of both tasks. Further evidence in support of the claim that that the MSR task indexes self-recognition is the significantly greater %LT in the mirror after the mark has been placed compared with before, and the significantly greater level of exploratory movements during self-videos exhibited by Recognisers. However, it is worth mentioning that the HRF plots showed an increase in HbO_2 blood flow in the

mPFC and in the left TPJ as ROI for Self-Live vs. Self-Recorded in Non-Recognisers as well. This might indicate a partial engagement of these regions in relation to self-recognition even in infants with less developed sense of self, suggesting that self-awareness gradually emerges throughout the second year of life (Bertenthal & Fischer, 1978; Neisser, 1993; Rochat, 1995). Therefore, one could conclude that traces or precursors of self-awareness might be present even before the self-recognition in the MSR task can be observed, given that the MSR task makes additional demands in terms of motor coordination that the fNIRS task may not. In this respect, brain responses might inform on a 'lower level' than the behavioural response exhibited during the MSR task. In fact, we might be able to detect evidence of self-recognition at an earlier age evidenced by different brain response to self and other-related stimuli than what it is indicated by the MSR task, which requires the infants to actually reach and touch the mark on their face. It would be interesting to follow the self-awareness development in the Non-Recognisers, and study how their brain response changes until the achievement of self-recognition indicated by the MSR. This might provide a deeper characterisation of the variability presented by the Non-Recognisers group, than the strict categorisation proposed by the MSR task. Moreover, future studies could use this fNIRS task in infants older than 2-3-years of age, when self-recognition in delayed videos should be established, to explore whether any differences in neural substrates of previously recorded self-videos compared to live ones are present. However, it is worth mentioning that while the engagement of the mPFC in both Self-Live vs. Self-Recorded and Self vs. Other was supported by the findings of a main effect of the Self-Live and the Self conditions in the repeated measures ANOVA analysis, no significant interaction with the MSR outcome was shown in neither

of the contrasts of interest. A post-hoc power analysis performed with G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) revealed that in order to detect a medium effect of this size as significant at the 5% level (d=0.5, Cohen, 1988), a sample of 42 participants would be required. This suggests that the sample of the current study might be underpowered to detect a significant interaction between the experimental conditions and the MSR outcome with a repeated measures ANOVA. The reader is advised to interpret results with cautious, as the significance of these findings was based on one sample t-tests and independent sample t-tests, which are less robust statistical analyses than the ANOVA approach.

Some channels over left and right STG showed a significantly greater activation in the baseline trials compared with the Other condition. None of the channels showed a significantly greater activation in the baseline trials compared with the Self-Live and Self-Recorded conditions. In this study, the baseline trials were videos of colourful swirly bubbles, with the intent of keeping participants engaged but not socially stimulated. It is possible that the STG activation is due to motion present in the baseline videos as the STG response to motion has been shown in several studies (for a review see Giese & Poggio, 2003). Therefore, it is possible that the videos used in this task as baseline might have inadvertently engaged the STG due to motion contained within them. The greater activation for Baseline compared to the Other but not for the Self conditions might be due to the fact that the baseline videos constituted a novel attractive element mainly in the first part of the block design, when they were alternated with Other trials. This is a significant limitation of this study, and thus a different choice of baseline should be examined whenever this fNIRS task will be used again in the future.

An additional limitation of the current study is the high variability and the unpredictable amount of observed and performed movements during the two Self conditions exhibited by the participants. Even though this aspect is not likely to have an effect on the results, researchers interested in using this task in the future should take into account the possibility to test more subjects than are usually tested in an fNIRS study. In fact, in this task the presence of movements in the Self trials was a necessary requirement in order to appreciate any differences between the conditions, yet this element is beyond experimental control. Therefore, this factor contributed to a very high exclusion rate, already exacerbated by the use of the high-chair. This requirement meant that many infants who sat perfectly still during the experiment did not provide the minimum number of valid trials to be included in the analysis, due to absence of their own movements needed for them to detect contingency. However, infants who moved too much were often excluded from the final sample, due to an excessive level of noise in the data. Any future replication of this study should consider an alternative to the use of the high chair, to limit the excessive exclusion rate presented by this study.

In conclusion, this is the first study to provide evidence for mPFC and the TPJ engagement in the process of self-recognition, in the developing brain. The frontal cortex in particular seems to be important for self-processing in infancy, supported by correlations with behavioural measurements and functional connectivity analysis. Only one previous study showed evidence for a role for the TPJ in self-processing in 18-month-olds (Lewis & Carmody, 2008), while this is the first time that the mPFC has been shown to be implicated in self-processing and self-other distinction in infancy. The results presented in this study are consistent with the vast literature in adults and with findings

presented in the previous chapter. This chapter and the previous one taken together have notably enriched the knowledge of the neural underpinnings of self-awareness in the developing brain and they both provide evidence to support the use of the MSR task as a valid tool to assess self-awareness in infancy. Moreover, as the study presented in Chapter 4 suggested that the significance of self-recognition goes beyond physical features, results from the current study might be interpreted as the neural underpinnings of emerging self-awareness, which comprehend, but it is not confined to, self-recognition.

While Chapter 4 and Chapter 5 provided evidence on the neural substrates of the sense of self in infancy, the next two chapters are dedicated to explore the relationship between emerging self-awareness and social interactions. This will further enrich the understanding of mechanisms underlying the development of the sense of self and how this may have an impact on social cognitive abilities.

Chapter 6

The role of self-awareness in
selective facial mimicry of linguistic
in-group over out-group members

6.1 Abstract

A link between the development of self-awareness and the interactions with others has been thought to be present from early in life. Moreover, research has shown that our identity is partially defined by our sense of belonging to certain social groups. Previous studies have shown that infants are sensitive to, and show a preference for in-group members from an early age. While this early sensitivity may be driven by a preference to interact with familiar others, it is likely that social categorisation based on self-comparison processes is only possible once infants have developed self-awareness. However, the relationship between emerging self-awareness and the tendency to identify with in-group members is still unexplored. Here I investigate this relationship by asking whether the tendency to selectively mimic linguistic in-group over out-group members is dependent on the presence of self-awareness. Mimicry, the spontaneous tendency to copy others' actions, has been shown to play an important role in social affiliation. 18-month-olds observed facial actions performed by either a native speaker or a foreign speaker model, while activation of the infants' corresponding facial muscles was measured using EMG to obtain an index of mimicry. fNIRS was simultaneously used to record neural responses to the stimuli. The MSR task assessed the infants' level of self-awareness. This study showed a general tendency to selectively mimic the facial actions of the native compared to the foreign speaker. More importantly, this effect was present only in those infants who showed self-recognition. Furthermore, Recognisers showed a greater engagement of one channel over the right posterior temporal gyrus compared with Non-Recognisers while observing facial actions performed by a native speaker rather than a foreign speaker. The facial mimicry findings are consistent with the idea that a more

advanced level of self-awareness may allow infants to identify with their social group, hereby enhancing their tendency to selectively mimic in-group members. However, the fNIRS results are less clear and not associated with the facial mimicry scores, therefore they should be interpreted with caution.

6.2 Introduction

The introduction of this thesis underlined the connection between the development of self-awareness and the interactions with others. The alternation between self-other integration and self-other distinction has been shown as fundamental for efficient social interactions (Decety & Sommerville, 2003; Sowden & Shah, 2014; Steinbeis, 2016). While the relationship between self and other representations, and social interactions, has been a topic extensively explored in adults, we know very little about the association of these two aspects in infancy. However, the idea of a social construction of the self recently proposed (Prinz, 2012; Rochat, 2003; Rochat & Zahavi, 2011) seems to favour the study of emerging self-awareness in relation to the social environment. In fact, the emerging sense of self likely has implications for the development of other social cognitive abilities, such as perspective taking, imitation, empathy, emotion recognition, and *vice versa* (Carpendale & Lewis, 2006).

Research has shown that our identity is partially defined by our sense of belonging to certain social groups (Bodenhausen, Kang, & Peery, 2012; Castelli, Tomelleri, & Zogmaister, 2008; Dasgupta, 2004; Devine, 1989; Fiske & Neuberg, 1990; Tajfel, 2010; Tajfel & Turner, 1986). A large body of research in social psychology has explored our natural disposition to perceive people as belonging to social categories, and has shown that our behaviours towards others are influenced by their group membership. For example, it has been shown that people judge members from their own group more positively (Gerard & Hoyt, 1974; Schmitt & Branscombe, 2001) they allocate more resources to them (Tajfel, 1978) and they are more likely to help in-group compared to out-group members (Levine, Prosser, Evans, & Reicher, 2005).

Social categorisation and preferences for in-groups have been shown to have their basis early in infancy (Liberman, Woodward, & Kinzler, 2017; Ziv & Banaji, 2012). For example, 10-month-olds prefer to interact with and to accept a toy from a native speaker compared to a foreign speaker (Kinzler, Dupoux, & Spelke, 2007) and they are more likely to choose a puppet who shares their food preferences (Mahajan & Wynn, 2012). Language seems to be a particularly strong cue to group membership (Liberman et al., 2017), with several studies demonstrating a preference for linguistic in-group compared to out-group members. For example, 12-month-olds are more likely to choose foods endorsed by a native speaker rather than by a foreign speaker (Shutts, Kinzler, McKee, & Spelke, 2009) and, by the second year of life, infants imitate novel object-directed actions of a linguistic in-group member more faithfully than actions performed by a linguistic out-group member (Buttelmann, Zmyj, Daum, & Carpenter, 2013; Howard, Henderson, Carrazza, & Woodward, 2015). Together these findings show an early-developing preference to interact with members of the same linguistic group. Interestingly though, mechanisms underlying the preference for linguistic in-group members might not be the same over the course of the development. Initially, the preference for linguistic in-group members in young infants could be driven by a preference for stimuli that the infant frequently encounters (Liberman et al., 2017). The finding that infants who are constantly exposed to different races do not exhibit an own-race preference seems to be consistent with this idea (Bar-Haim, Ziv, Lamy, & Hodes, 2006; Gaither et al., 2014). However, it is plausible that later in development self-identification and self-comparison processes may start to influence social categorisation. That is, whereas early preferences for in-group members may arise from familiarity, later preferences could plausibly be

influenced also by a process of comparing the other with the self. One of the key turning points in this respect may be the development of the sense of self, arising sometime between 18 and 24 months of age, which could permit this process of self-comparison. For example, to exhibit a preference for someone who has been arbitrarily assigned to the same group as yourself with a particular colour t-shirt (Dunham, Baron, & Carey, 2011; Tajfel, 1974), one would need to understand that we both share this characteristic. This understanding would seem to require a process of self-other comparison, or recognizing self-other similarity. To do this, a minimum requirement should be the development of self-awareness.

Although self-awareness is likely to affect how infants perceive, identify, and interact with others, to date we know little about how its development might influence infants' social categorisations. In this study, I investigate the relationship between the development of the sense of self during the second year of life and the preference for in-group members by exploring whether the tendency to selectively mimic native over foreign speakers is dependent on the presence of a sense of self. As explained in Chapter 1, mimicry plays a pivotal role in shaping social interactions, building relational bonds in every-day life (Lakin & Chartrand, 2003; Lakin et al., 2003) and increasing affiliation and cooperation (Chartrand et al., 2012; Cheng & Chartrand, 2003; Fischer et al., 2013; Stel et al., 2010). Several studies have explored the social modulation of mimicry in adulthood. For example, it has been shown that eye contact enhances mimicry (Wang, Newport, & Hamilton, 2011), and that people mimic more facial expressions of characters that have been judged positively (Likowski et al., 2008). Moreover, the influence of social groups in mimicry has been also explored in adults, showing that people mimic

more in-group that out-group members, and that among the in-group members people mimic more those that they evaluate more positively (Yabar, Johnston, Miles, & Peace, 2006). People selectively mimic ingroup and outgroup depending on their facial emotion expressions (Bourgeois & Hess, 2008). Despite the substantial volume of literature that explored the social modulation of mimicry in adults, research has only recently started to elucidate how social factors influence mimicry throughout the first few years of life. In a previous study from my team, 11-month-old infants showed greater facial mimicry of a model who spoke their native language compared to a foreign speaker (de Klerk et al., under review). At this age, it seems unlikely that the infants performed a conscious comparison between themselves and the model, or that they identified with her based on a process of self-comparison with their own linguistic group. Instead, the selective mimicry at this age may have mainly been driven by infants' tendency to prefer to interact with familiar others (Begus, Gliga, & Southgate, 2016; Liberman et al., 2017). However, the mechanisms underlying these selective mimicry processes may change once infants develop a sense of self, allowing them to generate more conceptually-rich social categories, and to start to actively categorise others in relation to their own social identity. Previous research has already demonstrated an association between self-recognition and the tendency to imitate others (Asendorpf & Baudonnière, 1994; Asendorpf, Warkentin, & Baudonni, 1996; Zmyj, Prinz, & Daum, 2013), but how emerging self-awareness interacts with the tendency to *selectively* imitate in-group others is still unknown.

In terms of neural activation, it is interesting to highlight that some of the regions that have been related to self-processing, are also involved during imitation. There are evidence of the MNS involved several during self-

processing tasks in adults (Kaplan et al., 2008; Uddin et al., 2007, 2005), but there is also an extensive literature that showed that the MNS is engaged during imitative behaviours (Iacoboni, 2005; Rizzolatti & Craighero, 2004). Given the positive association between imitation and emerging self-awareness (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013), the MNS has been proposed as a common neural substrate underlying both imitation and the sense of self, even during the first years of life. This functional substrate should support the integration between self and other perspectives (Iacoboni & Dapretto, 2006; Iacoboni, 2009). However, there are no evidence to support this hypothesis in developmental neuroscience.

Not only the MNS, but also the mPFC and the TPJ, two core regions of self-processing (for example see Arzy, Thut, Mohr, Michel, & Blanke, 2006; Jenkins & Mitchell, 2011), are also activated during imitation, in particular during inhibition of imitation (Brass, Ruby, & Spengler, 2009; Spengler et al., 2010; Spengler, Von Cramon, & Brass, 2009; Wang, Ramsey, Hamilton, 2011; Wang & Hamilton, 2012). A role for the mPFC has been also shown in social categorization, with an increasing activation related to in-group versus out-group stimuli, in both existing (Morrison, Decety, & Molenberghs, 2012) and newly created groups (Molenberghs, 2013). The authors associated the activation of the mPFC selectively for in-group stimuli with activation of this regions for self-processing, hypothesizing an overlapping neural activity as a marker of the social identity and group membership as parts of the self (Morrison, Decety, & Molenberghs, 2012). This is consistent with a previous study that found the activation of the mPFC for in-group favouritism during a minimal group paradigm (Volz, Kessler, & von Cramon, 2009). Both the mPFC and the TPJ have been shown to be activated when interacting with in-group

members during a decision making task, as a possible marker of self-comparison with the in-group features with self-referential mental activity (Rilling, Dagenais, Goldsmith, Glenn, & Pagnoni, 2008),

The TPJ activation is related to the ability to distinguish self- from other-generated actions (Decety & Lamm, 2007; Steinbeis, 2016), and an increase in TPJ activation has been shown during mimicry in affiliative contexts, suggesting that this region may play an important role in situations where salient affiliative signals increase mimicry, requiring one to disambiguate one's own actions from those of others' (Rauchbauer, Majdandžić, Hummer, Windischberger, & Lamm, 2015). Despite this extensive volume of neuroimaging literature that explores the relationship between self and other representations and imitation in adults, to date there is no evidence from infant studies showing an engagement of brain regions typically associated with self-awareness in social interactions. However, an investigation into this could shed light on the mechanisms that underlie the relationship between these two variables during the first years of life.

The current study aimed to investigate whether the emergence of the sense of self modulates the infants' tendency to selectively mimic linguistic in-group members and whether infants with more developed self-awareness activate different brain regions for facial actions performed by in-group rather than out-group members. Infants were tested with the MSR task to assess their level of self-awareness. Hereafter, activation of 18-month-olds' mouth and eyebrow muscle regions was measured using EMG - as an index of mimicry - while they observed facial actions performed either by a native or a foreign speaker. I expect to find a greater tendency to mimic facial actions performed by the native model in Recognisers than in Non-Recognisers. Simultaneously,

infants' brain activation was recorded using fNIRS. I hypothesize a greater engagement of MNS regions (i.e. IFG and STG) supporting a higher level of mimicry of the native model displayed by Recognisers. Moreover, I expect to find a crucial role of the mPFC that supports selective mimicry of in-group vs. out-group, especially in Recognisers. In particular, the mPFC activation during actions performed by the native model would be consistent with the role of the frontal cortex in social categorisation in relation to in-group members, as acknowledge as similar to oneself (Molenberghs, 2013; Morrison et al., 2012; Rilling et al., 2008; Volz et al., 2009). Alternatively, the mPFC activation during actions performed by the foreign model would be consistent with its role of inhibition of mimicry, modulating the activation of regions typically engaged in mimicry, such as the IFG and the STG, as previously shown in adults (Brass et al., 2009; Spengler et al., 2010, 2009; Wang et al., 2011; Yin Wang & Hamilton, 2012). Functional connectivity analysis can particularly inform on this latter hypothesis, investigating how regions known to be involved in mimicry are positively or negatively activated together, elucidating the role of the mPFC in respect to the other brain areas.

6.3 Methods

6.3.1 Participants

47 18-month-olds provided sufficient data to be included in the EMG analyses (26 males, age mean $\pm$ SD = 555.17 $\pm$ 12.93 days) and 57 18-month-olds provided sufficient data to be included in the fNIRS analyses (28 males, age mean $\pm$ SD = 552.88 $\pm$ 12.08 days). 36 participants contributed data both to the EMG and NIRS analyses.

48 infants were excluded from the EMG analyses due to: technical error (N=13), because they did not provide enough trials for analyses due to: fussiness (N=10), inattentiveness (N=23), or because they constantly hiccupped or repeatedly put their fingers in their mouth (N=2) - factors which were likely to have resulted in EMG activity unrelated to the stimulus presentation. 55 infants were excluded from the NIRS analyses due to (i) a refusal to wear the NIRS cap (N=10), (ii) excessive number of bad channels (>30% of the channels excluded due to poor light intensity readings) (N=14), (iii) because they did not provide the minimum of 3 good trials per condition due to fussiness (N=15) or inattentiveness (N=14), or technical error during the NIRS acquisition (N=2).

19 out of the 47 participants included in the EMG analyses and 22 out of the 57 participants included in the fNIRS analyses had also been exposed to the stimuli at 11 months[15] (de Klerk et al., under review). 6 of the infants included in the analyses were bilingual but heard English at least 60% of the time. In these participants, bilingualism might weaken the in-group/out-group distinction, although there is evidence that not only monolingual but also bilingual children prefer in-group members who use a familiar language (Souza, Byers-Heinlein, & Poulin-Dubois, 2013).

Power analysis performed with G*Power (Faul et al., 2007) revealed that in order to detect a medium effect of this size as significant at the 5% level (d=0.5, Cohen, 1988), a sample of 42 participants would be required.

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[15] Unfortunately, due to the small proportion of overlap between the participants who were included in the final analyses at 11 months and at 18 months (N=9) we are unable to perform any longitudinal comparison.

All included infants were born full-term, healthy and with normal birth weight. Written informed consent was obtained from the infant's caregiver prior to the start of the experiment.

6.3.2 Mirror self-recognition task

Prior to the fNIRS task, self-awareness was assessed with the MSR task (Amsterdam, 1972). The task took place in a room with a mirror positioned against one of the walls. For 27 infants, one camera was used to record the task, while for the rest of the sample three cameras recording from different angles were used. The MSR task procedure and the coding scheme used was the same as described in Chapter 4, section 4.3.2.

Two experimenters independently classified the infants as 'Recognisers', 'Ambiguous', or 'Non-Recognisers' based on their behaviours in front of the mirror after the red mark was placed, and they agreed in 94% of the cases. Discrepancies were discussed until agreement was reached.

6.3.3 EMG and fNIRS recording

6.3.3.1 Stimuli and procedure[16]

See section 2.3.2 for experimental set-up, fNIRS cap application and testing procedure.

Infants were presented with videos of two models who spoke either English (Native speaker) or Italian (Foreign speaker) (see Figure 6.1). Infants first observed 2 Familiarisation trials during which the models labelled familiar

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[16] Stimuli and procedure for this experiment were the same as those in our previous experiment with 11-month-olds (de Klerk et al., under review).

objects in either English or Italian. Thereafter, Reminder trials – in which one of the models labelled a familiar object, and Facial Action trials – in which the same model performed facial actions such as mouth opening and eyebrow raising- alternated. Facial Action trials started with 1000 ms during which the model did not perform any actions, followed by her performing three repeats of the same facial action, each lasting 3000 ms. The Reminder and Facial Action trials were alternated with pictures of houses, landscapes, and landscapes with and animals with a duration of 8000 ms to allow the haemodynamic response to return to baseline levels. The order of trials within the Familiarisation phase was randomised and the order of trials in the Reminder and Facial Action phase were pseudo-randomised to ensure that infants saw roughly the same number of eyebrow and mouth actions. The EMG analyses focused on the Facial Action trials. The role of the models (Native vs. Foreign speaker) was counterbalanced across infants[17].
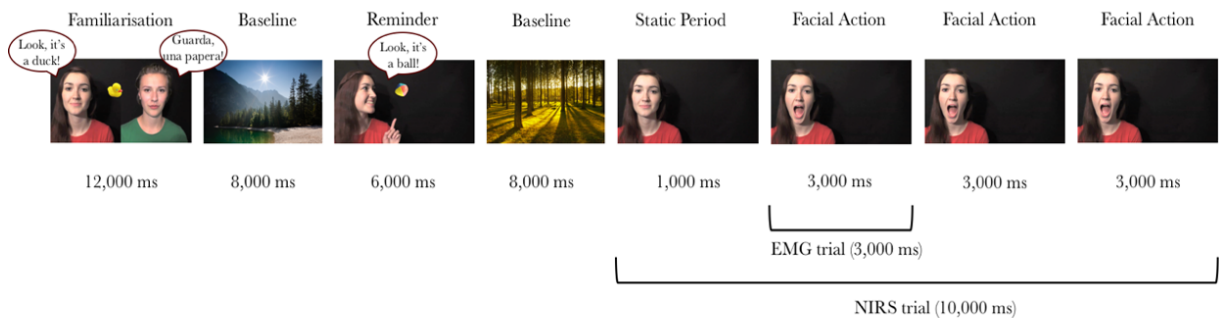
Figure 6.1 Schematic overview of the stimulus presentation (image reproduced with permission from de Klerk et al., under review).

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[17] For all of the participants who had been tested with the same paradigm at 11 months, the native speaker model and the foreign speaker model were the same at the 18-month visit, to avoid weakening the effect in case infants may have remembered which model was the native speaker in the previous testing session.

6.3.3.2 EMG recording and processing

Bipolar EMG recordings were made using paediatric surface Ag/AgCl electrodes that were placed on the cheek and forehead with an inter-electrode spacing of approximately 1 cm to measure activation over the masseter and frontalis muscle area, respectively (see Figure 6.2). The electrodes were connected to Myon wireless transmitter boxes that amplified the electrical muscle activation, which was recorded using ProEMG at a sampling rate of 2000 Hz. After recording, the EMG signal was filtered (high-pass: 30 Hz, low-pass: 500 Hz) smoothed (root mean square over 20 ms bins), and rectified. Each 3,000 ms period during which a facial action was performed was treated as a separate trial. The EMG signal was segmented into 3,000 ms epochs, and the average activity in each epoch was normalised (i.e. expressed as z-scores) within each participant and each muscle group (masseter and frontalis region), before the epochs for each trial type were averaged together. This allows for meaningful comparison of values between muscle regions, as well as reducing the impact of individual differences in reactivity on the group mean. Hereafter we calculated a mimicry score per trial by subtracting EMG activity over the non-corresponding muscle region from EMG activity over the corresponding muscle region (e.g. on an eyebrow trial we subtracted activity over the masseter region from activity over the frontalis region, so that a more positive score indicates more mimicry).

6.3.3.3 fNIRS recording and data analysis

See section 2.2.1 for information about the fNIRS cap and the arrays design. See section 2.2.3 for information about the NIRS system properties and the recording.

In this study, participants were tested with the two different fNIRS arrays described in Chapter 2, section 2.2.1[18]. The first array design, including 30 channels, was used to test 21 out of the 57 participants; the second design, including 44 channels, was used to test 36 out of the 57 participants. Both configurations shared the design and the location of the channels covering frontal, inferior frontal and temporal regions (30 channels out of 44), therefore the data acquired with the two different configurations can be analysed together. As mentioned in Chapter 2, the cap size was adapted to the infant's head circumference. Table 6.1 lists information concerning S-D separation and the number of infants included in the analysis who were tested with each cap size.

Cap size	S-D temporoparietal lobe	S-D frontal lobe	Number of participants
48 cm	25 mm	30 mm	36/57
50 cm	26 mm	31 mm	21/57

Table 6.1 S-D separation and number of infants tested with each cap size.

Figure 6.2 shows an example of infants wearing the two headgear configurations with the EMG electrodes.

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[18] The 44-channel configuration was an extension of the 30-channel configuration and included two additional rows of optodes that added 7 channels per hemisphere, in a superior location to the two existing lateral arrays. This allowed to improve detection of TPJ activation, a core region of interest for this study.

Configurations	Temporoparietal arrays	Frontal array
30 channels and EMG electrodes		
44 channels and EMG electrodes		
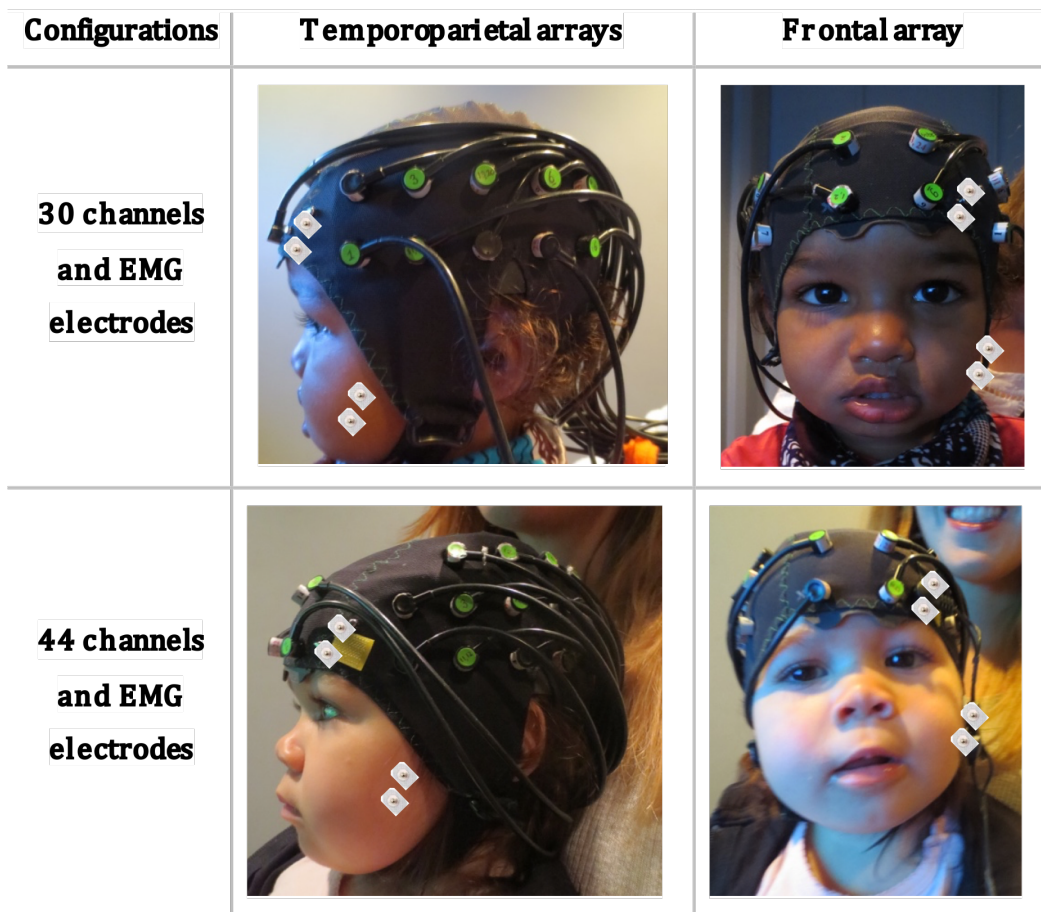
Figure 6.2 Infants wearing the fNIRS cap. A graphical representation of the EMG electrodes on the masseter and the frontalis regions was added on the pictures. The first row represents the cap with the 30-channel configuration, and the second row the cap with the 44-channel configuration (Parents provided consent for these images to be used).

6.3.4 Video coding and data exclusion

EMG trials in which the infant did not see at least two thirds of the action, or trials during which the infant vocalised, yawned, smiled, cried, or had something in their mouth (e.g. their hand) were excluded from the analyses as EMG activity in these cases was most likely due to the infants' own actions. Only infants with at least 2 trials per trial type (Native Mouth, Native Eyebrow, Foreign Mouth, Foreign Eyebrow) and at least 6 trials per condition (Native

Facial Actions and Foreign Facial Actions) were included in the analyses. Participants contributed an equal number of trials to the Native and Foreign condition (number of trials for the Native condition, mean $\pm$ SD = 12.30 $\pm$ 3.61; number of trials for the Foreign condition, mean $\pm$ SD = 11.74 $\pm$ 3.80), $t(46)$=1.36, p=0.406.

fNIRS trials in which the infant did not attend to at least 2 of the 3 facial actions, in addition to the general trial exclusion criteria[19], were excluded from further analyses (see section 2.3.1 for more details on trial exclusion). Only infants with at least 3 trials per experimental condition were included in the NIRS analyses (Lloyd-Fox, Blasi, Everdell, & Johnson, 2011; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014). Participants contributed an equal number of trials to the Native and Foreign condition (number of trials for the Native condition, mean $\pm$ SD = 4.84 $\pm$ 1.14; number of trials for the Foreign condition, mean $\pm$ SD = 4.88 $\pm$ 1.32), $t(56)$=0.26, p=0.792.

6.3.5 fNIRS data processing and analysis

See section 2.2.3 for information about the NIRS system properties and the recording. fNIRS data were pre-processed in Homer_2 (Huppert et al., 2009) following the pre-processing pipeline described in section 2.3.2. After the pre-processing, data were analysed using a combination of custom Matlab scripts and the SPM-NIRS toolbox (Ye et al., 2009), as described in section 2.3.3. For each participant, a design matrix was built modelling the 2 experimental conditions (Native Facial Actions, Foreign Facial Actions), the 2 Reminder

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[19] Trials were excluded if participant looked at the parent or anything social, if the experimenter or the parent talked.

conditions (Reminder Native, Reminder Foreign) and the baselines. Trials excluded due to the cleaning in the pre-processing or due to behavioural coding were removed from the analyses. Betas extracted from the design matrix were used to calculate contrasts of interest for each participant (Native Facial Actions>Foreign Facial Actions), and then submitted to statistical tests. Analysis of fNIRS data were based on changes in HbO_2, as fNIRS studies with infants do not consistently find statistically significant HHb changes (for some examples see: Grossmann, Cross, Ticini, & Daum, 2013; Lloyd-Fox et al., 2010; Lloyd-Fox, Széplaki-Köllod, Yin, & Csibra, 2015; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014). However, the pattern of HHb is plotted for completeness. As explained in section 2.3.3.1, fNIRS results are corrected for multiple comparisons using the FDR approach.

To further explore the role of the mPFC during facial actions performed by different social groups, functional connectivity was estimated using PPI (see section 3.1.2 for more details) (Friston et al., 1997). Consistently with the functional activation analysis, PPI analysis is performed only on the HbO_2 signal. In order to ensure statistical reliability, PPI results are corrected for multiple comparisons with FDR, as for the functional activation results.

6.4 Results

6.4.1 EMG

6.4.1.1 Characteristic of the sample

Out of the 47 infants that contributed data to the EMG analyses, 23 were classified as Recognisers and 24 as Non-Recognisers (see coding scheme described in paragraph 2.2). None of the infants included in the EMG analyses

were classified as Ambiguous. The two groups did not show any significant difference in parameters that could potentially affect mimicry outcomes, such as age (mean $\pm$ SD Recognisers = 555.52 $\pm$ 15.22 days, mean $\pm$ SD Non-Recognisers = 554 $\pm$ 10.93 days), $t(45)=0.13$, $p=0.89$, sex (Recognisers = 13 females, 10 males; Non-Recognisers = 13 females, 12 males), $\chi^2(1, N=47)=0.025$, $p=0.871$. A repeated measures ANOVA with number of included trials per condition (Native vs. Foreign) as within subject factor and MSR outcome (Recognisers vs. Non-Recognisers) as between subject factor demonstrated a significant interaction between number of trials per condition and MSR, $F(1, 45) = 6.70$, $p=0.013$, $\eta_p^2=0.130$. Follow up t-tests showed that there was no difference in the number of included trials between the two conditions in the Non-Recognisers, $t(23)=0.747$, $p=0.463$, but that in the Recogniser group there were significantly more valid trials in the Native condition compared to the Foreign condition, $t(22)=3.001$, $p=0.007$. In order to explore whether this could be related to a difference in the level of visual attention in the two groups, I performed a repeated measures ANOVA with number of trials excluded because of not looking per condition (Native vs. Foreign) as within subject factor and MSR outcome (Recognisers vs. Non-Recognisers) as between subject factor. The repeated measures ANOVA showed a non-significant interaction between number of trials excluded because of not looking per condition and MSR, $F(1, 45) = 0.28$, $p=0.264$, $\eta_p^2=0.028$.

6.4.1.2 EMG results

A repeated measures analysis on the Mimicry scores (activation over the corresponding muscle region minus activation over the non-corresponding

muscle region) with Linguistic group (Native vs. Foreign speaker), and Action type (Mouth vs. Eyebrow) as within subject factors demonstrated a significant main effect of linguistic group, $F(1, 45)=5.089$, $p=0.029$, $\eta_p^2=0.099$. Infants showed significantly greater mimicry in the Native compared to the Foreign condition (Figure 6.3-A). A repeated measures analysis on the Mimicry scores (activation over the corresponding muscle region minus activation over the non-corresponding muscle region) with Linguistic group (Native vs. Foreign speaker), and Action type (Mouth vs. Eyebrow) as within subject factors and the outcome on the MSR test as between subject factors (Recogniser vs. Non-Recogniser) did not show a significant interaction between Group and MSR, $F(1, 45)=0.009$, $p=0.924$, $\eta_p^2=0.001$ (Figure 6.3-B). However, a post-hoc paired-samples t-test on the average mimicry scores in the Native and Foreign condition showed a significant difference only in the Recognisers, $t(22) = 2.15$, $p = 0.043$, and not in the Non-Recognisers, $t(23) = 1.32$, $p = 0.198$ (Figure 6.3-C). Moreover, the average mimicry score in the Native condition was significantly different from 0 only in the Recognisers, $t(22) = 2.49$, $p=0.021$, and not in the Non-Recognisers, $t(23) = 0.23$, $p=0.841$.
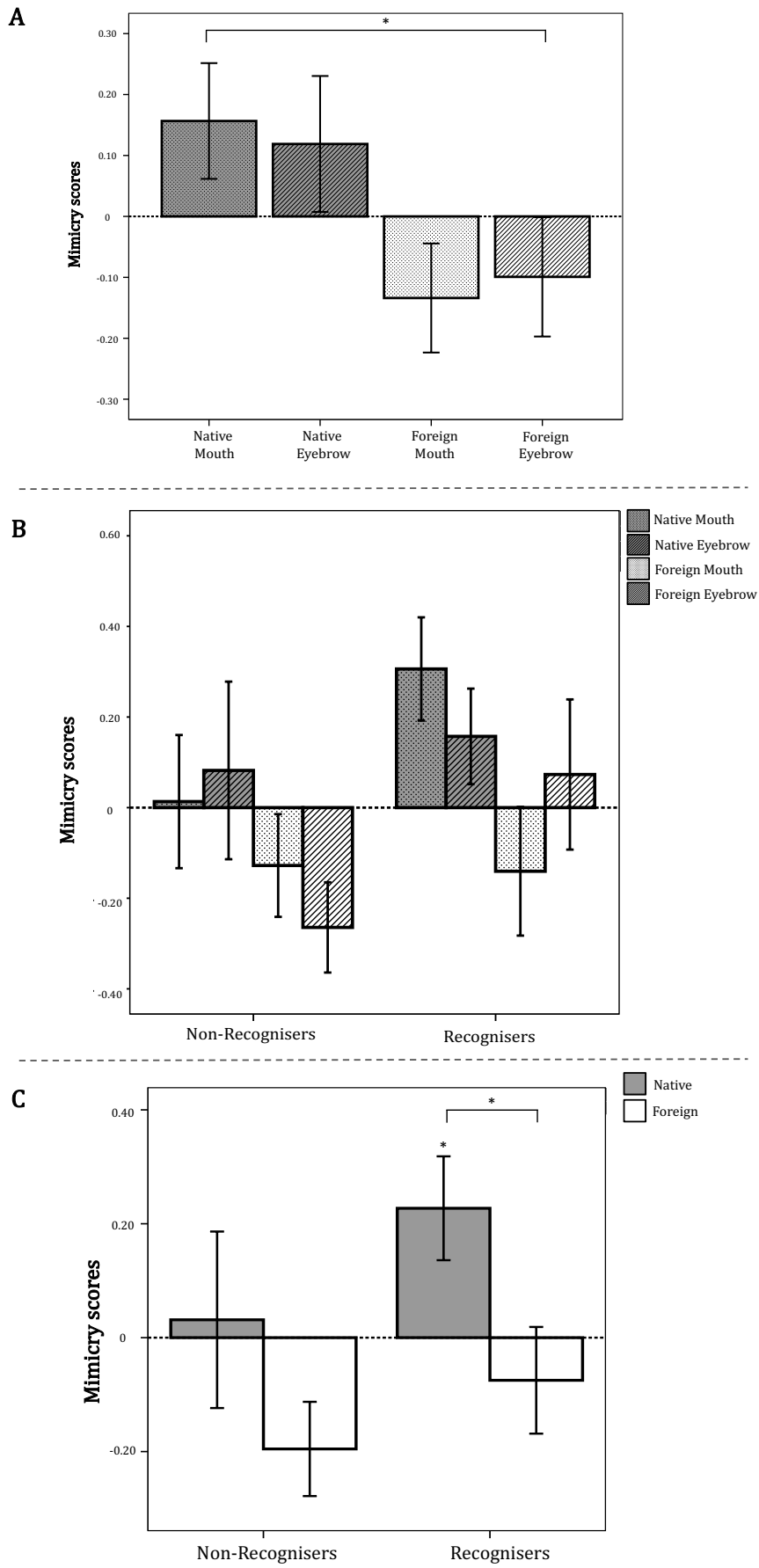
Figure 6.3. Graphical representation of the EMG results. A, Mean mimicry scores for the eyebrow and mouth actions in the Native and Foreign Mimicry condition. B, Mean mimicry scores for the eyebrow and mouth actions in the Native and Foreign condition displayed by Recognisers and Non-Recognisers at the MSR task. C, Average mimicry scores in the Native and Foreign condition in Recognisers and Non-Recognisers. The grey bars represent mimicry scores in the Native condition, the white bars represent scores in the Foreign condition, the dots pattern represent mimicry scores of the mouth actions, the stripes pattern represent mimicry scores of the eyebrow actions. Error bars indicate 1 SEM, * p < .05.

Correlational analyses to assess whether the mimicry scores were associated with the number of valid trials were performed. No relationship between the number of included trials and the mimicry scores in the Native condition was found, $r(45)=-0.480$, $p=0.750$ or between the number of valid trials and the mimicry scores in the Foreign condition, $r(45)=0.160$, $p=0.283$. As there was a significant difference in the number of valid trials between the two conditions in the Recogniser group specifically, I also performed these correlational analyses for the Recogniser group separately. There was no relationship between the number of included trials and the mimicry scores in the Native condition, $r(21)=0.273$, $p=0.207$ or between the number of valid trials and the mimicry scores in the Foreign condition, $r(21)=0.269$, $p=0.226$ in this group.

Considering that a subset of the included infants had already been exposed to the stimuli before (see de Klerk et al., under review), I also tested whether this may have influenced the results. A repeated measures analysis on the Mimicry scores (activation over the corresponding muscle region minus activation over the non-corresponding muscle region) with Linguistic group (Native vs. Foreign speaker), and Action type (Mouth vs. Eyebrow) as within subject factors and with the previous exposure to the stimuli as a between

subjects factor still demonstrated a significant main effect of linguistic group, $F(1, 45)=4.49$, $p=0.040$, $\eta_p^2=0.091$, and no significant interaction with previous exposure. A repeated measures analysis on the Mimicry scores (activation over the corresponding muscle region minus activation over the non-corresponding muscle region) with Linguistic group (Native vs. Foreign speaker), and Action type (Mouth vs. Eyebrow) as within subject factors and outcome on the MSR test as between subject factors (Recogniser vs. Non-Recogniser), and with the previous exposure to the stimuli as a between subjects factor demonstrated a significant main effect of linguistic group, and no significant interaction between Group and MSR, $F(1, 45)=0.037$, $p=0.849$, $\eta_p^2=0.001$. Thus, the previous exposure to the stimuli did not affect this result.

6.4.2 fNIRS

6.4.2.1 Characteristic of the sample

Out of the 57 infants that contributed data to the fNIRS analyses, 25 were classified as Recognisers and 31 as Non-Recognisers (see coding scheme described in paragraph 2.2). Only one participant was classified as Ambiguous. Recognisers and Non-Recognisers did not show any significant difference in parameters that could potentially affect infants' brain response, such as age (mean $\pm$ SD Recognisers $= 555.40 \pm 14.09$ days, mean $\pm$ SD Non- Recognisers $= 553.25 \pm 10.46$ days), $t(54)=0.26$, $p=0.795$, or gender (Recognisers,10 females, 15 males; Non-Recognisers $=$ 18 females, 13 males), $\chi^2(1, N=56)=1.48$, $p=0.223$. A repeated measures ANOVA with the number of valid trials per condition (Native vs. Foreign) as a within subject factor and MSR outcome (Recognisers vs. Non-Recognisers) as a between subject factor showed that there was neither a main effect of condition nor an interaction

between number of trials per condition and MSR, $F(1, 54)=0.143$, $p=0.707$, $\eta_p^2=0.003$.

6.4.2.2 fNIRS results

6.4.2.2.1 Native Facial Actions>Baseline and Foreign Facial Actions>Baseline

To explore which channels were activated by the task, both the Native (speaker) Facial Actions and the Foreign (speaker) Facial Actions conditions were contrasted to the Baseline. Table 6.2 shows the channels that are statistically significantly activated and marginally statistically significantly activated by the task.

channel	brain region	t value	p value	df
Native Facial Actions>Baseline				
28	mPFC	2.04	0.046*	54
29	mPFC	2.27	0.027*	55
43	Right TPJ	1.92	0.064†	30
Foreign Facial Actions>Baseline				
1	Left IFG	2.93	0.005*	43
6	Left STG	2.13	0.038*	49
16	Right IFG	2.11	0.039*	56
24	Right posterior temporal gyrus	2.57	0.013*	51
27	mPFC	3.55	0.001**	53
28	mPFC	2.23	0.03*	54
29	mPFC	2.38	0.021*	54

Table 6.2 Channels that showed a significant (p<0.05) and a marginally significant (p<0.065) greater activation in Native Facial Action>Baseline and in Foreign Facial Action>Baseline. **, p<0.05 that survived the FDR correction for multiple comparisons; *, p<0.05, †, p<0.065.

As can be seen from the table, contiguous channels over the mPFC are activated, both in the Native Facial Actions condition (channel 28 and 29) and in the Foreign Facial Actions condition (channel 27, 28 and 29). Moreover, while the Native Facial Actions condition engaged only one channel over the right TPJ, the Foreign Facial Actions engaged one channel over the left (channel 1) and one channel over the right IFG (channel 16), one channel over the left STG (channel 6) and one channel over the right posterior temporal gyrus (channel 24).

6.4.2.2.2 Repeated measures ANOVA

A repeated measures ANOVA with the betas from each condition compared with Baseline as a within subjects factor (Native Facial Actions>Baseline vs. Foreign Facial Actions>Baseline) and the MSR outcome as a between subjects factor revealed a main effect of condition in channel 1 (left IFG), $F(1, 42) = 5.35$, $p=0.026$, $\eta_P^2=0.113$, channel 4 (left IFG/left STG), $F(1, 44) = 5.57$, $p=0.023$, $\eta_P^2=0.112$, channel 9 (left STG), $F(1, 42) = 7.14$, $p=0.010$, $\eta_P^2=0.125$, and channel 27 (mPFC), $F(1, 50) = 5.22$, $p=0.027$, $\eta_P^2=0.088$ (not significant after FDR correction). Post-hoc analysis revealed that channels 1,4,9 and 27 that showed a main effect of condition were significantly more activated for Foreign Facial Actions than Native Facial Actions (channel 1: $t(43)=2.36$, $p=0.023$; channel 4: $t(45)=2.39$, $p=0.021$; channel 9: $t(51)=2.75$, $p=0.008$; channel 27: $t(52)=2.92$, $p=0.005$).

A significant interaction between condition and the MSR outcome was statistically significant only in channel 26 over the posterior temporal lobe, $F(1, 44) = 5.81$, $p=0.006$, $\eta_P^2=0.209$. A post-hoc independent sample t-test revealed that the Recognisers displayed a significantly greater activation in channel 26

than Non-Recognisers in the Native Facial Actions condition, $t(44)=2.19$, $p=0.034$, and that the Recognisers displayed a significantly greater activation in channel 26 in the Native Facial Actions condition rather than in the Foreign Facial Actions condition, $t(20)=2.34$, $p=0.029$. Figure 6.5 showed the HRF plots of the brain activation in channel 26 in the Recognisers and in the Non-Recognisers and the mean betas values for the two conditions compared to Baseline in channel 26 in the Recognisers and in the Non-Recognisers.

A

Channel 26 (right pSTS)
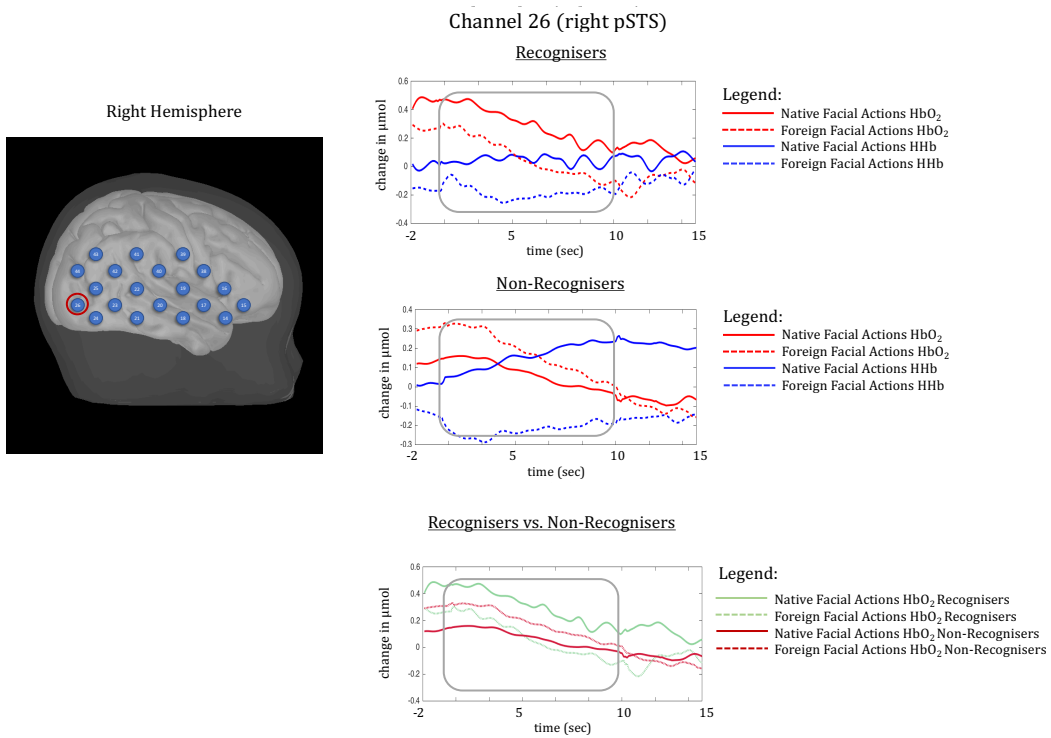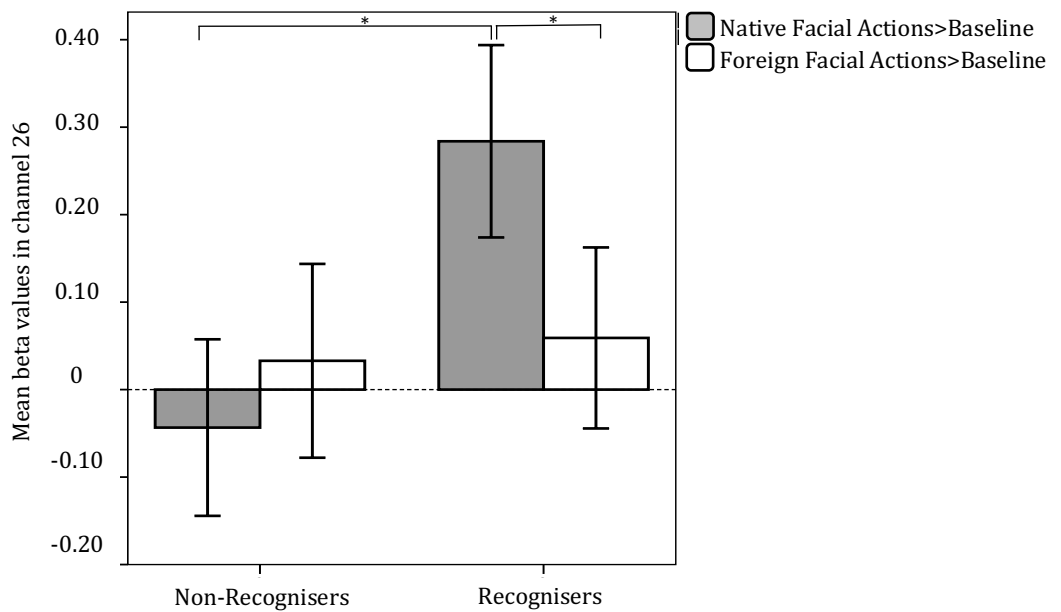
Figure 6.5 A, HRF plot of channel 26 in the Recognisers and in the Non-Recognisers. The grey square indicates the length of the experimental trial. B, Mean betas values from Native Facial Actions>Baseline and Foreign Facial Actions>Baseline in channel 26 in the Recognisers and in the Non-Recognisers.

6.4.2.2.3 One sample t-tests on the Native Facial Actions>Foreign Facial Actions

contrast in the Recognisers and the Non-Recognisers

To explore whether there are any brain regions that specifically respond to the observation of facial actions performed by native compared to foreign speakers (Native Facial Actions>Foreign Facial Actions) in the two groups, one-sample t-tests on the HRF contrast were performed in the Recognisers and in the Non-Recognisers by using the split analysis. This analysis might elucidate different neural brain regions activated by the two conditions in the two groups that can be related to the facial mimicry results. Table 6.3 shows the channels that showed greater activation in Native Facial Actions>Foreign Facial Actions and Foreign Facial Actions>Native Facial Actions in Recognisers and in Non-Recognisers (see figure 6.4 for the HRF plots).

Native Facial Actions>Foreign Facial Actions				
channel	brain region	*t* value	*p* value	df
Recognisers				
26	Right posterior temporal gyrus	2.07	0.050*	20
40	Right supramarginal gyrus	2.87	0.012*	15
Non-Recognisers				
/	/	/	/	/
Foreign Facial Actions>Native Facial Actions				
Recognisers				
16	Right IFG	2.17	0.039*	24
17	Right IFG/Right STG	2.00	0.057†	23
27	mPFC	2.19	0.038*	23
38	Right Supramarginal gyrus	2.53	0.023*	25
Non-Recognisers				
1	Left IFG	2.59	0.016*	24
4	Left IFG/left STG	1.98	0.059†	24

Table 6.3 Channels that showed a significant (p<0.05) and a marginally significant (p<0.065) greater activation to Native Facial Action>Foreign Facial Action and Foreign Facial Action>Native Facial Action, in the whole sample and in the subsets of Recognisers and Non-Recognisers. *, p<0.05; †, p<0.065.
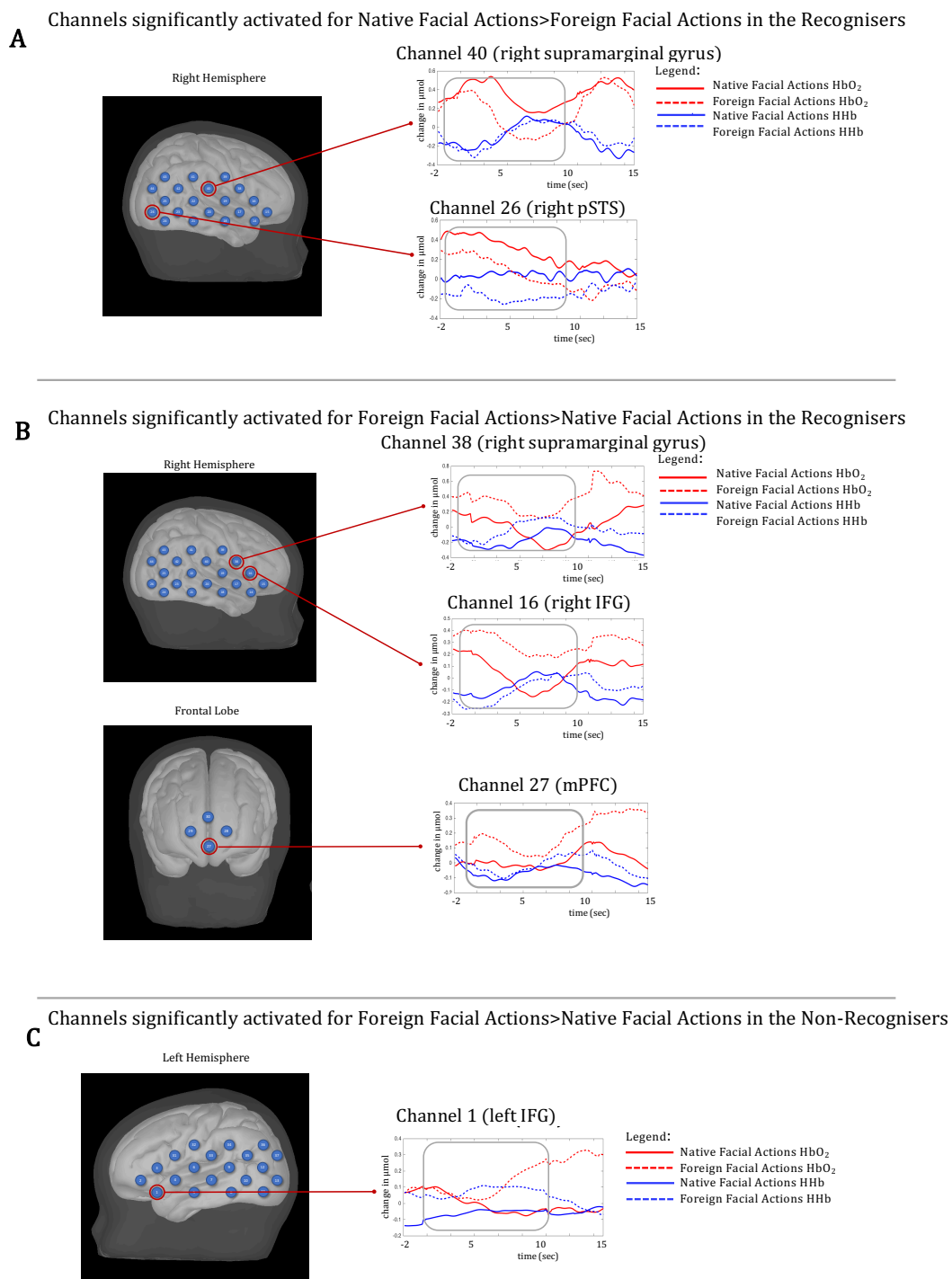
Figure 6.4. HRF plots of the channels that are significantly activated at the one-sample t-tests for the Native Facial Actions>Foreign Facial Actions contrast in the Recognisers and in the Non-Recognisers. A, channels significantly activated for Native Facial Actions>Foreign Facial Actions in the Recognisers; B, channels significantly activated for Foreign Facial Actions>Native Facial Actions in the Recognisers; C, channels significantly activated for Foreign Facial Actions>Native Facial Actions in the Non-Recognisers. The grey square indicates the length of the experimental trial.

As can be seen from the table, the IFG/STG showed a greater activation for Foreign Facial Actions>Native Facial Actions in both the Recognisers (channel 16 and 17) and the Non-Recognisers (channel 1,4,5), even though this activation was lateralised in the right hemisphere in the Recognisers and in the left hemisphere in the Non-Recognisers. Additionally, Recognisers showed a greater activation in channel 27 over mPFC for Foreign Facial Actions>Native Facial Actions. None of the channels showed greater activation for Native Action>Foreign Facial Action in the whole sample and in the Non-Recognisers group, but Recognisers showed a greater activation in channel 26 and channel 40 over the right temporal lobe in Native Facial Actions>Foreign Facial Actions.

6.4.2.3 Psychophysiological Interaction results

As it has been hypothesized that the mPFC is a crucial region for the modulation of mimicry, affecting the activity of other regions belonging to the MNS (Brass et al., 2009; Spengler et al., 2010, 2009; Wang et al., 2011; Wang & Hamilton, 2012), channels 27, 28, 29 and 30 over mPFC were chosen as region of interest for the PPI analyses.

Table 6.4 lists all pairs of channels that showed greater functional connectivity in response to the Foreign Facial Actions condition compared with the Native Facial Actions condition, in the whole sample, in Recognisers. None of the functional connections survived the FDR correction for multiple comparisons.

Foreign Facial Actions>Native Facial Actions				
Whole sample				
channel	brain region	*t* value	*p* value	df
28-23	mPFC – right STG	2.13	0.038*	52
29-2	mPFC – left IFG	2.17	0.034*	49
Recognisers				
28-15	mPFC-right IFG	2.45	0.023*	20
Non-Recognisers				
28-23	mPFC-right STG	2.00	0.054†	29
28-24	mPFC-right posterior temporal gyrus	2.59	0.015*	27
28-25	mPFC-right TPJ	2.98	0.006*	24

Table 6.4 Significant and marginally significant functional connections for Foreign Facial Actions > Native Facial Actions in the whole sample. *, p<0.05; †, p<0.065.

There was no statistically significant greater functional connectivity in the Native Facial Actions compared to the Foreign Facial Actions condition. Channel 2 (left IFG) and channel 23 (right STG) displayed greater functional connectivity with channel 28 and 29 over the mPFC in the Foreign Facial Actions rather than in the Native Facial Actions condition. While Recognisers showed only one statistically significant greater functional connection between channel 28 (mPFC) and channel 15 (right IFG) in the Foreign Facial Actions rather than in the Native Facial Actions condition, the Non-Recognisers displayed greater functional connectivity between channel 28 (mPFC) and two contiguous channels, channel 24 (right posterior temporal gyrus) and channel 25 (right TPJ) in the Foreign Facial Actions rather than in the Native Facial Actions condition.

6.4.3 Relationship between EMG and fNIRS data

Hereafter I investigated the relationship between the haemodynamic response over the channels significantly activated for the Native Facial Actions>Foreign Facial Actions and the Foreign Facial Actions>Native Facial Actions contrast and infants' facial mimicry. To limit the number of correlational analyses, a differential mimicry score was calculated (facial mimicry score in the Native condition minus facial mimicry score in the Foreign condition). The differential mimicry score was negatively correlated only with greater activation in channel 27 (mPFC), $r(31)=-0.364$, $p=0.037$ (not significant after FDR correction), and channel 4 (left IFG/left STG), $r(29)=-0.395$, $p=0.034$ (not significant after FDR correction) (Figure 6.5). Thus, infants who showed a greater HbO_2 response over channel 27 and channel 4 when observing facial actions performed by the Native speaker compared to facial actions performed by the Foreign speaker, showed less mimicry of facial actions of the Native speaker compared to facial actions of the Foreign speaker. No significant correlation was observed between the pairs of channels that displayed significant functional connections in the Foreign Facial Actions rather than in the in the Native Facial Actions results and the infants' facial mimicry scores.
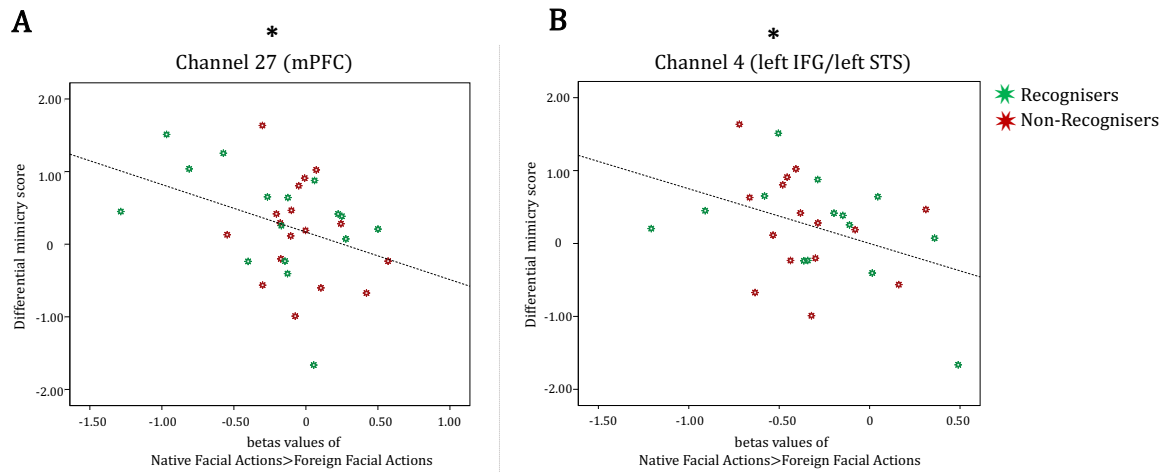
Figure 6.5 Scatterplot of the relationship between activation in channel 27 (A) and channel 4 (B) in Native Facial Actions>Foreign Facial Actions and the differential mimicry score. *, p<0.05.

6.5 Discussion

How the emergence of self-awareness during the second year of life affects the ability to identify with one's social group is still unknown. While infants' preference for in-group members early in life may be driven by a preference to interact with familiar others, mechanisms related to self-comparison might plausibly start to play a more important role once infants have developed a sense of self. To test this, the current study aimed to investigate whether the emergence of a sense of self modulates infants' tendency to selectively mimic linguistic in-group members – an index of in-group preference - and whether infants with more developed self-awareness activate different brain regions for facial actions performed by in-group rather than out-group members.

6.5.1 Facial mimicry results

In this study, I explored how infants' developing self-awareness impacts on their tendency to affiliate with in-group members, as indicated by selective mimicry of linguistic in-group over out-group members. Only those 18-month-olds with a more advanced level of self-awareness – as indexed by self-recognition during the MSR task – exhibited significantly greater mimicry of the facial actions performed by the native speaker, compared to the foreign speaker. These findings are consistent with previous studies that have shown an effect of the emerging sense of self on other imitative behaviours in young children (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013). However, the current work is the first to additionally investigate the interaction with group status. Our results suggest that instead of making infants generally more imitative, a more advanced level of self-awareness may instead make infants more aware of themselves in relation to others, enhancing imitative responses selectively of those that they are motivated to affiliate with (e.g. with in-group members). This is an effect that the previous studies were unable to pick up on because only native language models or peers were used (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013).

This study is also consistent with the idea that the MSR task measures something more than physical self-recognition. In fact, our findings suggest that passing the MSR task may reflect a change in the infants' ability to form a representation of themselves or a 'self-concept', that can be perceived in relation to others (Asendorpf & Baudonnière, 1994; Nielsen & Dissanayake, 2004; Suddendorf & Whiten, 2001), rather than a mere detection of visual-motor contingencies (Heyes, 1994; Mitchell, 1993).

Consistent with the idea that the Recognisers may have preferred to interact with the in-group member, we found that the Recognisers had significantly more valid trials in the Native compared to the Foreign condition. One may argue that our results could be explained by the fact that the Recognisers observed more trials of the in-group model's facial actions, therefore leading to higher mimicry levels. However, it is worth mentioning that Recognisers had only two more valid trials than the Non-Recognisers in the Native condition. Additionally, Recognisers had only two more valid trials in the Native than in the Foreign condition. Moreover, the non-significant correlations between the mimicry scores and the number of included trials (both in the whole sample and in the Recognisers) suggest that the mimicry scores are not purely driven by the different number of trials included in the analysis. Furthermore, there was no significant difference in the number of trials excluded because of not looking between the Recognisers and the Non-Recognisers, suggesting that the mimicry scores are not driven by a different level of attention in the two groups. However, further work may explore the role of attention in influencing social categorisation in more detail. As there is evidence showing that people pay less attention to out-group members (Graen, Novak, & Sommerkamp, 1982; Martiny-Huenger, Gollwitzer, & Oettingen, 2014), it would be interesting to test whether different levels of attention can interact with self-related processes in influencing affiliation with the in-group.

Nevertheless, the absence of a significant interaction between Linguistic group and MSR requires us to be cautious when generalising these findings. The absence of an interaction might be driven by the large amount of variability in our data, in particular in the Non-Recognisers group. The high variability in the mimicry scores of the Non-Recognisers might reflect the fact

that the emergence of self-awareness is a gradual process (Bertenthal & Fischer, 1978; Neisser, 1993; Rochat, 1995), rather than a stage-like transition. Potentially some of the infants included in this study had an intermediate stage of self-awareness resulting in selective mimicry behaviours that were more similar to those displayed by infants categorised as Recognisers than those displayed by true Non-Recognisers.

6.5.2 Brain response results

The haemodynamic response patterns in the Recognisers and the Non-Recognisers are less clear than the facial mimicry results. The channels activated by the task or that showed a greater activation in one condition compared to the other are often not clustered together. Moreover, among all the statistical comparisons performed, only channel 27 over the mPFC significantly activated by the Foreign Facial Actions when compared with Baseline survived the FDR correction for multiple comparisons. This makes the interpretation of the results difficult, and therefore these findings must be generalised with caution.

6.5.2.1 The IFG and the STG in the Foreign Facial Actions condition

One of my hypotheses predicted a greater activation of areas belonging to the MNS in the Native rather than in the Foreign Facial Action condition, which would have been consistent with the facial mimicry results. In fact, there is evidence of the IFG and the STG as region involved in mimicry (Likowski et al., 2012; Rymarczyk, Zurawski, Jankowiak-Siuda, & Szatkowska, 2018; Wang et al., 2011). The repeated measure ANOVA revealed a significant interaction between the experimental condition and the MSR outcome in channel 26 over

the posterior temporal lobe, with the Recognisers significantly engaging the posterior temporal lobe in the Native Facial Actions rather than in the Foreign Facial Actions condition, showing a significant greater activation in the Native Facial Actions compared with the Non-Recognisers. A greater activation of the temporal lobe in the Recognisers was confirmed by the one-sample t-test performed on the Native Facial Actions>Foreign Facial Actions contrast, where the Recognisers displayed a significantly greater activation in two channels over the temporal lobe. However, they are not spatially contiguous - aspect that might suggest they belong to the same cluster of activation - with one being more anterior (channel 40) and one more posterior (channel 26). As there is evidence that the temporal lobe is engaged during mimicry (Iacoboni, 2005; Rizzolatti & Craighero, 2004), the activation of these two channels might reflect the greater tendency to mimic the Native rather the Foreign model, which was exhibited by the Recognisers only. However, the single-channel activation and the absence of significant correlations between betas in these channels and the facial mimicry scores cannot validate this hypothesis.

The repeated measures ANOVA revealed a main effect of the Foreign Facial actions condition over the left IFG/STG (channel 1,4,9). Consistent with findings from the repeated measures ANOVA, the one sample t-tests on the HRF contrast in the Recognisers and the Non-Recognisers revealed that both groups exhibited greater activation for the Foreign Facial Actions rather than the Native Facial Actions condition in some channels over IFG. The activation is lateralised in the right hemisphere for the Recognisers and in the left hemisphere for the Non-Recognisers. Even though I did not have any predictions in terms of lateralisation of activation, this seems to indicate the recruitment of regions typically involved in mimicry (Rizzolatti & Craighero,

2004). While some suggested that the IFG but it is unclear why this is stronger in the Foreign rather than in the Native Facial Actions condition. Moreover, this is not consistent with the facial mimicry results that showed a greater tendency to mimic the Native rather than the Foreign model. However, the grater activation of the IFG/STG in the Foreign Facial Actions rather than in the Native Facial Actions condition is supported by a negative correlation between betas of the Native rather than the Foreign facial actions in channel 4 (left IFG/left STG) and the differential mimicry score. This suggests that infants who presented a greater activation of the IFG/STG for Foreign Facial Actions>Native Facial Actions also showed greater mimicry of the Foreign rather than for the Native model, which is consistent with the idea that IFG may be involved in supporting mimicry (Rizzolatti & Craighero, 2004). However, why the relationship between the IFG activation and the facial mimicry scores has been found to be significant only in the Foreign and not in the Native Facial Actions condition is unclear. When looking at the scatterplots of the significant correlations, it is difficult to identify a clear pattern of relationship between haemodynamic response and facial mimicry that distinguish Recognisers and Non-Recognisers. In fact, both groups are distributed along the fitted line without any clustering. This makes it difficult to draw any conclusions about how emerging self-awareness may influence the relationship between facial mimicry and neural responses to facial actions.

6.5.2.2 The mPFC in the Foreign Facial Actions condition

The third hypothesis was related to a crucial role of mPFC that supports selective mimicry of in-group vs. out-group, especially in Recognisers. As explained in the introduction of this study, there is evidence of the mPFC

activation for actions performed by in-group members, indicating self-processing (Molenberghs, 2013; Morrison et al., 2012; Rilling et al., 2008; Volz et al., 2009), but also during actions performed by the out-group members, indicating inhibition of mimicry (Brass et al., 2009; Spengler et al., 2010, 2009; Wang et al., 2011; Wang & Hamilton, 2012). In the whole sample, the mPFC was activated to both the Native Facial Actions and the Foreign Facial Actions (and this latter condition the activation in channel 27 survived the FDR correction for multiple comparison, therefore suggesting higher statistical interpretability). The one sample t-tests on the HRF in the two groups revealed a greater activation in Foreign Facial Actions>Native Facial Actions over mPFC only in the Recognisers. At a first sight, this might appear as an index of inhibition of facial mimicry of the actions performed by the foreign speaker. This would be consistent with the significant greater tendency to selectively mimic the Native rather than the Foreign facial actions, which was exhibited only by infants with more advanced self-awareness. However, the negative correlation between betas of Foreign Facial Actions>Native Facial Actions in channel 27 (mPFC) and the differential mimicry score disconfirmed this hypothesis. In fact, this correlation analysis shows that participants that presented greater activation over mPFC in Foreign Facial Actions rather than in Native Facial Actions displayed also greater facial mimicry of the Foreign rather than the Native model, which is not in line with the facial mimicry results.

6.5.2.4 Functional connectivity

Connectivity analyses performed with PPI did not provide further clarification to the haemodynamic activation results. Moreover, none of the statistically significant functional connections survived the FDR correction for multiple

corrections. The greater functional coupling between mPFC-IFG and mPFC-STG in the Foreign rather than in the Native facial actions conditions can be interpreted as a modulation of the mimicry of the foreign model suggested by previous studies (Wang, Ramsey, & Hamilton, 2011; Wang & Hamilton, 2012). This would be consistent with the greater tendency to mimic the native rather than the foreign model as displayed by the facial mimicry scores. However, this inference is limited to only 2 pairs of connections (28-23 and 29-2), and the absence of significant correlations between the functional connectivity values and the facial mimicry scores (even when looking at it in the two groups separately) does not provide support for this interpretation.

6.5.3 Conclusions

To summarise, the facial mimicry findings confirmed my predictions, with the Recognisers showing a selectively greater tendency to mimic the in-group rather than the out-group model, which suggest that a more advanced level of self-awareness may allow infants to identify with their social group. Moreover, the facial mimicry results inform mechanisms underlying self-recognition, as passing the MSR task may reflect a change in the infants' ability to form a representation of themselves, that can be perceived in relation to others (Asendorpf & Baudonnière, 1994; Nielsen & Dissanayake, 2004; Suddendorf & Whiten, 2001). However, the fNIRS results are difficult to interpret. As indicated by the power analysis, sample sizes are big enough to potentially detect a statistically significant effect, therefore the unclear fNIRS results cannot be attributed to an underpowered study. Moreover, the inconsistent relationship between facial mimicry and the haemodynamic responses does not help the understanding of the fNIRS results. In the previous study

performed by my team on the 11-month-old sample (de Klerk et al., under review), participants showed greater activation over the TPJ for Native rather than Foreign facial actions. The study was conducted in the same way and data analyses have been performed with the same toolboxes. Therefore, I would not attribute any differences in the fNIRS results to methodological aspects.

It would be interesting for future research to explore whether other cues to group membership would show similar effects, such as race and gender, making our results more generalizable. In fact, we know that language is a potent cue to group membership (Liberman et al., 2017), but other social categories have been less investigated. Moreover, future research can focus on those infants who are constantly exposed to different social categories, such as bilingual children. As it has been shown that the affiliation with a social group becomes part of the psychological self (Tajfel & Turner, 1986), one may hypothesize that mechanisms related to self-comparison identify more than one social group as in-groups in those infants that are constantly exposed to some social groups for the same social category. Moreover, future studies can explore how emerging self-awareness may influence the affiliation with groups which are clearly not depending on familiarity, for example a coloured t-shirt assigned on the day of the testing session (based on the minimal group paradigm, Tajfel, 1974). In this case, only infants which are able of self-comparison processes would exhibit greater tendency of affiliation, as expressed by mimicry, which would be consistent with the influence of the emergence of self-awareness during the second year of life on the ability to identify with one's social group and with the idea that the MSR task measures something more than physical self-recognition.

This chapter showed the first investigation into the relationship between self-awareness and social interactions in infancy, showing that the sense of self may allow infants to identify with their social group. With the next chapter, I explored the relationship between self-awareness and social interactions from another angle. Based on the hypothesis of a social shaping of the sense of self through the interactions with others (Prinz, 2012; Rochat & Zahavi, 2011), the next chapter investigates whether the early interactions with the mother may influence the emergence of the sense of self at 18 months.

Chapter 7

An investigation into the relationship
between the mothers' tendency
to imitate their 4-month-olds and
emerging self-awareness at 18 months

7.1 Abstract

The literature reviewed in this thesis has revealed a remarkable link between emerging self-awareness and social interactions. Recent theories on the development of the sense of self have hypothesized a social construction of the self through interactions with others, especially with the mother. The first mother-child interactions are usually characterized by a high level of contingency and maternal imitation, and some studies showed that this aspect is fundamental for the later development of social cognitive abilities. It has been hypothesized that the first mother-child social interactions constitute the foundations of a *primary subjectivity* in the infant, suggesting a positive relationship between the mother's early imitation of the infant and emerging self-awareness. However, it has been also hypothesized that being mimicked blurs self-other boundaries, suggesting a negative relationship between the mother's early imitation of the infant and emerging self-awareness. Despite the ubiquity of mother-child contingency during the first years of life, it is unclear how these early social interactions are related to the emergence of self-awareness later in the development. In the current study, I aimed to test whether mothers' tendency to imitate their 4-month-olds predicts emerging self-awareness – as indexed by the MSR task at 18 months.

   Results showed no significant relationship between the mothers' tendency to imitate their infants at 4 months and the MSR outcome at 18 months. However, the absence of significant relationships does not necessarily provide evidence against the hypothesis that suggests a social construction of the self, hence the results are discussed in terms of methodological limitations. Specifically, factors such as samples size, age gap between the time points, and a limitation of the strict categorisation of the MSR task are examined.

7.2 Introduction

Recent theories proposed a strong link between the emerging self and the interaction with others, suggesting a social nature of the sense of self, where others serve as *social mirrors* (Prinz, 2012; Rochat & Zahavi, 2011). Through the interaction with others, there is also a gradual development the idea of 'me', which is the ability to understand how others perceive oneself, a foundational aspect of the development of self-awareness (Lewis, 2011; Rochat, 1995, 2003; Rochat & Zahavi, 2011). Consistent with this, researchers in this field have proposed an association between emerging self-awareness and social cognitive abilities (Iacoboni, 2009; Rochat & Zahavi, 2011; Southgate, 2018; Steinbeis, 2016). In particular, imitation has been thought to be remarkably associated with emerging self-awareness, possibly supported by the MNS as a mechanism for shared neural substrates (Iacoboni, 2009). In fact, as areas belonging to the MNS system have been found to be engaged both during imitative behaviours (Iacoboni, 2005; Rizzolatti & Craighero, 2004) and self-related processing (Kaplan et al., 2008; Uddin et al., 2007, 2005), and developmental studies have found a positive association between emerging self-awareness and imitation (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013), it has been proposed that the MSN may be the functional link between imitation and the sense of self even during the first years of life (Iacoboni & Dapretto, 2006; Iacoboni, 2009). However, to date there is a lack of empirical evidence to support this idea.

The study presented in the previous chapter is in agreement with the idea of an association between emerging self-awareness and social interactions, showing that infants with a more developed sense of self significantly exhibited a greater tendency to selectively affiliate with in-group members rather than

outgroup ones, indexed by a greater level of facial mimicry of the native rather than foreign speaker. While Chapter 6 provided evidence supporting the influence of emerging self-awareness on social interactions, it does not inform about the social nature of self. There is very limited evidence supporting the idea that social interactions play a role in shaping the self, and the current study aims to go some way towards filling this gap.

When considering early interactions with others, it is worth mentioning that the first fundamental *other* for the infant is the mother (Prinz, 2012). For example, infants prefer to look at their own mother's face compared to a stranger's face (Bushnell, Sai, & Mullin, 1989; Field, Guy, & Umbel, 1985; Field, Cohen, Garcia, & Greenberg, 1984), and they recognize their mother's voice from about 3 days of age (Decasper & Fifer, 1980). From an evolutionary perspective, this mother-infant bond is thought to be crucial not only for a survival purpose, but also for the development of self-related processes (Bowlby, 1958; Fonagy, Gergely, & Target, 2007; Mayes, Fonagy, & Target, 2007). In fact, the first mother-child interactions are usually characterized by a high level of contingency (Leclère et al., 2014), which has been suggested to be crucial for the later development of social cognitive abilities, such as communication abilities (Kaye, 1982), but also for self-related aspects, such as self-consciousness (Tronick, 2012), self-other differentiation and orientation towards the social environment (Gergely & Watson, 1996, 1999). Therefore, it has been hypothesized that the first mother-child social interactions constitute the foundations of a *primary subjectivity* of the infant (Fonagy, Gergely, & Target, 2006). In this framework, it has been proposed that the mother covers a 'pedagogy function', where the infant learn through continuous social communications, especially with the help of *ostensive cues*, such as eye contact,

calling the infant by name, and using specific type of voice intonation (Fonagy et al., 2006). During the mother-child interactions, the mothers are naturally predisposed to imitate their infants' facial actions (Lenzi et al., 2009). This might promote social dialogs that contribute to the infants' development of a sense of self, where the infant learns to switch between self and other representations (Emde, 1992). However, it has been also hypothesized that being mimicked increases the overlap between self and other, promoting bodily closeness and interpersonal fusion (Ashton–James et al., 2007). A parental style with these characteristics of higher proximity has been associated with a lower successful rate on the MSR task (Keller et al., 2004, 2005; Ross et al., 2017). Based on this, it also is reasonable to hypothesize a negative relationship between early maternal imitation and emerging self-awareness.

Despite the ubiquity of mother-child contingency in the first years of life, the mechanisms underlying the relationship between these early social interactions and the emergence of self-awareness later in the development is still not clear. Moreover, the literature on this topic lacks empirical evidence, and possible processes related to a positive association between the early mother-child interactions and the later self-awareness are not always described clearly. This study aims to shed light on the social construction of the self, and given the crucial role of the high level of contingency during the first mother-child interactions, the mothers' tendency to imitate their infants early in life is investigated as a possible predictor of self-awareness at 18 months. As during the first few months of their life infants spend most of their time in face-to-face interactions (Rayson, Bonaiuto, Ferrari, & Murray, 2017), in this study 4-month-old infants were exposed to a face-to-face mother-child interaction, which allows the measurement of parental imitation of the infant's facial

actions. The same infants were tested again at 18 months, a crucial age for emerging self-awareness, with the MSR task. I hypothesized that the mothers' tendency to imitate their 4-month-olds' facial actions would predict emerging self-awareness, which would support the fundamental role of maternal imitation in the development of the sense of self. A positive association between the mothers' tendency to imitate their infants and emerging self-awareness would support the idea of a pedagogic role of the mother, where the infant learns about self and other representations (Emde, 1992; Fonagy et al., 2006). A negative association between the mothers' tendency to imitate their infants and emerging self-awareness would support the idea an inverse relationship between the development of the sense of self and a proximal parenting style fusion (Keller et al., 2004, 2005; Ross et al., 2017).

7.3 Methods

7.3.1 Participants

The final sample consisted of 31 4-month-olds (18 males, age mean $\pm$ SD=119.81 $\pm$ 8.57 days). All the infants that participated in the parent-child interaction at 4 months were also tested with the MSR task at 18 months (18 males, age mean $\pm$ SD = 551.65 $\pm$ 9.50 days).

All included infants were born full- term, healthy and with normal birth weight. Written informed consent was obtained from the infant's caregiver prior to the start of the experiment.

7.3.2 4 month session: the Parent-Child Interaction

This section is the same as the one described in a previous study performed by members of my team (de Klerk, under review).

Infants participated in a five-minute face-to-face Parent-Child Interaction (PCI). Infants were placed in a semi-reclined infant seat facing their mother. Parents were informed that the researchers would be out of the room for 5 minutes and that during this time they were to play with their infant however they would at home, without any toys around. Three cameras recorded a frontal view of the infant's face, a frontal view of the mother's face, and a side view of the infant's face and body.

As some of the infants were fussy by the end of the PCI session, a total of three minutes of the interaction was video-coded for the amount of parental imitation. To obtain an index of the infants' opportunity to associate visual and motor representations of facial actions, we calculated the probability that the mother would imitate her infant's facial action within a three second time window. This time window was chosen based on the finding that infants younger than six months do not experience events as contingent if they occur more than three seconds after their own actions (Gergely & Watson, 1999). Videos were coded for facial actions such as frowning, eyebrow raising, mouth opening, tongue protrusion[20] using Mangold INTERACT coding software. To ensure an objective measure of maternal imitation, the videos of the infants and mothers were coded separately - i.e. the coder never played the footage of the

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[20] These actions were chosen as the PCI has been also associated with the infants' tendency to mimic others' facial actions at 4 months in a study performed by members of my team. In this study, infants observed models performing frowning, eyebrow raising, mouth opening, tongue protrusion, therefore the PCI videos were coded for the same facial actions (de Klerk et al., under review).

infant and the mother simultaneously. A maternal imitation score was calculated by dividing the number of infant facial actions that the mother imitated within three seconds by the total number of facial actions that the infant performed.

7.3.3 18 month session: the MSR task

Self-awareness was assessed with the MSR task (Amsterdam, 1972). The task took place in a room with a mirror positioned against one of the walls, with one camera recording the task. The MSR task procedure and the coding scheme used was the same as described in Chapter 4, section 4.3.2.

Two experimenters independently classified the infants as 'Recognisers', 'Ambiguous', or 'Non-Recognisers' based on their behaviours in front of the mirror after the red mark was placed, and they agreed in 98% of the cases. Discrepancies were discussed until agreement was reached.

7.4 Results

Out of the 31 participants that provided data for the PCI, 19 were categorised as Non-Recognisers, 1 as Ambiguous and 11 as Recognisers. The Recognisers and the Non-Recognisers groups did not show any significant difference in parameters that could potentially affect the outcome, such as age at the 4 months session (mean $\pm$ SD Recognisers $= 118.91 \pm 8.19$ days, mean $\pm$ SD Non-Recognisers $= 120 \pm 9.08$ days), $t(28)=0.32$, $p=0.745$, age at the 18 months session (mean $\pm$ SD Recognisers $= 551.25 \pm 10.58$ days, mean $\pm$ SD Non-Recognisers $= 552.75 \pm 9.40$ days), $t(28)=0.30$, $p=0.769$, sex (Recognisers $=$ 6 females, 5 males; Non-Recognisers $=$ 7 females, 12 males), $\chi^2(1,$

N=30)=0.889, p=0.346. A binomial logistic regression with a bootstrap method (1000 samples) was performed to test the relationship between the mothers' tendency to imitate their 4-month-old's facial actions and emerging self-awareness at 18 months, as indexed by the MSR task. There was no significant relationship between the mothers' tendency to imitate their 4 months' facial actions and the infants' MSR outcome at 18 months, $\chi^2(1)$=0.645, p=0.434, C.I.=-3.68 – 11.44. Even though I did not have a prediction in terms of a different effect of the mouth and eyebrow maternal imitation at 4 months on emerging self-awareness at 18 months, I performed an exploratory level analysis investigating whether there was any relationship between the mothers' tendency to imitate their 4 months' eyebrow or mouth actions and self-awareness at 18 months. The mothers' tendency to imitate their 4 months' eyebrow actions and mouth actions did not predict infants at the MSR outcome at 18 months (eyebrow: $\chi^2(1)$=0.017, p=0.872, C.I.=-4.55 – 6.98; mouth: $\chi^2(1)$=0.46, p=0.478, C.I.=-3.59 – 6.50) (Figure 7.1).
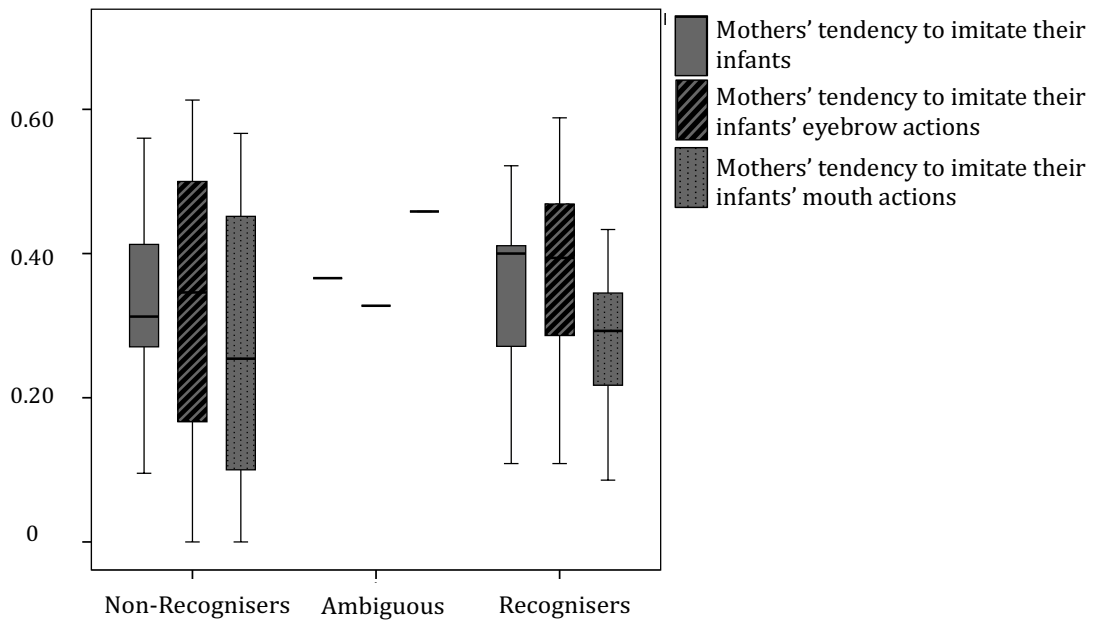
Figure 7.1 Graphical representation of the relationship between the mothers' tendency to imitate their 4 months' facial actions and success at the MSR at 18 months.

7.5 Discussion

Recent theories on the development of the sense of self advanced the hypothesis of a social construction of the self through interactions with others, especially with the mother (Prinz, 2012; Rochat & Zahavi, 2011). In particular, imitation is thought to play a crucial role in shaping the sense of self from early in life (Emde, 1992; Iacoboni, 2009), and the first mother-child interactions are usually characterized by a high level of imitation and contingency (Leclère et al., 2014; Lenzi et al., 2009). These interactions have been hypothesized to constitute the foundations of a *primary subjectivity* of the infant (Fonagy et al., 2006), where the infant gradually learns about self and other representations (Emde, 1992). However, it has been also hypothesized that being mimicked increase the overlap between self and other, therefore promoting interpersonal fusion (Ashton–James et al., 2007). To date, it is unclear how these early social

interactions are associated with the emergence of self-awareness later in the development. To test this, in the current study I investigated whether the mothers' tendency to imitate their 4-month-olds predicted emerging self-awareness at 18 months, but there was no significant relationship between these two variables.

The absence of a significant effect of the mothers' tendency to imitate their infants on emerging self-awareness does not imply an evidence for the absence of the hypothesized relationship. Bayes statistical analysis has recently enriched the interpretation of findings, providing a further exploration of non-significant results (Morey & Rouder, 2011). In fact, this approach can inform on whether non-significant results do actually support the null-hypothesis, or whether the data are not sensitive enough to support the experimental hypothesis, such as due to an underpowered study (Dienes, 2014; Hartgerink, Wicherts, & Van Assen, 2017). Unfortunately, it seems that this method not applicable on binomial logistic regressions, which have been performed in this study.

There are some possible reasons to explain the absence of a predictive association between the mothers' tendency to imitate their 4 months and the tendency to mimic others and emerging self-awareness at 18 months. First, the age gap between 4 months and 18 months might have been too big. Future studies focusing on assessing the parent-child contingency closer in time to emerging-self-awareness might provide more reliable information. However, one may also think that many months of experience of mother-child interaction precede the emergence of self-awareness, therefore a big age gap between the two observations may be accurate. Second, the wide variance observed in the extent of parent-child contingent interaction might have obscured a

relationship between these two aspects. Therefore, in order to answer the question of this study and to elude the high variance of this data, a bigger sample size is likely to be necessary. In particular, as evidenced by the plot in the results section (figure 7.1), the mothers' tendency to imitate their infants' mouth actions at 4-months presented a greater variance in the group of those that at 18 months were classified as Non-Recognisers at the MSR task than Recognisers. This aspect might shed light on the categorisation provided by the MSR task. In fact, as evidenced already in other studies of this thesis, the high variance related to the Non-Recognisers data may suggest inaccuracy in classifying the Non-Recognisers with the MSR task, with some 18-month-olds which might be capable of self-recognition being erroneously classified as Non-Recognisers due to lack of motivation or a shy temperament during the MSR task. Alternatively, this may reflect a gradual emergence of self-awareness, with some of the Non-Recognisers possibly being close to recognising themselves in the mirror at the time of the MSR task even if without a clear touch of their faces, which may had been exposed to high level of maternal imitation at 4 months.

It is worth mentioning that the absence of a significant relationship between mothers' tendency to imitate their infants and the infants' later self-awareness might suggest that the key mechanism predicting the emergence of self-awareness at 18 months is not specifically the mothers' imitation of infants' facial actions, but rather the contingency of maternal responding. This would be consistent with the wider literature suggesting a fundamental role of contingency response during mother-infant interactions (e.g. Gergely & Watson, 1996, 1999a; van der Meer et al., 1995). In this framework, the temporal relationship between the infant's action and the mother's response is

key to the infant learning how to switch between self and other representations (Emde, 1992), rather than the contingent imitation of the same action.

Although maternal imitation has only been included in the current analysis if contingent, an alternative way to analyse this dataset would be to consider all the possible contingent mother responses to infant actions, for example, the mother smiling after the infant opens his mouth as a more sensitive predictor of emerging self-awareness later in development. Additionally, this would represent a more realistic and naturalistic way of investigating mother-infant interactions as it is more likely that a wide range of the mother's contingent responses follows the infant's actions. This includes but is not limited to the imitation of exactly the same facial action. One can hypothesise a positive association between contingency of maternal responding early in life and emerging self-awareness at 18 months, which would provide evidence for the pedagogy role of mother-infant interactions when scaffolding a *primary subjectivity* of the infant (Emde, 1992; Fonagy et al., 2006).

In conclusion, this study did not provide any evidence supporting a social construction of the self, as there was no significant relationship between maternal imitation and emerging self-awareness. Future studies are needed to overcome the aforementioned methodological limitations of this study, recruiting bigger samples, assessing the mothers' tendency to imitate their infants at older ages than at 4 months, and considering the mother's contingency response to the infant's actions as a more realistic predictor of emerging self-awareness at 18 months.

Chapter 8

General Discussion and Conclusions

The sense of self is a person's essential being that makes them different from others. While as adults we tend to take our self-concepts for granted, mechanisms that underlie their development are still largely unknown.

Until now, self-awareness in infancy has been assessed with the MSR task (Amsterdam, 1972). Despite the criticisms around this test (Heyes, 1996; Loveland, 1986; Mitchell, 1993), no real alternative measures to assess self-awareness in infancy have been developed. This field of research has progressed very little since the development of the MSR task, which is in contrast to the extensive volume of studies, especially neuroimaging ones, that have started to shed light on the sense of self in adulthood. However, the interest in exploring mechanisms underlying emerging self-awareness has undergone a revival recently. In fact, it has been hypothesized that there is an association between self-processing and social cognitive abilities (Santiesteban et al., 2012), which might be in place even during the first years of life (Southgate, 2018). Given this, a deeper understanding of the development of the sense of self is needed, and this PhD work aimed to fill this gap. With this project, I intended to bring the topic of the development of the sense of self into research again. The focus of this project was to provide evidence for the accuracy of the MSR task, to explore the neural underpinnings of emerging self-awareness with a focus on brain networks, and to understand how the development of the sense of self is associated with social interactions, especially mimicry.

Specifically, the overarching aim of this PhD thesis was to elucidate the mechanisms underlying the development of self-awareness in infancy, by investigating the following questions:

- What is the significance of visual self-recognition in infancy?

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- May functional connections in brain networks at rest be a marker of self-awareness in infants, as it is in adults?

- Are the brain areas that are typically engaged in adult self-processing also engaged in emerging self-awareness?

- What role do others play in the construction of our sense of self?

- How does self-awareness influence how infants interact with the social world?

This chapter summarises the experimental findings of this PhD work, and discusses them in relation to each other and the existing literature. The following sections also acknowledge possible limitations of the studies, and propose potential directions for future research.

8.1 Summary of findings

In order to discuss the main findings of this PhD work in detail, Table 8.1 provides a brief summary of each study and its results, with the aim to remind the reader of the experimental studies presented in this thesis.

	Study	Method	Main Findings
Chapter 3	**Dynamic Causal Modelling on infant fNIRS data: a validation study on a simultaneously recorded fNIRS-fMRI dataset**	fNIRS and fMRI on a single 6-month-old, comparison of the DCM method on the two techniques	Converging results between the DCM models and parameters estimated with fMRI and fNIRS
	The developmental trajectory of the fronto-temporoparietal connectivity: a longitudinal fNIRS investigation	fNIRS, longitudinal resting-state fronto-temporoparietal connectivity in awake infants at 11, 18, 24, 30, 36 months	Gradual increase of the fronto-temporoparietal connectivity. The 24-month-olds showed the greatest increase in connectivity.
Chapter 4	**Fronto-temporoparietal connectivity as a potential neural marker of self-awareness in 18-month-olds: a resting state fNIRS study**	18 months, MSR and fNIRS resting-state fronto-temporoparietal connectivity	Recognizers showed significantly stronger fronto-temporoparietal connectivity compared to Non-Recognizers.
Chapter 5	**Neural underpinnings of self-recognition in 18-month-olds**	18 months, MSR and fNIRS while looking at matching and mismatching participants' own movements and an unfamiliar other infant	Recognisers showed a greater activation of the mPFC and the TPJ for Self-Live>Self-Recorded. Recognisers also showed a greater activation of the mPFC for Self>Other. Behavioural measures indicating self-recognition were positively correlated with the mPFC activation

Chapter			
Chapter 6	The role of self-awareness in selective facial mimicry of linguistic in-group over out-group members	18 months, MSR, fNIRS and EMG while looking at facial actions of in-group and out-group models	Recognisers showed significant greater mimicry of Native>Foreign Facial Action and a greater engagement of the mPFC for Foreign>Native Facial Actions. Non-Recognisers engaged left STG for Foreign>Native Facial Actions. No relationships were found between the fNIRS and the EMG.
Chapter 7	An investigation into the relationship between the mothers' tendency to imitate their 4-month-olds and emerging self-awareness through the infants' tendency to mimic others at 18 months	PCI at 4 months and MSR at 18 months	The mothers' tendency to mimic their infants at 4 months did not significantly predict the infants' MSR outcome at 18 months.

Table 8.1 Summary of the main results of each study in this PhD thesis.

Chapter 3 focused on methodological improvements in connectivity analyses for fNIRS to explore brain networks supporting the emergence of self-awareness and to enhance this neuroimaging technique for more sophisticated analyses. Tracking the development of brain networks, both spontaneous fluctuations and task-related, is a hot topic in neurodevelopmental research. In this respect, fNIRS is a valuable technique, allowing the acquisition of brain fluctuations and responses in awake infants, which is more similar to adult fMRI studies. The first study presented in this chapter validated the use of DCM with

infant fNIRS data. DCM estimates effective connectivity, which informs about directionality of the connections and how they are modulated by experimental conditions. Taking advantage of a unique dataset where fNIRS and fMRI data were recorded simultaneously, a high correspondence between the DCM models and connectivity parameters estimated with fMRI and fNIRS was demonstrated. Although I was not able to apply this technique on any other datasets in this thesis, this study opens new lines of research in developmental neuroscience, providing a better understanding of networks in the brain under certain experimental conditions. The second experiment presented in Chapter 3 examined the longitudinal trajectory of the fronto-temporoparietal connectivity - as a proxy of the DMN - acquired during quiet rest in awake infants. A vast adult literature has shown that the DMN is a network of brain regions activated when we are not engaged in any particular task, and it is related to psychological self-processing (Qin & Northoff, 2011; Raichle, 2015). This study demonstrated a gradual increase of the fronto-temporoparietal connections with age, with a peak at around 24 months. This seem to be consistent with a previous fMRI resting-state study that showed that by 2 years, the DMN is similar to that observed in adults (Gao et al., 2009; Gao, Lin, Grewen, & Gilmore, 2016). For the first time, this study validated a method of resting-state data acquisition from awake infants, and provided a data analysis pipeline that will open new lines of research for the investigation of functional connectivity at rest.

The second aim of this thesis was to investigate the neuronal underpinnings of emerging self-awareness. Taking advantage of the analysis pipeline provided by the longitudinal resting-state study in Chapter 3, the study in Chapter 4 demonstrated that infants who displayed self-recognition in the

mirror showed significantly stronger fronto-temporoparietal connectivity compared to those who did not. As the DMN appears to be primarily involved in psychological self-processing and less in physical self-recognition in adults (Qin & Northoff, 2011), this result suggests that passing the MSR task may indicate broader self-awareness than mere physical self-recognition. This interpretation is consistent with previous studies that showed a relationship between self-recognition in the mirror and empathy and personal pronoun use (Bischof-Köhler, 2012; Lewis & Ramsay, 2004). Therefore, results from this study inform the debate surrounding the significance of visual self-recognition in infancy and the validity of the MSR task as an indicator of self-awareness beyond physical self-recognition (Suddendorf & Butler, 2013) (this topic is expanded in sections 8.2.1). Additionally, this study showed for the first time that fronto-temporoparietal connectivity is a neural correlate of self-awareness not only in adults, but in infants as well.

Chapter 5 aimed to explore which areas of the developing brain respond during self-recognition. 18-month-olds' brain responses were acquired while they looked at videos of themselves, either live video feed or a previously recorded video of themselves. Participants were also presented with videos of an unfamiliar infant. 18-month-olds that exhibited self-recognition in the mirror showed greater activation of the mPFC and the TPJ when looking at the live video of themselves compared to the previously recorded video. They also showed greater mPFC activation when looking at their own live videos compared with those of an unfamiliar infant. The mPFC seems to play a crucial role in self-processing in infancy as two behavioural measures used in this study as indexes of self-recognition (looking time in the mirror during the MSR task and level of movements during the self-videos in the fNIRS task) were

found to be positively correlated with the mPFC activation during the observation of themselves. The key function of the mPFC in self-processing is consistent with animal studies showing that primates that exhibited self-recognition are those with more developed frontal lobes (Platek et al., 2008; Semendeferi, Damasio, Frank, & Van Hoesen, 1997), and that in human beings, the frontal lobes are developing over the first three years of life (Bell & Fox, 1992; Fuster, 2003; Johnson, 2001), a fundamental period for developing capacities to represent self and other (Amsterdam, 1972). Functional connectivity analysis on this task provided further evidence for the importance of the mPFC for self-processing. Stronger connections between the mPFC and the right TPJ were exhibited during videos with matching rather that mismatching self-movements, and in self-videos rather than in other-videos. These findings are consistent with those from the previous chapter showing a crucial role of the mPFC and the TPJ in a functional network related to self-processing, and with the adult literature that extensively demonstrated the engagement of the mPFC and the TPJ in self-processing tasks (Davey et al., 2016; Northoff et al., 2006)

Recent theories in developmental psychology have emphasised the importance of social interactions in emerging self-awareness, and that others play a fundamental role in constructing one's own self-concept by acting as *social mirrors* (Prinz, 2012; Rochat, 2003; Rochat & Zahavi, 2011). Therefore, it seems crucial to study emerging self-awareness in the context of infants' interactions with others and the social environment. Moreover, some adult work has suggested a link between imitation and self-awareness or self-other distinction. For example, it has been shown that imitation–inhibition training enhances self-other processes in adults (Santiesteban et al., 2012). A positive

relationship between imitation and emerging self-awareness has been demonstrated by some developmental studies (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013). In this PhD project, the relationship between emerging self-awareness and social interactions was explored by focusing on mimicry, a form of imitation, through Chapters 6 and 7. The study presented in Chapter 6 aimed to investigate how emerging self-awareness can influence infants' mimicry of linguistic in-group and out-group members. Only infants with a more advanced self-awareness showed significantly greater facial mimicry of a native compared to a foreign speaker. fNIRS results displayed a few single-channel activations which were not statistically associated with the facial mimicry results, therefore these findings should be treated cautiously. The facial mimicry results are consistent with the idea that a more advanced level of self-awareness may allow infants to identify with their social group, hereby enhancing their tendency to selectively affiliate with in-group members.

Chapter 7 aimed to investigate the role of others in constructing the self, which refers to the idea of the social nature of the self. In particular, it has been hypothesized that infants' early imitative interactions with their mother contribute to the formation of the self (Prinz, 2012; Rochat & Zahavi, 2011). Moreover, through frequent mother-child exchanges, infants are also exposed to the perceptual-motor coupling that will lead them to copy others' actions. With this study, I investigated whether the mothers' tendency to imitate their infants at 4 months is a predictor of self-awareness. However, results showed no significant relationship between the mothers' tendency to imitate their infants and emerging self-awareness. The absence of significant relationships between the mothers' tendency to imitate their infants during the first months

of life and emerging self-awareness later in the development does not provide any support for that the self is socially constructed. However, from a methodological perspective, statistical analyses were underpowered, and the gap between the two observations may have been excessively wide.

8.2 Synthesis and theoretical implications

This section provides a discussion of the studies conducted in this PhD thesis, in relation to each other and to the previous literature. The theoretical implications of these findings have been synthesised into four general themes: i) the significance of visual self-recognition in infancy; ii) considerations on the accuracy of the MSR task; iii) the role of the mPFC and the TPJ in emerging self-awareness; iv) a note on brain network analyses with fNIRS; v) the interplay between emerging self-awareness and social interactions.

8.2.1 The significance of visual self-recognition in infancy

The development of the MSR as a test of self-awareness in infancy dates back to 1972 (Amsterdam, 1972). Self-recognition in the mirror has been thought to indicate a broader sense of self beyond bodily awareness, as success on the MSR task has been associated with empathy (Bischof-Köhler, 2012), personal pronoun use (Lewis & Ramsay, 2004), and capacity for 'symbol-mindedness' (Savanah, 2013). It has been also suggested that self-recognition in the mirror indicates the ability to understand how others see oneself (Lewis, 2011; Rochat, 1995, 2003; Rochat & Zahavi, 2011). Critics of this test argued that infants' self-recognition reflects a pure detection of matching visual and kinaesthetic information (Heyes, 1996; Mitchell, 1993), or the understanding of the

reflective proprieties of the mirror (Loveland, 1986). Despite the controversy surrounding this task, this field of research has progressed very little over the last decades. Given this, one of the purpose of this PhD thesis was to provide evidence for the validity of the MSR task, exploring the significance of self-recognition.

Chapter 4 showed that infants who displayed self-recognition had stronger fronto-temporoparietal connectivity at rest, which is consistent with a rich interpretation of the MSR task. The fronto-temporoparietal connectivity was considered to be a proxy for the DMN, which is a network that has been associated with abstract self-processing in adults (for example sees Davey, Pujol, & Harrison, 2016; Golland, Golland, Bentin, & Malach, 2008; Molnar-Szakacs & Uddin, 2013). Therefore, the study presented in Chapter 4 suggests that the fronto-temporoparietal connectivity may be a marker of emerging self-awareness in infancy. More importantly, this neural correlate may elucidate which components of the 18-month-olds' self-awareness arose at this stage of the development. As regions comprising the DMN have been associated with abstract self-processing in adults, and functional connectivity in regions belonging to this network differentiate those infants who did and did not recognize themselves in the mirror, the MSR task may indeed be a test for self-related processing, and not merely physical self-recognition, or a matching of seen and felt movements.

Consistent with the idea of self-recognition as an index of self-awareness, Chapter 6 showed that only infants that displayed self-recognition showed a greater tendency to mimic in-group versus out-group models. This might be associated with self-comparison and identification processes, which are arguably only possible if infants have a self-awareness. Given that mere

physical self-recognition or a detection of seen and felt movements should be insufficient for such a self-comparison process involving the detection of shared language use, a more plausible explanation for this relationship is that MSR indexes something more profound about the self than physical self-recognition. That infants may be able to compare features that goes beyond physical appearance is more consistent with an interpretation of self-recognition that encompasses also abstract characteristics related to the self.

Taken together, that infants who recognized themselves in the mirror evidenced stronger fronto-temporoparietal connectivity (which is a neural marker that may be related to abstract self-processing), and a greater tendency to affiliate with the in-group rather than the out-group (which in the case of more abstract markers of group similarity should be related to self-comparison and identification processes), is consistent with previous studies that have suggested that self-recognition is as an index of a broader concept of self-awareness (Bischof-Köhler, 2012; Lewis, 2011; Lewis & Ramsay, 2004; Rochat, 1995, 2003; Rochat & Zahavi, 2011; Savanah, 2013). It is important to note here that it is still possible that the observed stronger fronto-temporoparietal connectivity may also be an index of a general maturation of the brain.

8.2.2 Considerations on the accuracy of MSR task

The previous section described some of the evidence from this PhD work supporting the idea that the MSR task assesses self-awareness - defined as knowledge of oneself as a peculiar individual with both physical and mental features- therefore encompassing also abstract self-concepts (Rochat, 2003). Nevertheless, some further considerations on the results from this PhD work may inform us about the accuracy of the MSR test.

The investigation into the neural underpinnings of self-processing presented in Chapter 5 showed that Recognisers displayed a significant activation of the mPFC and the TPJ while looking at live videos of themselves. However, the HRF plots showed an increase in HbO_2 blood flow in the mPFC and in the left TPJ for Self-Live vs. Self-Recorded in Non-Recognisers as well, even though this difference did not reach statistical significance. The study presented in Chapter 6 showed that the Non-Recognisers had a high variability in the facial mimicry results, as was illustrated in the plots in the results section. Moreover, the absence of a predictive relationship between the mothers' tendency to imitate their 4-month-olds' facial actions and emerging self-awareness at 18 months (Chapter 7) may be due to a high variability in the mothers' tendency to mimic those infants that were classified as Non-Recognisers at 18 months, as evidenced by the plots in the results section.

There are two possible explanations for the high variability presented by the Non-Recognisers in some of the data in this PhD thesis. First, although my own data suggests that the MSR task is a valuable tool with which to assess infants' self-awareness, it might also provide false negatives, i.e. categorising some infants as Non-Recognisers while they were actually capable of self-recognition. This idea is consistent with some of the criticisms of the MSR test, such as the fact that it is difficult to control for factors not related to self-awareness, such as a timid personality or motivation in touching the mark on the face, which might affect the outcome at the MSR task (Brandl, 2016). Therefore, it is plausible that while the Recognisers group is homogeneous and less likely to include infants that had not actually developed self-awareness, it is possible that some infants who had the ability to recognise themselves were erroneously included in the Non-Recognisers group due to factors unrelated to

self-awareness (such as shyness). Alternatively, the high variability in the neural and electromyographical data recorded from the Non-Recognisers might reflect the gradual process of the development of self-awareness (Bertenthal & Fischer, 1978; Neisser, 1993; Rochat, 1995). This may be consistent with the fact that some of the Non-Recognisers displayed patterns of brain activation and facial mimicry similar to the ones exhibited by the Recognisers, aspect that increased the variance of the Non-Recognisers results. Therefore, these infants may have been close to the self-recognition in the mirror, even if they did not exhibited a clear touch of the face. This suggests that there may be evidence for self-recognition at an earlier age and that self-awareness gradually emerges throughout the second year of life.

The inaccuracy in the classification of the Non-Recognisers may indeed reflect the gradual emergence of the sense of self, which is an aspect that cannot be traced by the categorisation provided by the MSR test. In fact, the stringent categorisation that the MSR test requires may be too limited when facing a complex psychological domain that gradually develops over a period of time. Instead of a strict categorical response, researchers in this field could think about some additional continuous variables to better characterise the emergence level of self-awareness (this topic is expanded on section 8.5.4). For example, behavioural measurements as those considered in Chapter 5, such as infants' looking time in the mirror after the mark placement or number of testing behaviours while infants are looking at themselves, can provide a better description of the level of self-awareness.

8.2.3 The role of the mPFC and the TPJ in emerging self-awareness

Neuroimaging studies can shed light on mechanisms underlying developmental changes, providing a unique insight that complements behavioural assessments (Skerry & Saxe, 2015). However, while there is an extensive body of research that investigated the neural underpinnings of the sense of self in adults, knowledge of the neural substrates related to its development were still unexplored when I began this PhD project. In adult research, the mPFC and the TPJ have been described as the 'self' brain regions by many (for reviews see Northoff et al., 2006; Northoff & Bermpohl, 2004; Ruby & Legrand, 2007), as they have been extensively found to be engaged in self-processing tasks (Davey et al., 2016; Kaplan et al., 2008; Kelley et al., 2002; Kircher et al., 2000; Uddin et al., 2005). Moreover, the mPFC and the TPJ are two core hubs of the DMN, our 'intrinsic system' that deals with self-related signals and self-processing (Davey et al., 2016; Golland et al., 2008; Molnar-Szakacs & Uddin, 2013; Raichle, 2015; Sporns, 2010). As mentioned in the introduction of this work, the literature review on neuroimaging adult research was not performed with the intent of equating the infant with the adult brain functions and networks. However, considering the very limited number of studies performed so far to investigate neural underpinnings of self-awareness in the developing brain, understanding which are the 'self' brain regions in adults constituted a necessary starting point for this PhD work.

The studies presented in Chapter 4 and 5 investigated the neural underpinnings of emerging self-awareness and, consistent with previous work in adults, they showed that mPFC and TPJ are recruited during a self-processing task and as hubs of a brain network at rest. Both regions have been the focus of much interest in relation to social cognition in infancy (for a review see

Grossmann, 2013b), and this PhD thesis implicates these regions in emerging self-awareness. Interestingly, the mPFC and the TPJ are also crucial regions of the mentalizing network (for a recent review see Mahy, Moses, & Pfeifer, 2014). This overlap between regions implicated in mentalizing and self-processing seems to be consistent with the idea of a strong link between self and other perspectives (Saxe et al., 2006). The next challenge would be to identify the dependence relationship between self and other perspectives, informing on which is fundamental for the development of the other one. Consistent with the *like-me* perspective described in the introduction of this thesis, one may think that mentalizing skills, i.e. understanding the other's perspective, depend on self-processing (Gallese, 2005; Meltzoff, 2007; Meltzoff & Moore, 1997). However, the activation of the TPJ already at 7 months related to other's false belief (Hyde et al., 2018) and the successful performance of infants younger than 18 months, crucial age of emerging self-awareness (Amsterdam, 1972), on implicit false belief tasks (for some examples see Baillargeon, Scott, & He, 2010; Onishi and Baillargeon, 2005; Song & Baillargeon, 2008; Southgate, Chevallier, & Csibra, 2010) seem to support the *like-you* perspective, where infants achieve a self-perspective through the understanding of other's perspective (Prinz, 2012; Rochat & Zahavi, 2011).

8.2.4 A note on brain network analyses with fNIRS

Perceiving the brain as a network of integrated regions, and not only as a sum of localised activations, can enrich our understanding of multifaceted and complex psychological domains, such as self-awareness (Petersen & Sporns, 2015). In particular, the investigation of the fronto-temporoparietal connectivity – as a proxy of the DMN – in Chapter 4 would not have been

possible without an approach focused on brain networks. In fact, I would consider the finding on the fronto-temporoparietal connectivity as a possible marker of emerging self-awareness as one of the most novel results of this thesis, as it may inform on the psychological aspects of self-processing present already early in life. For the purpose of investigating neural underpinnings of self-awareness, in this PhD project I took advantage of fNIRS and, with this work, I provided evidence for its suitability for connectivity analyses, as discussed in Chapter 3. The exponential use of fNIRS throughout the last decades is promising for an increasing use of this neuroimaging method for future research, in particular in developmental neuroscience (Pinti et al., 2018). Moreover, the importance of exploring functional connectivity and brain trajectories across human development is increasingly being recognized. Therefore, I hope that this thesis has contributed to improve the use of fNIRS for more sophisticated analyses that can shed light on functional activation and network development in the future of developmental research.

8.2.5 The interplay between emerging self-awareness and social interactions

A complete investigation into the mechanisms underlying the development of the sense of self has to take into account social interaction with others, as these interactions have been suggested to be a fundamental component of the shaping of the self (Hauf & Prinz, 2005; Prinz, 2003, 2012). As highlighted by the *like-you* perspective, minds are conceived as open and interchangeable systems and subjectivity is defined through social interactions (Hauf & Prinz, 2005; Prinz, 2003, 2012). In adult neuroimaging research, this constant interplay between self and other perspectives is consistent with the finding of

some shared neural systems that represent self and other (e.g. the MNS), with also some brain regions (e.g. TPJ and mPFC) designated to clearly distinguish between self and other (Decety & Sommerville, 2003; Santiesteban, 2014). In this PhD work, the link between emerging sense of self and social interactions has been explored from two points of view: first, how emerging self-awareness affects social interactions (Chapter 6); second, how early social interactions affect emerging self-awareness (Chapter 7). To test this, in this PhD project I focused on mimicry, a form of imitation that has been shown to play a role in shaping social interactions and building relational bonds in everyday life (Lakin & Chartrand, 2003; Lakin et al., 2003).

In the introduction of this thesis, two possible directions of the relationship between emerging self-awareness and mimicry have been postulated: i) a positive relationship between these two aspects, where infants with a more developed sense of show a higher tendency to mimic others. This would be consistent with previous studies showing that self-recognition in the mirror is associated with a greater tendency to imitate peers and models (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013); ii) a negative relationship between these two aspects, where infants with a less developed sense of show a higher tendency to mimic others. This would be consistent with adult studies suggesting that boundaries between self and other become blurred during mimicry, suggesting an overlapping of self and other perspectives (Ashton–James et al., 2007; Georgieff & Jeannerod, 1998; Hale & Hamilton, 2016). Results from Chapter 6 showed that infants who exhibited MSR showed a greater tendency to selectively mimic the in-group over the out-group, suggesting that infants exhibiting self-recognition may interpret the in-group member differently from infants who do not exhibit self-recognition.

Specifically, I propose that infants who exhibit self-recognition have a self-awareness that allows them to compare the other with the self (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013). The fact that infants with self-awareness selectively mimicked more the in-group rather than the out-group model might indicate a clear distinction between self and other (Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Zmyj et al., 2013). Alternatively, one may think that the higher mimicry of the in-group is an indicator of the blurred boundaries between the self and the model recognised as in-group member, therefore with some similar features (Ashton–James et al., 2007; Georgieff & Jeannerod, 1998; Hale & Hamilton, 2016).

The relationship between emerging sense of self and mimicry has been explored from another point of view in the last experimental chapter, where being mimicked early in life has been hypothesized to have an effect on the later development of the sense of self, with two possible predictions. One may think that an higher level of infant's imitation by the mother could promote social dialogs that contribute to the infants' development of a sense of self, where the infant learns to switch between self and other representations (Emde, 1992). Alternatively, it has been also hypothesized that being mimicked increases the overlap between self and other, promoting bodily closeness and interpersonal fusion (Ashton–James et al., 2007). Based on this, the mothers' tendency to imitate their infants could lead to a more delayed emergence of self-awareness. Unfortunately, a role of early social interactions in influencing the emerging sense of self has not been demonstrated in Chapter 7, and this study has been discussed especially in terms of methodological limitations (future recommendations for exploring the role of the mother-infant interactions in emerging self-awareness are provided in section 8.4.2).

8.3   Limitations

This section aims to critically explore possible limitations of this PhD work, which might also help to identify future lines of research. In particular, I acknowledge the absence of an assessment of the infant's general developmental level, the absence of an investigation into early exposure to self-pictures and self-videos, and methodological issues related to fNIRS data analysis.

8.3.1 The absence of an assessment of general developmental level

In this PhD thesis, the general cognitivwe development of the participants was not taken into account as a factor that could potentially influence the development of the sense of self. One of the main criticisms of the MSR task is that infants may require certain cognitive skills to 'pass' the task (Loveland, 1986). Therefore, it would have been beneficial to measure infants' general developmental level to control for such factors. Indeed, one may argue that the differences in functional connections suggested in Chapter 4 and the stronger activation of core regions related to self-processing in Chapter 5 might be driven by a greater general maturation of the brain, which also gives rise to a more advanced level of self-awareness. However, assessing the general level of brain maturation requires the acquisition of MRI images to assess structural connectivity and cortical thickness in each participant. As cognitive abilities are likely to be positively related to the general maturation of the brain through the first years of life (for example see Casey, Tottenham, Liston, & Durston, 2005; Deoni et al., 2016; Nagy, Westerberg, & Klingberg, 2004; Peterson et al., 2000),

a cognitive assessment may indirectly provide information concerning the brain maturation of the participants. Therefore, the integration of a cognitive assessment (such as the *Mullen Scales of Early Learning* (Mullen, 1995), the *Bayley Scales of Infant and Toddler Development* (Macha & Petermann, 2015), Vineland Adaptive Behaviour Scales (Sparrow, Balla, & Cicchetti, 1984)) would have enriched the study of the emerging self-awareness, potentially ruling out the possible interpretation that general cognitive development, or general brain maturation, may lead to a positive association between stronger functional connectivity within the DMN brain regions and self-recognition.

8.3.2 The possible influence of the early exposure to self-pictures and self-videos in emerging self-recognition and self-awareness

The advent of social media and smartphones has extensively changed our way of living. This has an impact also on infants' daily routine, as they are born surrounded by videos and images of themselves. Parents are increasingly documenting their infants' lives, and infants are exposed to their images and videos to a greater extent now than only a few years ago. Additionally, the use of video-calls, especially in cities like London where many families are geographically separated from their relatives, increases the exposure of infants to self-videos (McClure, Chentsova-Dutton, Barr, Holochwost, & Parrott, 2015). However, to date an effect of the early exposure to self-pictures and self-videos on emerging self-recognition and self-awareness has not been investigated. One may think that this experience could possibly accelerate the classic milestone of self-recognition, but whether this is the case has not been studied. In this PhD work, the proportion of infants who successfully recognised themselves in the mirror was consistent with the proportion documented in previous studies

(Amsterdam, 1972; Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Rochat, 1995). Therefore, it does not seem likely that higher levels of the exposure to self-pictures and self-videos affected the outcome of the studies in this PhD thesis, and did not have an impact on emerging self-awareness. Although the internet is pervaded by blogs and articles speculating on how the early exposure to self-pictures and self-videos may affect later self-awareness, there currently is no scientific investigation into this topic.

8.3.3 Methodological issues related to fNIRS data analysis: a note on data quality based on the HRF plots

In Chapters 5 and 6, which reported brain functional activation studies, some of the channels plotted in the results section did not show a smooth, canonical HRF. While most of the activations in this work are inferred and discussed based on the channels that showed a canonical HRF, it is worth acknowledging that the HRF plots that did not show a canonical HRF indicate that data quality might have not been high in all channels and/or participants. While some variability in shape and length of the HRF in very young infants has been reported, several studies with infants after the first year of life documented an HRF resembling the adult one, regardless of the location of the activation or the task used (for a review see Issard & Gervain, 2018). Therefore, considerations regarding the data quality in infant studies based on the HRF plots should not differ much from the adult ones.

The canonical HRF should have a gaussian shape, which is generally characterised by a peak and an undershoot (Poldrack & Nichols, 2011). This shape reflects the increase in oxygenated blood to the brain areas that are activated (Attwell & Iadecola, 2002). Given the physiological nature of the HRF,

one has to bear in mind that adequate fNIRS recordings should contain information about the participants' physiological activation, for example, heart rate is usually easily visible in fNIRS data. Therefore, excluding channels that do not show the participants' heart rate preserves only those with good data quality and means they are reliable for inferring brain activation. In fact, detecting a participant's heart rate in the fNIRS recording suggests a good coupling between the scalp and the optodes (Perdue, Westerlund, McCormick, & Nelson, 2014). This channel rejection step can be easily implemented in the analysis pipeline by plotting the fNIRS raw data by power spectrum, where a small peak around 2 Hz[21] showing the participant's heart rate can be considered as an indicator of good data quality. Channels that do not show evidence of the participant's heart rate are more likely to be characterised by noise instead of cerebral blood flow, therefore, they should be excluded from further data analysis.

It is important to note that more rigorous criteria for data cleaning and channel selection would necessarily lead to a higher exclusion rate of channels and participants. As a result, a high-quality dataset composed of a small number of participants may not be representative of the general population. For example, participants who moved more than average during the experimental sessions or those with dark hair that prevent the light from the optodes efficaciously reaching the brain and the detectors may be excluded. The danger of a massive rejection is likely to characterise infants neuroimaging studies, not always meeting time constraints during a PhD project, or the increasing

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[21] As infants have a faster heartbeat than adults, the infant heartrate is normally observed at around 2Hz and the adult one at 1 Hz.

requests of reviewers and editors of well-regarded scientific journals to publish with a considerable number of participants (Button et al., 2013).

In Chapter 6, some of the HRF plots showed a non-canonical shape as there was an increase in HbO_2 before the stimulation. This may indicate an effect of habituation to the task, where the participant expects a certain video to appear due to the regular alternation between the experimental conditions. In the study in Chapter 6, the anticipatory brain response may be facilitated by the structure of the experimental design as every mimicry trial was anticipated by a reminder trial of the same speaker. Future studies similar to the one presented in Chapter 6 should jitter the baseline, which is a strategy commonly used to avoid habituation effects in brain responses (Lloyd-Fox et al., 2010). As participants cannot precisely anticipate when the experimental condition begins, their brain response is more likely to be 'time-locked' to the beginning of the trial (Lloyd-Fox et al., 2010).

8.4   Recommendations for future research

Some suggestions for future studies were already given in the discussion section of each chapter. However, this PhD project has given rise to some new questions, and the current section is focused on describing potential future research on the topic of self-awareness in infancy.

8.4.1 How does emerging self-awareness affect theory of mind?

This PhD work was partially motivated by the hypothesis of a link between self-processing and social cognitive skills, which renewed the interest in

understanding the mechanisms underlying emerging self-awareness. In fact, self and other perspectives need to be integrated but also separated to achieve efficient social interactions (Santiesteban, 2014). In this project, the relationship between the development of the sense of self and social interactions was explored by focusing on mimicry. However, there are hypotheses of an influence of self-awareness also on higher social processes, such as theory of mind (ToM) (Southgate, 2018).

In developmental psychology, how and when infants and older children are able to make inferences about others' mental states and perspectives is a hot topic. However, although there is a high volume of studies focusing on perspective taking abilities in infants and children, results are not always consistent and researchers still do not agree on the mechanisms that underlie the development of mentalizing skills (Rakoczy, 2012; Southgate, 2018). One of the unsolved questions is why young infants are able to successfully predict other' perspectives during implicit false belief tasks, but older children seem to fail explicit false belief tasks. While going into details about this debate is beyond the aim of this section (for more information on this see Heyes, 2014; Rakoczy, 2012; Schaafsma, Pfaff, Spunt, & Adolphs, 2015; Southgate, 2018; Wellman, Cross, & Watson, 2001), it has been proposed that one of the reasons why young infants are able to predict others' perspectives is that they have not yet acquired a distinct self-perspective (Southgate, 2018). In fact, when this eventually develops in the second year of life, it has to be inhibited in order to fully understand others' perspectives (Southgate, 2018). This theory would explain findings of successful performances on false-belief tasks in infants younger than between 18 and 24 months (for some examples see Baillargeon, Scott, & He, 2010; Hyde, Simon, Ting, & Nikolaeva, 2018; Onishi and Baillargeon,

2005; Luo, 2011; Song & Baillargeon, 2008; Southgate, Chevallier, & Csibra, 2010), before the development of the sense of self (Amsterdam, 1972; Rochat, 2003).

Based on this theory, one can hypothesise that Non-Recognisers, as indicated by the MSR task, might successfully perform on a false-belief task, while Recognisers might not be able to correctly represent other's perspectives. Even if Recognisers successfully represent other's perspectives, they might encounter more difficulties in doing so as compared with Non-Recognisers, as indexed for examples by the need for more trials to correctly predict the other's perspective. To provide evidence supporting this hypothesis, during the next months[22] I will be analysing some data that I have collected during my PhD, aimed to assess false belief understanding in 18-month-olds. In this study, participants watched a video sequence similar to that previously used by several studies of my supervisor Professor Victoria Southgate and colleagues (Senju et al., 2010; Southgate, Senju, & Csibra, 2007; Southgate & Vernetti, 2014). In this video, a female actor sat behind two windows, in front of which there were placed two boxes. The participants know which one of the two contains a ball and that the actor's aim is to reach for the ball at the end of every trial. The capacities to understand false belief are tested when the actor is looking away, and a puppet moves the location of the ball. During this task, eye-tracking data were acquired, to measure the infants' anticipatory looking to the two boxes. Participants' brain response was simultaneously recorded with fNIRS, to try to isolate any brain activation in relation to the false belief trials. The same participants underwent the assessment of their level of self-

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awareness with the MSR task. Based on Southgate's hypothesis, I predict that the 18 months-olds classified as Non-Recognisers will show a more accurate performance on the false-belief task - exhibited by anticipatory looking to the correct box that the actor will reach for - than 18-month-olds classified as Recognisers. In addition, the Recognisers might show a greater engagement of the IFG, the mPFC and the TPJ, brain regions of the ToM network typically involved in dealing with conflicting perspectives during the false belief task (Frith & Frith, 2006; Hartwright, Hansen, & Apperly, 2016; Saxe & Wexler, 2005), likely to characterise only those infants who have to inhibit their self-perspective, in order to understand others' perspectives (Southgate, 2018). However, there is also evidence for the TPJ activation in relation to overlapping boundaries between self and others (Lombardo, Chakrabarti, Bullmore, Wheelwright, et al., 2010), which may be more evident in Non-Recognisers than Recognisers. Therefore, a greater activation of the right TPJ in the Non-Recognisers than in the Recognisers, might support the successful performance of the Non-Recognisers on the false-belief task.

8.4.2 How does the early relationship with the mother affect emerging self-awareness? The fundamental role of the frontal cortex

A social shaping of the self has been hypothesized, where the interactions with others are a fundamental foundation of the construction of the self (Prinz, 2012; Rochat & Zahavi, 2011). In this context, the mother is the first source of social interaction (Prinz, 2012; Rochat & Zahavi, 2011). Researchers belonging to the tradition of a social construction of the self consider bidirectional imitative

interactions and proto-conversational turn-taking as fundamental for the construction of the self (Gergely & Watson, 1996; Mayes et al., 2007; Rochat & Striano, 1999). In particular, it has been highlighted how this primary intersubjectivity is indeed possible because of the infants' tendency to identify temporal contingency between stimuli and response (Gergely & Watson, 1996, 1999). Although the work in this thesis contributed to a better understanding of the mechanisms underlying the development of the sense of self, I have not been able to demonstrate an association between the early social interactions with the mother and the later emerging self-awareness (see Chapter 7). However, as previously highlighted, it is possible that this was due to methodological constraints. It would be interesting for future research to further investigate mechanisms underlying the association between the mother-child relationship and emerging self-awareness. In this respect, neuroimaging studies might shed light on processes related to this interaction, enriching the evidence obtained by previous behavioural assessments (Gergely & Watson, 1996; Mayes et al., 2007; Rochat & Striano, 1999).

In terms of neuroimaging findings, we know very little about how the developing brain responds during the social exchanges with the mother through the first years of life and whether this may be related to later self-awareness. There is evidence for temporal synchronisation of the brain of the mother and the child during social interaction recorded with EEG (Leong et al., 2017; Neale et al., 2018), showing that social cues increase the adult–infant connectivity during communication. However, these studies do not provide information on which brain regions are involved in mother-infant social exchanges. To my knowledge, there is only one study that used fNIRS to record activation from the frontal cortex in mother-infant dyads, showing that both the

mother and the infant activated the frontal cortex when looking at videos of the other one (Minagawa-Kawai et al., 2009). However, in this study the brain responses of the mother and the infant were not recorded simultaneously during a live interaction, preventing a description of a possible temporal synchronisation of the two brain responses, which may be informative about the mechanisms underlying the mother-child interaction. Moreover, the fNIRS acquisition was focused on the frontal cortex only, but exploring the functional connections between the mPFC and other regions that play a role in self-processing, such as TPJ (Decety & Sommerville, 2003; Lewis & Carmody, 2008; Murray, Debban, Fox, Bzdok, & Eickhoff, 2015) during live interactions would be a fascinating topic for future studies. In fact, as it has been shown that functional connectivity in regions belonging to the DMN is positively associated with emotional synchrony between adolescents and their parents (Lee, Miernicki, & Telzer, 2017), one may hypothesize that the strength of fronto-temporoparietal connections in the infants and their mothers is positively associated with the mother-infant contingency during social interactions.

There has been a lot of interest to the role of the mPFC region in social interactions, both in adults (Van Overwalle, 2009) and during the first years of life (Grossmann, 2013b). Very young infants seem to engage the mPFC when detecting communicative cues (Grossmann, 2013a; Grossmann et al., 2008) and with this thesis, for the first time, a key role of the mPFC in emerging self-awareness has been shown in 18-month-olds (see Chapter 4 and 5). Based on this, future studies should investigate the role of the mPFC, which rapidly develops between the first and third years of life (Bell & Fox, 1992; Fuster, 2003; Johnson, 2001), as a shared neural underpinning of the mother-infant relationship and emerging self-awareness. In particular, an impaired or a

delayed emergence of self-awareness may be associated with a reduced contingency of the mother, which would be consistent with the previous theories that highlighted a fundamental role the mother of social mirror during social interactions (Csibra & Gergely, 2006; Prinz, 2012; Rochat & Zahavi, 2011). Alternatively, a delayed or impaired emergence of self-awareness may be also associated with a reduced infants' sensitivity for communicative and social cues, which would be consistent with some theories that related impairments in the social cognition skills with a lack of detection of communicative cues (Elsabbagh & Johnson, 2007; Grossmann, 2013b; Zwaigenbaum et al., 2005). I predict that this relationship between mother-infant social interaction and emerging self-awareness at around 18 months may be mediated by the engagement of the mPFC during social interactions. Future research may test this hypothesis in a mediation model (Mackinnon, 2010). For this purpose, fNIRS can shed light on young infants' brain response during mother-infant interactions, as this method has been established in neuroimaging research to be used both with infants and during live social interactions (Lloyd-Fox, Blasi, & Elwell, 2010; Pinti et al., 2015, 2018).

Moreover, adult research has shown evidence for a subdivision of functional activation and connections of the more superior and inferior portions of the mPFC (Amodio & Frith, 2006; Bzdok et al., 2013; Grossmann, 2013b; Ongür & Price, 2000). While the central portion of the mPFC has been found to be related to self-processing and understanding of other's perspectives (Gusnard, Akbudak, Shulman, & Raichle, 2001; Mitchell, Banaji, & Macrae, 2005), a more superior portion of the mPFC, has been related to monitoring self-related actions, due also to the connections with the motor cortex (Cavada & Goldman-Rakic, 1989; Walton, Devlin, & Rushworth, 2004),

which may be related to the development of a sense of agency, the sense of control over one's actions (Moore, 2016). The more inferior portion of the mPFC, also known as orbitofrontal cortex, seems to be fundamental for integrating sensory information that contributes to bodily self-awareness, due also to the connections with the insular cortex and the somatosensory cortex (Rolls, 2004). Based on this subdivision of the mPFC which has been related to different aspect of the self in adults, future research may offer a map of the frontal cortex through the first years of life, providing specific information on the consequential stages of the development of the sense of self. In fact, as described in the introduction of this thesis, it has been thought that different aspects of the self arise at different ages. The bodily self-awareness seems to be achieved in the first months after birth (Filippetti et al., 2015; Rochat & Hespos, 1997); emerging self-awareness has been shown from 18 months with this thesis, consistent with previous studies (Amsterdam, 1972; Asendorpf & Baudonnière, 1994; Asendorpf et al., 1996; Rochat, 1995); finally, the sense of agency, as defined by Moore (2016), is achieved only later than 18 months, with capacities of reflection on one's own actions (Stephens & Graham, 1994). Moreover, it would be interesting to look at patterns of functional connectivity between the frontal cortex and other regions that are fundamental for emerging self-awareness and whether the strength of these connections can predict emerging self-awareness at 18 months. Lastly, the activation of these three portions of the frontal cortex can be explored also during mother-infant interaction, to better understand which aspects of the self are related to the early interaction with the mother.

From a methodological perspective, these future studies would be possible as a result of the recent improvements of the fNIRS method in terms of

spatial registration and functional connectivity analyses tools, which this PhD

project contributed to.

8.4.3 How to test the hypothesis of a synchronous development of self-awareness and social emotions?

Rochat hypothesized that self-recognition in the mirror might indicate not only

self-awareness, but also the development of social emotions, such as shame

(Rochat et al., 2012; Rochat & Zahavi, 2011). This hypothesis is based on the

idea that successful performance on the MSR task, which involves detecting

something unusual on one's face, is also linked to understanding how others see

and perceive ourselves (Lewis, 2011; Rochat & Zahavi, 2011). To support this,

Rochat (2012) demonstrated the influence of social norms on self-recognition

by placing a sticker on the infant's face during the MSR task, with a similar

sticker being worn by everyone else in the room. Under this condition, infants

were more hesitant to remove the sticker, whereas this reaction was not

observed when self-recognition was tested in a set-up in which the other people

in the room did not wear the sticker (Rochat et al., 2012). Rochat interpreted

this finding as an evidence for the fact that under a 'shared' condition of having

something unusual on the face, infants are less likely to experience shame

compared with a condition where only the infant has been marked on his/her

cheek, therefore attempting to take it off immediately (Rochat et al., 2012).

Although the presence of an association between the development of self-

awareness and social emotions seems plausible, given the fact that awareness

of oneself might indicate also awareness of others, to date there are no

empirical studies that support a synchronous development of self-awareness

and social emotions. Moreover, during the MSR task, shame or puzzlement are

only sometimes observed in the infants who exhibit self-recognition, but there is not a constant association between the two aspects. However, investigating the relationship between emerging self-awareness, as indicated by the MSR task, and social emotions might provide further information on the significance of self-recognition. For this purpose, adding the use of an infrared camera during the MSR task would be a possible way to perform a systematic investigation into the emotional reactions during self-recognition, detecting blush on infants' cheeks as an index of shame (Leary, Britt, Cutlip, & Templeton, 1992; Lewis, 1992). This method, called infrared thermography, records temperature changes on the participant's face, and it has been validated by previous studies as a valuable tool to measure emotional arousal (Clay-Warner & Robinson, 2015; Kolli, Fasih, Machot, & Kyamakya, 2011) even with infants (Esposito et al., 2015).

8.4.4 Are there any differences in emerging self-awareness between typical infants and infants with Autism Spectrum Disorder?

 A large body of research has shown that individuals with ASD exhibit impairments in several domains that have been thought to be related to self-other awareness, such as imitation (Dawson & Adams, 1984; Stone, Lemanek, Fishel, Fernandez, & Altemeier, 1990; Williams, Whiten, & Singh, 2004), emotion recognition (Hobson, Ouston, & Lee, 1988; Uljarevic & Hamilton, 2013), and perspective taking (Baron-Cohen, 2001; Baron-Cohen, Leslie, & Frith, 1985). Therefore, it is plausible to think that children with ASD, who have deficits in recognizing other's perspectives, might have an impairment in self-

processing as well (Frith & Happe, 1999; Uddin, 2011). This would be consistent with the hypothesis of a synchronous development of self-awareness and social cognitive abilities highlighted in the previous section. Surprisingly though, children with ASD showed no difficulties in 'passing' the MSR task. However, it has been documented that they do not show any signs of embarrassment or perplexity when they notice the mark (Dawson & McKissick, 1984; Neuman & Hill, 1978; Rochat & Zahavi, 2011; Spiker & Ricks, 1984). As previously mentioned, Rochat hypothesized an association between emerging self-awareness and social emotions (Rochat et al., 2012; Rochat & Zahavi, 2011). However, this hypothesis leaves unexplained why autistic children have no difficulties in passing the MSR task. Interestingly, it has been shown that children with ASD who failed to recognise themselves were more likely to have more severe ASD symptomatology, as evidenced by the fact that they were non-verbal, while children with ASD who were capable of self-recognition exhibited higher levels of social functioning (Spiker & Ricks, 1984). Consistent with this, Dawson reported that the few children with ASD that did not exhibit self-recognition also showed a reduced performance in other cognitive domains, such as object permanence (Dawson & McKissick, 1984). The fact that studies on self-recognition in ASD found an association between an unsuccessful performance on the MSR task and more severe symptomatology may be consistent with some of the criticisms regarding this task, where a certain level of cognitive development has been thought to be necessary to exhibit self-recognition (Loveland, 1986). Alternatively, one can also think that more severely impaired individuals with ASD are unsuccessful at the MSR task due to a possible more delayed development of the self.

In contrast to the studies that showed a typical performance of the children with ASD on the MSR task, neuroimaging studies have provided evidence for an altered brain response in relation to self-awareness in ASD. It has been shown that the functional connectivity between regions belonging to the DMN and the CMS, the central portions of the DMN, is decreased in both adults and children diagnosed with ASD (Lynch et al., 2013; Müller et al., 2011; Uddin & Menon, 2009; Washington et al., 2014). While this knowledge came from resting-state studies, there is also evidence for differences in brain responses between typically developing children and children with ASD during self-processing tasks. It has been shown that individuals with ASD show a reduced activation in the ACC when they imagine themselves performing an action compared to when the see others performing an action (Chiu et al., 2008), and a reduced activity in the mPFC and reduced functional connectivity between the mPFC and the somatosensory cortex while they made judgments on both the self and other (Kennedy & Courchesne, 2008; Lombardo, Chakrabarti, Bullmore, Sadek, et al., 2010). Moreover, 10-year-old children with ASD showed hypoactivation of the right IFG compared to typically developing children when looking at their own face (Kita et al., 2011). Lastly, while typically developing children showed activation of prefrontal regions when looking at their own face and others' faces, children with ASD activated these regions for images of their own face only. This finding has been interpreted as evidence for a lack of shared representation between self and other, which instead characterised typically developing children (Uddin et al., 2008).

This section highlighted how current knowledge of self-awareness and ASD are controversial and not always coherent. Performance of the children with ASD on the MSR task has been described as typical (Dawson & McKissick,

1984; Neuman & Hill, 1978; Rochat & Zahavi, 2011; Spiker & Ricks, 1984), but there is a large body of neuroimaging literature showing that individuals with ASD exhibited reduced activation and functional connectivity in core regions for self-processing (Chiu et al., 2008; Kennedy & Courchesne, 2008; Kita et al., 2011; Lombardo, Chakrabarti, Bullmore, Sadek, et al., 2010; Lynch et al., 2013; Müller et al., 2011; Uddin et al., 2008; Uddin & Menon, 2009; Washington et al., 2014). Giving this inconsistency between behavioural and neuroimaging findings, further research is needed to systematically explore emerging self-awareness in ASD. In particular, studying the development of the sense of self, i.e. during the second year of life, might better elucidate any differences in mechanisms underlying it the development of self-awareness in typically developing children and children with ASD. For example, it would be interesting to test infants at high-risk of ASD (which have at least one older sibling with a clinical diagnosis in the autism spectrum) with the fNIRS paradigm presented in Chapter 5. This study may inform on a possible hypoactivation of core regions related to self-processing early in life and which may be related to the behavioural assessment of the MSR task. Moreover, implementing the infrared thermography suggested in the previous section for the study of emerging self-awareness in high-risk of ASD infants can inform on the emotional reaction during self-recognition.

8.5   Concluding remarks

This thesis work investigated the mechanisms underlying the development of self-awareness. Taken together, the results of this PhD project have provided evidence for the significance of visual self-recognition in infancy, suggesting that a broad sense of self may emerge between 18 and 24 months, indicating not only a recognition of physical features, but also psychological self-awareness. In terms of neuroimaging findings, the mPFC and the TPJ were identified as key brain regions for self-processing in infancy, and also functionally synchronised as part of a wider brain network measured during quiet rest in infants with a more developed sense of self. This PhD work focused also on the relationship between self-awareness and social interactions in infancy, showing that self-awareness influences the way that infants perceive the social environment, and, if mimicry does indeed reflect a motivation to affiliate, affecting their tendency to selectively affiliate with social groups.

The present novel findings represent a pioneering starting point for future investigations into a deeper understanding of self-awareness in infancy. This PhD thesis opens up avenues for future studies interested in the relationship between developing self-awareness with other social domains, such as theory of mind, social emotions and the early mother-infant relationship. Moreover, based on the findings of this work, future research can explore any differences in emerging self-awareness between typically developing infants, and infants at high-risk of ASD. From a methodological perspective, the fNIRS community may benefit from the connectivity analyses tools advanced in this PhD that can open new avenues of research on understanding the trajectory of functional networks in the developing brain.

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channels

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		2	2	2	3	2	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	2
2	2		2	2	3	2	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	2
3	2	2		2	3	2	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	2
4	2	2	2		3	2	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	2
5	3	3	3	3		3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
6	2	2	2	2	3		3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	2
7	3	3	3	3	3	3		3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
8	3	3	3	3	3	3	3		3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
9	3	3	3	3	3	3	3	3		3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
10	3	3	3	3	3	3	3	3	3		2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
11	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
12	3	3	3	3	3	3	3	3	3	3	2		2	3	3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
13	2	2	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
14	3	3	3	3	3	3	3	3	3	3	2	3	2		3	3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
15	3	3	3	3	3	3	3	3	3	3	2	3	2	3		3	3	3	3	3	2	3	2	2	3	3	3	2	3	2
16	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3		3	3	3	3	2	3	2	2	3	3	3	2	3	2
17	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3		3	3	3	2	3	2	2	3	3	3	2	3	2
18	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3		3	3	2	3	2	2	3	3	3	2	3	2
19	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3		3	2	3	2	2	3	3	3	2	3	2
20	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3	3		2	3	2	2	3	3	3	2	3	2
21	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	2	2	2	2
22	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3	3	2	3		2	2	3	3	3	2	3	2
23	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	2	2
24	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2		2	2	2	2	2	2
25	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2		3	3	2	3	2
26	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3		3	2	3	2
27	3	3	3	3	3	3	3	3	3	3	2	3	2	3	3	3	3	3	3	3	2	3	2	2	3	3		2	3	2
28	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2		2	2
29	2	2	2	2	3	2	3	3	3	3	3	2	3	2	3	3	3	3	3	3	2	3	2	2	3	3	3	2		2
30	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	

channels

Supplementary Table 1 Degrees of freedom of the paired t-tests between 11 months and 18 months in each connection.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		4	3	2	3	3	3	3	4	3	3	4	3	4	4	4	4	4	4	4	4	4	3	4	3	3	4	4	4	4
2	4		4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	5	5
3	3	4		2	2	4	4	4	4	4	3	4	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	4	4
4	2	2	2		2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	1	2	2	2	2
5	3	3	2	2		2	2	2	3	2	2	3	2	3	3	3	3	3	3	3	3	3	2	3	2	2	3	3	3	3
6	3	4	4	2	2		4	4	4	4	3	4	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	4	4
7	3	4	4	2	2	4		4	4	4	3	4	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	4	4
8	3	4	4	2	2	4	4		4	4	3	4	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	4	4
9	4	5	4	2	3	4	4	4		4	3	5	3	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	5	5
10	3	4	4	2	2	4	4	4	4		3	4	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	4	4
11	3	3	3	2	2	3	3	3	3	3		3	3	3	3	3	3	3	3	3	3	3	2	3	2	2	3	3	3	3
12	4	5	4	2	3	4	4	4	5	4	3		3	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	5	5
13	3	3	3	2	2	3	3	3	3	3	3	3		3	3	3	3	3	3	3	3	3	2	3	2	2	3	3	3	3
14	4	5	4	2	3	4	4	4	5	4	3	5	3		5	5	5	5	5	5	4	5	3	4	4	4	5	5	5	5
15	4	5	4	2	3	4	4	4	5	4	3	5	3	5		5	5	5	5	5	4	5	3	4	4	4	5	5	5	5
16	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5		5	5	5	5	4	5	3	4	4	4	5	5	5	5
17	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5		5	5	5	4	5	3	4	4	4	5	5	5	5
18	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5		5	5	4	5	3	4	4	4	5	5	5	5
19	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5		5	4	5	3	4	4	4	5	5	5	5
20	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5		4	5	3	4	4	4	5	5	5	5
21	4	4	3	2	3	3	3	3	4	3	3	4	3	4	4	4	4	4	4	4		4	3	4	3	3	4	4	4	4
22	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5	5	4		3	4	4	4	5	5	5	5
23	3	3	2	1	2	2	2	2	3	2	2	3	2	3	3	3	3	3	3	3	3	3		3	2	2	3	3	3	3
24	4	4	3	2	3	3	3	3	4	3	3	4	3	4	4	4	4	4	4	4	4	3			3	3	4	4	4	4
25	3	4	3	1	2	3	3	3	4	3	2	4	2	4	4	4	4	4	4	4	3	4	2	3		4	4	4	4	4
26	3	4	3	1	2	3	3	3	4	3	2	4	2	4	4	4	4	4	4	4	3	4	2	3	4		4	4	4	4
27	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5	5	4	5	3	4	4	4		4	5	5
28	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5	5	4	5	3	4	4	4	4		5	5
29	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5		5
3	4	5	4	2	3	4	4	4	5	4	3	5	3	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	5	0

channels

Supplementary Table 2 Degrees of freedom of the paired t-tests between 11 months and 24 months in each connection. Connections highlighted in grey are those excluded from the analysis as only half or less than half of the sample contribuited to the statistical test.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		2	1	1	5	1	4	4	5	5	4	2	3	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	1	1
2	2		2	2	6	1	5	4	5	5	4	3	3	6	6	6	6	6	5	6	4	6	3	4	4	4	6	6	2	2
3	1	2		2	5	1	5	4	4	4	3	3	3	5	5	5	5	5	4	5	3	5	2	3	3	3	5	5	1	1
4	1	2	2		5	1	5	4	4	4	3	3	3	5	5	5	5	5	4	5	3	5	2	3	3	3	5	5	1	1
5	5	6	5	5		4	5	4	5	5	4	3	3	6	6	6	6	6	5	6	4	6	3	4	4	4	6	6	5	5
6	1	1	1	1	4		4	4	4	4	3	2	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	0	0
7	4	5	5	5	5	4		4	4	4	3	3	3	5	5	5	5	5	4	5	3	5	2	3	3	3	5	5	4	4
8	4	4	4	4	4	4	4		4	4	3	2	3	4	4	4	4	4	4	4	3	4	2	3	3	3	4	4	3	3
9	5	5	4	4	5	4	4	4		5	4	2	3	5	5	5	5	5	5	4	5	3	4	4	4	4	5	5	4	4
10	5	5	4	4	5	4	4	4	5		4	2	3	5	5	5	5	5	5	4	5	3	4	4	4	4	5	5	4	4
11	4	4	3	3	4	3	3	3	4	4		1	3	4	4	4	4	4	4	4	4	3	4	3	3	4	4	4	4	4
12	2	3	3	3	3	2	3	2	2	2	1		1	3	3	3	3	3	2	3	1	3	1	1	1	1	3	3	2	2
13	3	3	3	3	3	3	3	3	3	3	3	1		3	3	3	3	3	3	3	3	3	2	3	2	2	3	3	3	3
14	5	6	5	5	6	4	5	4	5	5	4	3	3		6	6	6	6	5	6	4	6	3	4	4	4	6	6	5	5
15	5	6	5	5	6	4	5	4	5	5	4	3	3	6		6	6	6	5	6	4	6	3	4	4	4	6	6	5	5
16	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6		6	6	5	6	4	6	3	4	4	4	6	6	5	5
17	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6	6		6	5	6	4	6	3	4	4	4	6	6	5	5
18	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6	6	6		5	6	4	6	3	4	4	4	6	6	5	5
19	5	5	4	4	5	4	4	4	5	5	4	2	3	5	5	5	5	5		5	4	5	3	4	4	4	5	5	4	4
2	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6	6	6	6	5		4	6	3	4	4	4	6	6	5	5
21	4	4	3	3	4	3	3	3	4	4	4	1	3	4	4	4	4	4	4	4		4	3	4	3	3	4	4	4	4
22	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6	6	6	6	5	6	4		3	4	4	4	6	6	5	5
23	3	3	2	2	3	2	2	2	3	3	3	1	2	3	3	3	3	3	3	3	3	3		3	2	2	3	3	3	3
24	4	4	3	3	4	3	3	3	4	4	4	1	3	4	4	4	4	4	4	4	4	3	3		3	3	4	4	4	4
25	4	4	3	3	4	3	3	3	4	4	3	1	2	4	4	4	4	4	4	4	3	4	2	3		4	4	4	3	3
26	4	4	3	3	4	3	3	3	4	4	3	1	2	4	4	4	4	4	4	4	3	4	2	3	4		4	4	3	3
27	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6	6	6	6	5	6	4	6	3	4	4	4		6	5	5
28	5	6	5	5	6	4	5	4	5	5	4	3	3	6	6	6	6	6	5	6	4	6	3	4	4	4	6		5	5
29	1	2	1	1	5	0	4	3	4	4	4	2	3	5	5	5	5	5	4	5	4	5	3	4	3	3	5	5		2
30	1	2	1	1	5	0	4	3	4	4	4	2	3	5	5	5	5	5	4	5	4	5	3	4	3	3	5	5	2	

channels

channels

Supplementary Table 3 Degrees of freedom of the paired t-tests between 11 months and 30 months in each connection. Connections highlighted in grey are those excluded from the analysis as only half or less than half of the sample contribuited to the statistical test.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		3	2	2	6	2	5	5	6	6	5	6	5	6	6	6	6	6	6	6	5	6	4	5	5	5	6	6	3	3
2	3		3	3	7	2	6	5	7	6	5	7	5	7	7	7	7	7	7	7	5	7	4	5	5	5	7	7	4	3
3	2	3		3	6	2	6	5	6	5	4	6	4	6	6	6	6	6	6	6	4	6	3	4	4	4	6	6	3	2
4	2	3	3		6	2	6	5	6	5	4	6	4	6	6	6	6	6	6	6	4	6	3	4	4	4	6	6	3	2
5	6	7	6	6		5	6	5	7	6	5	7	5	7	7	7	7	7	7	7	5	7	4	5	5	5	7	7	7	6
6	2	2	2	2	5		5	5	5	5	4	5	4	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	2	2
7	5	6	6	6	6	5		5	6	5	4	6	4	6	6	6	6	6	6	6	4	6	3	4	4	4	6	6	6	5
8	5	5	5	5	5	5	5		5	5	4	5	4	5	5	5	5	5	5	5	4	5	3	4	4	4	5	5	5	5
9	6	7	6	6	7	5	6	5		6	5	7	5	7	7	7	7	7	7	7	5	7	4	5	5	5	7	7	7	6
10	6	6	5	5	6	5	5	5	6		5	6	5	6	6	6	6	6	6	6	5	6	4	5	5	5	6	6	6	6
11	5	5	4	4	5	4	4	4	5	5		5	5	5	5	5	5	5	5	5	5	5	4	5	4	4	5	5	5	5
12	6	7	6	6	7	5	6	5	7	6	5		5	7	7	7	7	7	7	7	5	7	4	5	5	5	7	7	7	6
13	5	5	4	4	5	4	4	4	5	5	5	5		5	5	5	5	5	5	5	5	5	4	5	4	4	5	5	5	5
14	6	7	6	6	7	5	6	5	7	6	5	7	5		7	7	7	7	7	7	5	7	4	5	5	5	7	7	7	6
15	6	7	6	6	7	5	6	5	7	6	5	7	5	7		7	7	7	7	7	5	7	4	5	5	5	7	7	7	6
16	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7		7	7	7	7	5	7	4	5	5	5	7	7	7	6
17	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7		7	7	7	5	7	4	5	5	5	7	7	7	6
18	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7	7		7	7	5	7	4	5	5	5	7	7	7	6
19	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7	7	7		7	5	7	4	5	5	5	7	7	7	6
20	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7	7	7	7		5	7	4	5	5	5	7	7	7	6
21	5	5	4	4	5	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5		5	4	5	4	4	5	5	5	5
22	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7	7	7	7	7	5		4	5	5	5	7	7	7	6
23	4	4	3	3	4	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4		4	3	3	4	4	4	4
24	5	5	4	4	5	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4		4	4	5	5	5	5
25	5	5	4	4	5	4	4	4	5	5	4	5	4	5	5	5	5	5	5	5	4	5	3	4		5	5	5	5	5
26	5	5	4	4	5	4	4	4	5	5	4	5	4	5	5	5	5	5	5	5	4	5	3	4	5		5	5	5	5
27	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7	7	7	7	7	5	7	4	5	5	5		7	7	6
28	6	7	6	6	7	5	6	5	7	6	5	7	5	7	7	7	7	7	7	7	5	7	4	5	5	5	7		7	6
29	3	4	3	3	7	2	6	5	7	6	5	7	5	7	7	7	7	7	7	7	5	7	4	5	5	5	7	7		3
30	3	3	2	2	6	2	5	5	6	6	5	6	5	6	6	6	6	6	6	6	5	6	4	5	5	5	6	6	3	

channels (rows) × channels (columns)

Supplementary Table 4 Degrees of freedom of the paired t-tests between 11 months and 36 months in each connection. Connections highlighted in grey are those excluded from the analysis as only half or less than half of the sample contribuited to the statistical test.

channels

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		6	6	5	5	6	6	6	6	6	6	5	5	6	6	6	6	6	6	6	6	6	6	5	6	5	5	6	6	8
2	6		10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
3	6	10		5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
4	5	5	5		5	5	5	5	5	5	5	8	8	5	5	5	5	5	5	5	5	5	5	8	5	8	8	5	5	7
5	5	5	5	5		5	5	5	5	5	5	8	8	5	5	5	5	5	5	5	5	5	5	8	5	8	8	5	5	7
6	6	10	10	5	5		9	10	10	10	9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	6
7	6	9	9	5	5	9		9	9	9	9	8	8	9	9	9	9	9	9	9	9	9	9	8	9	8	8	8	9	6
8	6	10	10	5	5	10	9		10	10	9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
9	6	10	10	5	5	10	9	10		10	9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
10	6	10	10	5	5	10	9	10	10		9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
11	6	9	9	5	5	9	9	9	9	9		8	8	9	9	9	9	9	9	9	9	9	9	8	9	8	8	8	9	6
12	5	9	9	8	8	9	8	9	9	9	8		9	9	9	9	9	9	9	9	9	9	9	8	9	8	8	8	9	6
13	5	9	9	8	8	9	8	9	9	9	8	9		9	9	9	9	9	9	9	9	9	9	8	9	8	8	8	9	6
14	6	10	10	5	5	10	9	10	10	10	9	9	9		10	10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
15	6	10	10	5	5	10	9	10	10	10	9	9	9	10		10	10	10	10	10	10	10	10	9	10	9	9	9	10	7
16	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10		10	10	10	10	10	10	10	9	10	9	9	9	10	7
17	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10		10	10	10	10	10	10	9	10	9	9	9	10	7
18	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10		10	10	10	10	10	9	10	9	9	9	10	7
19	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10		10	10	10	10	9	10	9	9	9	10	7
20	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10		10	10	10	9	10	9	9	9	10	7
21	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10		10	10	9	10	9	9	9	10	7
22	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10	10		10	9	10	9	9	9	10	7
23	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10	10	10		9	10	9	9	9	10	7
24	5	9	9	8	8	9	8	9	9	9	8	8	8	9	9	9	9	9	9	9	9	9	9		9	9	9	8	9	7
25	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10	10	10	10	9		9	9	9	10	7
26	5	9	9	8	8	9	8	9	9	9	8	8	8	9	9	9	9	9	9	9	9	9	9	9	9		9	8	9	7
27	5	9	9	8	8	9	8	9	9	9	8	8	8	9	9	9	9	9	9	9	9	9	9	9	9	9		6	9	7
28	6	9	9	5	5	9	8	9	9	9	8	8	8	9	9	9	9	9	9	9	9	9	9	8	9	8	6		9	7
29	6	10	10	5	5	10	9	10	10	10	9	9	9	10	10	10	10	10	10	10	10	10	10	9	10	9	9	9		7
30	8	7	7	7	3	7	6	7	7	7	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	

channels

Supplementary Table 5 Degrees of freedom of the paired t-tests between 18 months and 24 months in each connection.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
2	9		9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
3	9	9		9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
4	9	9	9		9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
5	9	9	9	9		9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
6	9	9	9	9	9		9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
7	9	9	9	9	9	9		9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
8	9	9	9	9	9	9	9		9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
9	9	9	9	9	9	9	9	9		9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
10	9	9	9	9	9	9	9	9	9		9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
11	9	9	9	9	9	9	9	9	9	9		6	7	9	9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
12	6	6	6	6	6	6	6	6	6	6	6		5	6	6	6	6	6	6	6	6	6	6	5	6	5	6	5	5	5
13	7	7	7	7	7	7	7	7	7	7	7	5		7	7	7	7	7	7	7	7	7	7	6	7	6	7	6	6	5
14	9	9	9	9	9	9	9	9	9	9	9	6	7		9	9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
15	9	9	9	9	9	9	9	9	9	9	9	6	7	9		9	9	9	9	9	9	9	9	8	9	8	9	8	8	7
16	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9		9	9	9	9	9	9	9	8	9	8	9	8	8	7
17	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9		9	9	9	9	9	9	8	9	8	9	8	8	7
18	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9		9	9	9	9	9	8	9	8	9	8	8	7
19	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9		9	9	9	9	8	9	8	9	8	8	7
20	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9		9	9	9	8	9	8	9	8	8	7
21	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9		9	9	8	9	8	9	8	8	7
22	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9		9	8	9	8	9	8	8	7
23	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9		8	9	8	9	8	8	7
24	8	8	8	8	8	8	8	8	8	8	8	5	6	8	8	8	8	8	8	8	8	8	8		8	8	8	7	7	6
25	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8		8	9	8	8	7
26	8	8	8	8	8	8	8	8	8	8	8	5	6	8	8	8	8	8	8	8	8	8	8	8	8		8	7	7	6
27	9	9	9	9	9	9	9	9	9	9	9	6	7	9	9	9	9	9	9	9	9	9	9	8	9	8		8	8	7
28	8	8	8	8	8	8	8	8	8	8	8	5	6	8	8	8	8	8	8	8	8	8	8	7	8	7	8		8	7
29	8	8	8	8	8	8	8	8	8	8	8	5	6	8	8	8	8	8	8	8	8	8	8	7	8	7	8	8		7
30	7	7	7	7	7	7	7	7	7	7	7	5	5	7	7	7	7	7	7	7	7	7	7	6	7	6	7	7	7	

channels

Supplementary Table 6 Degrees of freedom of the paired t-tests between 18 months and 30 months in each connection.

channels

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1		14	14	14	14	14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
2	14		14	14	14	14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
3	14	14		14	14	14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
4	14	14	14		14	14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
5	14	14	14	14		14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
6	14	14	14	14	14		13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
7	13	13	13	13	13	13		13	13	12	13	13	13	13	13	13	13	13	13	13	13	12	13	12	13	11	12	12	13	11
8	13	13	13	13	13	13	13		13	12	13	13	13	13	13	13	13	13	13	13	13	12	13	12	13	11	12	12	13	11
9	14	14	14	14	14	14	13	13		12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
10	12	12	12	12	12	12	12	12	12		12	12	12	12	12	12	12	12	12	12	12	11	12	12	12	11	12	11	12	11
11	14	14	14	14	14	14	13	13	14	12		13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
12	13	13	13	13	13	13	13	13	13	12	13		13	13	13	13	13	13	13	13	13	12	13	12	13	11	12	12	13	11
13	13	13	13	13	13	13	13	13	13	12	13	13		13	13	13	13	13	13	13	13	12	13	12	13	11	12	12	13	11
14	14	14	14	14	14	14	13	13	14	12	14	13	13		14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
15	14	14	14	14	14	14	13	13	14	12	14	13	13	14		14	14	14	13	13	13	12	13	12	13	11	13	13	14	12
16	14	14	14	14	14	14	13	13	14	12	14	13	13	14	14		14	14	13	13	13	12	13	12	13	11	13	13	14	12
17	14	14	14	14	14	14	13	13	14	12	14	13	13	14	14	14		14	13	13	13	12	13	12	13	11	13	13	14	12
18	14	14	14	14	14	14	13	13	14	12	14	13	13	14	14	14	14		13	13	13	12	13	12	13	11	13	13	14	12
19	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	13	13	13		13	13	12	13	12	13	11	12	12	13	11
20	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	13	13	13	13		13	12	13	12	13	11	12	12	13	11
21	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	13	13	13	13	13		12	13	12	13	11	12	12	13	11
22	12	12	12	12	12	12	12	12	12	11	12	12	12	12	12	12	12	12	12	12	12		12	11	12	10	11	11	12	10
23	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	13	13	13	13	13	12	12		12	13	11	12	12	13	11
24	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	11	12		12	11	12	11	12	11
25	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	13	13	13	13	13	13	12	13	12		11	12	12	13	11
26	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	10	11	11	11	11		11	10	11	10
27	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	13	13	13	13	13	12	13	12	12	12	11		11	13	12
28	13	13	13	13	13	13	12	12	13	11	13	12	12	13	13	13	13	13	12	12	12	11	12	11	12	10	11		13	12
29	14	14	14	14	14	14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13		12
30	0	14	14	14	14	14	13	13	14	12	14	13	13	14	14	14	14	14	13	13	13	12	13	12	13	11	13	13	14	

channels

Supplementary Table 7 Degrees of freedom of the paired t-tests between 18 months and 36 months in each connection.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1		9	9	8	8	9	9	9	9	7	9	7	9	9	9	9	8	8	8	9	8	9	9	9	9	9	9	9	9	9	8	9	9	9	9	9	9	8	9	9	9	9	8	8
2	9		14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
3	9	14		8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
4	8	8	8		8	8	8	8	8	7	9	9	9	8	8	8	10	10	10	8	10	8	8	8	8	8	8	8	8	10	8	8	8	8	8	8	10	9	9	8	8	8	10	10
5	8	8	8	8		8	8	8	8	10	9	9	9	8	8	8	10	10	10	8	10	8	8	8	8	8	8	8	8	10	8	8	8	8	8	8	10	9	9	8	8	8	10	10
6	9	14	14	8	8		13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	13	14	14	14	14	14	13	12	14	13	14	13	13	12	11	10	10	12	12	13	10	11
7	9	13	13	8	8	13		12	13	11	10	11	10	13	13	13	12	12	11	13	12	13	13	13	13	13	13	13	12	11	13	12	13	13	13	12	11	10	10	12	12	13	10	11
8	9	13	13	8	8	13	12		13	11	9	11	9	13	13	13	12	12	12	13	12	13	13	13	13	13	13	13	13	12	11	13	13	13	12	12	11	11	10	10	13	13	13	12
9	9	14	14	8	8	14	13	13		12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
10	10	12	12	10	10	12	11	11	12		10	11	10	12	12	12	11	11	10	12	11	12	12	12	12	12	12	12	11	10	12	11	12	11	11	10	11	10	10	11	11	12	10	11
11	9	10	10	9	9	10	10	9	10	10		9	10	10	10	10	10	10	9	10	10	10	10	10	10	10	10	10	9	9	10	9	10	10	10	9	9	9	9	9	9	10	8	9
12	10	12	12	9	9	12	11	11	12	11	9		9	12	12	12	11	11	10	12	11	12	12	12	12	12	12	12	11	10	12	11	12	11	11	10	11	9	9	11	11	12	10	11
13	9	10	10	9	9	10	10	9	0	10	9	9		10	10	10	10	10	9	10	10	10	10	10	10	10	10	10	9	10	9	10	10	10	10	9	9	9	9	9	9	10	8	9
14	9	14	14	8	8	14	13	13	14	12	10	12	10		14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
15	9	14	14	8	8	14	13	13	14	12	10	12	10	14		14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
16	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14		13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
17	8	13	13	10	10	13	12	12	13	11	10	11	10	13	13	13		13	12	13	13	13	13	13	13	13	13	13	12	12	13	12	13	12	11	11	11	11	11	12	12	13	10	11
18	8	13	13	10	10	13	12	12	13	11	10	11	10	13	13	13	13		12	13	13	13	13	13	13	13	13	13	12	12	13	12	13	12	11	11	11	11	11	12	12	13	10	11
19	8	12	12	10	10	12	11	12	12	10	9	10	9	12	12	12	12	12		12	12	12	12	12	12	12	12	12	11	11	12	12	12	11	11	10	10	10	10	12	12	12	10	11
20	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12		13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
21	8	13	13	10	10	13	12	12	13	11	10	11	10	13	13	13	13	12	13	13		13	13	13	13	13	13	13	12	11	13	12	13	12	12	11	11	11	11	11	12	12	13	10
22	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13		14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
23	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14		14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
24	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14		14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
25	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14		14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
26	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14		14	14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
27	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	13	14	14	14		14	13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
28	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	12		13	12	14	13	14	13	13	12	12	11	11	13	13	14	11	12
29	9	13	13	8	8	13	12	12	13	11	9	11	9	13	13	13	12	12	11	13	12	13	13	13	13	13	13	13		12	13	12	13	12	12	11	11	10	10	12	12	13	11	11
30	8	12	12	10	10	12	11	11	12	10	9	10	9	12	12	12	12	12	11	12	12	12	12	12	12	12	12	12	0		12	11	12	11	11	10	10	10	10	11	11	12	10	10
31	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12		13	14	13	13	12	12	11	11	13	13	14	11	12
32	9	13	13	8	8	13	12	13	13	11	9	11	9	13	13	13	12	12	12	13	12	13	13	13	13	13	13	13	12	11	13		13	12	12	11	11	10	10	13	13	13	11	12
33	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13		13	13	12	12	11	11	13	13	14	11	12
34	9	13	13	8	8	13	12	12	13	11	10	11	10	13	13	13	12	12	11	13	12	13	13	13	13	13	13	13	13	12	11	13	12		12	11	11	10	10	12	12	13	10	11
35	9	13	13	8	8	13	12	12	13	11	10	11	10	13	13	13	12	12	11	13	12	13	13	13	13	13	13	13	12	11	13	12	13	13		12	11	10	10	12	12	13	10	11
36	9	12	12	8	8	12	12	11	12	10	9	10	9	12	12	12	11	11	10	12	11	12	12	12	12	12	12	12	11	10	12	11	12	11	12		11	9	9	11	11	12	9	10
37	8	12	12	10	10	12	11	11	12	11	9	11	9	12	12	12	11	11	10	12	11	12	12	12	12	12	12	12	11	10	12	11	12	11	11	11		9	9	11	11	12	10	11
38	9	11	11	9	9	11	10	10	11	10	9	9	9	11	11	11	11	11	10	11	11	11	11	11	11	11	11	11	10	10	11	10	11	10	11	10	9		11	10	10	11	8	9
39	9	11	11	9	9	11	10	10	11	10	9	9	9	11	11	11	11	11	10	11	11	11	11	11	11	11	11	11	10	10	11	10	11	10	11	10	10	9		10	10	11	8	9
40	9	13	13	8	8	13	12	13	13	11	9	11	9	13	13	13	12	12	12	13	12	13	13	13	13	13	13	13	12	11	13	13	13	12	12	11	11	10	10		13	13	11	12
41	9	13	13	8	8	13	12	13	13	11	9	11	9	13	13	13	12	12	12	13	12	13	13	13	13	13	13	13	12	11	13	13	13	12	12	11	11	10	10	13		13	11	12
42	9	14	14	8	8	14	13	13	14	12	10	12	10	14	14	14	13	13	12	14	13	14	14	14	14	14	14	14	13	12	14	13	14	13	13	12	12	11	11	13	13		11	12
43	8	11	11	10	10	11	10	11	11	10	8	10	8	11	11	11	10	10	10	11	10	11	11	11	11	11	11	11	11	10	11	11	11	10	10	9	10	8	8	11	11	11		11
44	8	12	12	10	10	12	11	12	12	11	9	11	9	12	12	12	11	11	11	12	11	12	12	12	12	12	12	12	11	10	12	12	12	11	11	10	11	9	9	12	12	12	11	

channels

Supplementary Table 8 Degrees of freedom of the paired t-tests between 24 months and 30 months in each connection.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1		13	13	11	11	13	13	12	12	10	10	13	11	13	13	13	12	13	11	12	13	13	13	13	13	13	13	13	13	12	13	13	13	13	12	13	13	9	9	12	10	12	11	13
2	13		17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
3	13	17		11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
4	11	11	11		11	11	11	10	10	9	9	11	10	11	11	11	10	11	9	10	11	11	11	11	11	11	11	11	11	11	10	11	11	11	11	10	11	11	11	11	10	11	10	9	11
5	11	11	11	11		11	11	10	10	9	9	11	10	11	11	11	10	11	9	10	11	11	11	11	11	11	11	11	11	11	10	11	11	11	11	10	11	11	11	11	10	11	10	9	11
6	13	16	16	11	11		16	15	15	13	13	16	14	16	16	16	15	16	14	15	16	16	16	16	16	16	16	16	16	16	15	16	16	16	16	15	15	15	12	12	15	13	15	13	16
7	13	16	16	11	11	16		15	15	13	13	16	14	16	16	16	15	16	14	15	16	16	16	16	16	16	16	16	16	16	15	16	16	16	16	15	15	15	12	12	15	13	15	13	16
8	12	15	15	10	10	15	15		14	12	13	15	13	15	15	15	15	15	14	14	15	15	15	15	15	15	15	15	15	15	14	15	15	15	15	14	14	14	12	12	14	12	14	12	15
9	12	15	15	10	10	15	15	14		13	13	15	14	15	15	15	14	15	13	14	15	15	15	15	15	15	15	15	15	15	14	15	15	15	15	14	14	14	11	11	14	12	14	13	15
10	10	14	14	9	9	13	13	12	13		13	14	14	14	14	13	12	14	11	13	14	14	14	14	14	14	14	14	13	12	14	13	13	13	14	13	13	11	11	12	11	14	12	14
11	10	14	14	9	9	13	13	13	13	13		14	14	14	14	13	13	14	12	13	14	14	14	14	14	14	14	14	13	12	14	13	13	13	14	13	13	12	12	12	10	13	11	14
12	13	17	17	11	11	16	16	15	15	14	14		15	17	17	16	15	17	14	16	17	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
13	11	15	15	10	10	14	14	13	14	14	15	15		15	15	14	13	15	12	14	15	15	15	15	15	15	15	15	14	13	15	14	14	14	15	14	14	12	12	13	11	14	12	15
14	13	17	17	11	11	16	16	15	15	14	14	17	15		17	16	15	17	14	16	17	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
15	13	17	17	11	11	16	16	15	15	14	14	17	15	17		16	15	17	14	16	17	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
16	13	16	16	11	11	16	16	15	15	13	13	16	14	16	16		15	16	14	15	16	16	16	16	16	16	16	16	16	16	15	16	16	16	16	15	15	15	12	12	15	13	15	13	16
17	12	15	15	10	10	15	15	15	14	12	13	15	13	15	15	15		15	14	14	15	15	15	15	15	15	15	15	14	15	15	15	15	14	14	14	12	12	14	12	14	12	15
18	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15		14	16	17	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
19	11	14	14	9	9	14	14	14	14	13	11	12	14	12	14	14	14	14		14	14	14	14	14	14	14	14	14	13	14	14	14	14	13	13	13	12	12	14	12	13	11	14
20	12	16	16	10	10	15	15	14	14	13	13	16	14	16	16	16	15	14	16		16	16	16	16	16	16	16	16	15	14	16	15	15	15	15	15	15	13	13	15	13	15	12	16
21	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16		17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
22	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17		17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
23	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17		17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
24	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17		17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
25	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17		17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
26	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17		17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17	
27	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17	17		15	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
211	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17	17	15		16	15	17	16	16	16	16	16	16	13	13	15	13	16	13	17
29	13	16	16	11	11	16	16	15	15	13	13	16	14	16	16	16	15	16	14	15	16	16	16	16	16	16	16	16		15	16	16	16	16	16	15	15	15	12	12	15	13	15	13	16
30	12	15	15	10	10	15	15	14	14	12	12	15	13	15	15	15	14	15	13	14	15	15	15	15	15	15	15	15	15		15	15	15	15	14	14	14	11	11	14	13	14	12	15
31	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17	17	16	15	17	17		16	16	16	16	16	16	13	13	15	13	16	13	17
32	13	16	16	11	11	16	16	15	15	13	13	16	14	16	16	16	15	16	14	15	16	16	16	16	16	16	16	16	16	15	16		16	16	15	15	15	12	12	15	13	15	13	16
33	13	16	16	11	11	16	16	15	15	13	13	16	14	16	16	16	15	16	14	15	16	16	16	16	16	16	16	16	16	15	16	16		16	15	15	15	12	12	15	13	15	13	16
34	13	16	16	11	11	16	16	15	15	13	13	16	14	16	16	16	15	16	14	15	16	16	16	16	16	16	16	16	16	15	16	16	16		15	15	15	12	12	15	13	15	13	16
35	12	16	16	10	10	15	15	14	15	14	14	16	15	16	16	15	14	16	13	15	16	16	16	16	16	16	16	16	15	14	16	15	15	15		15	15	12	12	14	12	15	13	16
36	13	16	16	11	11	15	15	14	14	13	13	16	14	16	16	15	14	16	13	15	16	16	16	16	16	16	16	16	15	14	16	15	15	15	15		16	12	12	14	12	15	12	16
37	13	16	16	11	11	15	15	14	14	13	13	16	14	16	16	15	14	16	13	15	16	16	16	16	16	16	16	16	15	14	16	15	15	15	15	16		12	12	14	12	15	12	16
38	9	13	13	11	11	12	12	12	11	11	12	13	12	13	13	12	12	13	12	13	13	13	13	13	13	13	13	13	12	11	13	12	12	12	12	12	12		13	12	10	12	9	13
39	9	13	13	11	11	12	12	12	11	11	12	13	12	13	13	12	12	13	12	13	13	13	13	13	13	13	13	13	12	11	13	12	12	12	12	12	13		12	10	12	9	13	
40	12	15	15	10	10	15	15	14	14	12	12	15	13	15	15	15	14	15	14	15	15	15	15	15	15	15	15	15	15	14	15	15	15	15	14	14	14	12	12		13	14	12	15
41	10	13	13	11	11	13	13	12	11	10	10	13	11	13	13	13	12	13	13	13	13	13	13	13	13	13	13	13	13	12	13	13	13	13	13	14	12	10	10	13		13	11	13
42	12	16	16	10	10	15	15	14	14	14	13	16	14	16	16	15	14	16	13	15	16	16	16	16	16	16	16	16	16	15	14	16	15	15	15	15	15	12	12	14	13		13	16
43	11	13	13	9	9	13	13	12	13	12	11	13	12	13	13	13	12	13	11	12	13	13	13	13	13	13	13	13	12	13	13	13	13	13	12	12	9	9	12	11	13		13	
44	13	17	17	11	11	16	16	15	15	14	14	17	15	17	17	16	15	17	14	16	17	17	17	17	17	17	17	16	15	17	16	16	16	16	16	16	13	13	15	13	16	13		

channels

Supplementary Table 9 Degrees of freedom of the paired t-tests between 24 months and 36 months in each connection.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1		21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
2	21		21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
3	21	21		21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
4	21	21	21		21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
5	21	21	21	21		19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
6	19	19	19	19	19		19	18	18	18	18	15	16	19	19	19	19	18	19	18	18	18	19	17	18	16	19	19	19	17	19	19	19	19	17	18	17	19	19	19	19	19	16	17
7	20	20	20	20	20	19		19	18	18	19	16	17	20	20	20	20	19	20	19	19	19	20	18	18	16	20	20	20	17	20	20	20	19	17	19	18	20	20	20	20	19	16	17
8	20	20	20	20	20	18	19		17	18	20	16	18	20	20	19	19	20	18	19	20	19	20	18	18	16	20	20	19	17	20	19	19	18	17	19	18	20	20	20	20	19	15	16
9	18	18	18	18	18	18	18	17		17	17	15	16	18	18	18	18	17	18	17	17	17	18	16	17	15	18	18	18	16	18	18	18	18	17	17	17	18	18	18	18	18	16	17
10	19	19	19	19	19	18	18	18	17		18	15	16	19	19	18	18	18	18	19	18	18	19	17	19	16	19	19	18	16	19	18	18	18	17	18	17	19	19	19	19	19	16	17
11	20	20	20	20	20	18	19	20	17	18		16	18	20	20	19	19	20	18	19	20	19	20	18	18	16	20	20	19	17	20	19	19	18	17	19	18	20	20	20	20	19	15	16
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13	18	18	18	18	18	16	17	18	16	16	18	15		18	18	17	17	18	16	17	18	17	18	16	16	14	18	18	17	15	18	17	17	16	16	17	17	18	18	18	18	17	14	15
14	21	21	21	21	21	19	20	20	18	19	20	17	18		21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
15	21	21	21	21	21	19	20	20	18	19	20	17	18	21		20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
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17	20	20	20	20	20	19	20	19	18	18	19	16	17	20	20	20		19	19	19	19	19	20	18	18	16	20	20	20	17	20	20	20	19	17	19	18	20	20	20	20	19	16	17
18	20	20	20	20	20	18	19	20	17	18	20	16	18	20	20	19	19		18	19	20	19	20	18	18	16	20	20	19	17	20	19	19	18	17	19	18	20	20	20	20	19	15	16
19	19	19	19	19	19	19	19	18	18	18	18	15	16	19	19	19	19	18		18	18	18	19	17	18	16	19	19	19	17	19	19	19	19	17	18	17	19	19	19	19	19	16	17
20	20	20	20	20	20	18	19	19	17	19	19	16	17	20	20	19	19	19	18		19	19	20	18	19	16	20	20	19	16	20	19	19	18	17	19	18	20	20	20	20	19	16	17
21	20	20	20	20	20	18	19	20	17	18	20	16	18	20	20	19	19	20	18	19		19	20	18	18	16	20	20	19	17	20	19	19	18	17	19	18	20	20	20	20	19	15	16
22	20	20	20	20	20	18	19	19	17	18	19	17	17	20	20	19	19	19	18	19	19		20	18	18	16	20	20	19	17	20	19	19	18	18	20	18	20	20	20	20	19	16	16
23	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20		19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
24	19	19	19	19	19	17	18	18	16	17	18	15	16	19	19	18	18	18	17	18	18	18	19		17	17	19	19	18	15	19	18	18	17	16	18	17	19	19	19	19	18	14	15
25	19	19	19	19	19	18	18	18	17	19	18	15	16	19	19	18	18	18	18	19	18	18	19	17		16	19	19	18	16	19	18	18	18	17	18	17	19	19	19	19	19	16	17
26	17	17	17	17	17	16	16	16	15	16	16	13	14	17	17	16	16	16	16	16	16	16	17	17	16		17	17	16	14	17	16	16	16	15	16	15	17	17	17	17	17	13	14
27	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17		21	20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
28	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21		20	17	21	20	20	19	18	20	19	21	21	21	21	20	16	17
29	20	20	20	20	20	19	20	19	18	18	19	16	17	20	20	20	20	19	19	19	19	19	20	18	18	16	20	20		17	20	20	20	19	17	19	18	20	20	20	20	19	16	17
30	17	17	17	17	17	17	17	17	16	16	17	14	15	17	17	17	17	17	17	16	17	17	17	15	16	14	17	17	17		17	17	17	17	16	17	16	17	17	17	17	17	15	15
31	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17		20	20	19	18	20	19	21	21	21	21	20	16	17
32	20	20	20	20	20	19	20	19	18	18	19	16	17	20	20	20	20	19	19	19	19	19	20	18	18	16	20	20	20	17	20		20	19	17	19	18	20	20	20	20	19	16	17
33	20	20	20	20	20	19	20	19	18	18	19	16	17	20	20	20	20	19	19	19	19	19	20	18	18	16	20	20	20	17	20	20		19	17	19	18	20	20	20	20	19	16	17
34	19	19	19	19	19	19	19	18	18	18	18	15	16	19	19	19	19	18	19	18	18	18	19	17	18	16	19	19	19	17	19	19	19		17	18	17	19	19	19	19	19	16	17
35	18	18	18	18	18	17	17	17	16	16	18	16	16	18	18	17	17	17	17	17	18	18	16	17	17	15	18	18	17	16	18	17	17	17		18	18	18	18	18	18	18	16	16
36	20	20	20	20	20	18	19	19	17	18	19	17	17	20	20	19	19	19	18	19	20	20	18	18	16	20	20	19	17	20	20	19	19	18	18		19	20	20	20	20	19	16	16
37	19	19	19	19	19	17	18	18	17	17	18	17	17	19	19	18	18	18	17	18	18	19	19	17	15	19	19	18	16	19	19	18	18	17	18	19		19	19	19	19	18	16	16
38	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19		21	21	21	20	16	17
39	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21		21	21	20	16	17
40	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21		21	20	16	17
41	21	21	21	21	21	19	20	20	18	19	20	17	18	21	21	20	20	20	19	20	20	20	21	19	19	17	21	21	20	17	21	20	20	19	18	20	19	21	21	21		20	16	17
42	20	20	20	20	20	18	19	19	17	18	19	16	17	20	20	19	19	19	18	19	19	18	20	18	19	16	20	20	19	17	20	19	19	18	18	20	18	20	20	20	20		16	17
43	16	16	16	16	16	16	16	15	16	16	15	14	14	16	16	16	16	15	16	16	15	16	16	14	16	13	16	16	16	15	16	16	16	16	16	16	16	16	16	16	16	16		16
44	17	17	17	17	17	17	17	16	17	17	16	14	15	17	17	17	17	16	17	17	16	16	17	15	17	14	17	17	17	15	17	17	17	17	16	16	16	17	17	17	17	17	16	

channels

Supplementary Table 10 Degrees of freedom of the paired t-tests between 30 months and 36 months in each connection.

Appendix B

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
1		36	36	35	35	35	34	36	35	35	33	30	29	36	36	36	35	36	35	34	35	34	36	35	34	32	33	33	35	33	18	17	18	17	17	15	16	18	17	17	15	15	14	17
2	36		38	35	35	36	35	38	35	35	35	32	31	38	38	38	37	38	36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
3	36	38		35	35	36	35	38	35	35	35	32	31	38	38	38	37	38	36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
4	35	35	35		35	34	34	35	34	34	33	29	29	35	35	35	34	35	34	34	34	33	35	34	34	32	32	33	34	33	18	17	18	17	17	15	16	18	17	17	15	15	14	17
5	35	35	35	35		34	34	35	34	34	33	29	29	35	35	35	34	35	34	34	34	33	35	34	34	32	32	33	34	33	18	17	18	17	17	15	16	18	17	17	15	15	14	17
6	35	36	36	34	34		35	36	35	34	33	31	30	36	36	36	35	36	35	34	35	34	36	35	35	33	33	33	35	33	19	18	19	18	18	16	17	19	17	18	16	16	14	18
7	34	35	35	34	34	35		35	36	35	34	33	33	30	30	35	35	35	34	34	34	33	35	34	35	33	32	33	34	33	19	18	19	18	18	16	17	19	17	18	16	16	14	18
8	36	38	38	35	35	36	35		35	35	35	32	31	38	38	38	37	38	36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
9	35	35	35	34	34	35	34	35		34	32	30	29	35	35	35	34	35	34	33	34	33	35	34	34	32	32	32	34	32	18	17	18	17	17	15	16	18	17	17	15	15	14	17
10	35	35	35	34	34	34	33	35	34		32	29	29	35	35	35	34	35	34	33	34	33	35	34	33	31	32	32	34	32	17	16	17	16	16	14	15	17	16	16	14	14	14	16
11	33	35	35	33	33	33	33	35	32	32		30	30	35	35	35	35	35	34	35	35	34	35	34	34	32	32	33	33	33	18	17	17	17	17	15	17	18	15	18	15	15	14	17
12	30	32	32	29	29	31	30	32	30	29	30		30	32	32	32	32	32	31	31	32	31	32	31	31	29	29	29	30	29	18	17	17	17	18	16	17	18	15	18	15	15	14	17
13	29	31	31	29	29	30	30	31	29	29	30	30		31	31	31	31	31	30	31	31	30	31	30	31	29	28	29	29	29	18	17	17	17	17	15	17	18	15	18	15	15	14	17
14	36	38	38	35	35	36	35	38	35	35	35	32	31		38	38	37	38	36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
15	36	38	38	35	35	36	35	38	35	35	35	32	31	38		38	37	38	36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
16	36	38	38	35	35	36	35	38	35	35	35	32	31	38	38		37	38	36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
17	35	37	37	34	34	35	34	37	34	34	35	32	31	37	37	37		37	36	36	37	36	37	36	35	33	34	34	35	34	19	18	18	18	18	16	18	19	16	19	16	16	15	18
18	36	38	38	35	35	36	35	38	35	35	35	32	31	38	38	38	37		36	36	37	36	38	37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
19	35	36	36	34	34	35	34	36	34	34	34	31	30	36	36	36	36	36		35	36	35	36	35	34	32	33	33	35	33	18	17	18	17	17	15	17	18	16	18	16	16	14	17
20	34	36	36	34	34	34	34	36	33	33	35	31	31	36	36	36	36	36	35		36	35	36	35	35	33	33	34	34	34	19	18	18	18	18	16	18	19	16	19	16	16	15	18
21	35	37	37	34	34	35	34	37	34	34	35	32	31	37	37	37	37	37	36	36		36	37	36	35	33	34	34	35	34	19	18	18	18	18	16	18	19	16	19	16	16	15	18
22	34	36	36	33	33	34	33	36	33	33	34	31	30	36	36	36	36	36	35	35	36		36	35	34	32	33	33	34	33	18	17	17	17	17	15	17	18	15	18	15	15	14	17
23	36	38	38	35	35	36	35	38	35	35	35	32	31	38	38	38	37	38	36	36	37	36		37	36	34	35	35	36	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
24	35	37	37	34	34	35	34	37	34	34	34	31	30	37	37	37	36	37	35	36	35	37	36		35	34	35	34	35	35	20	19	19	19	19	17	18	20	17	19	16	16	15	19
25	34	36	36	34	34	35	35	36	34	33	34	31	31	36	36	36	35	36	34	35	35	34	36	35		34	33	34	34	34	20	19	19	19	19	17	18	20	17	19	16	16	15	19
26	32	34	34	32	32	33	33	34	32	31	32	29	29	34	34	34	33	34	32	33	33	32	34	34	34		32	32	32	33	20	19	19	19	19	17	18	20	17	19	16	16	15	19
27	33	35	35	32	32	33	32	35	32	32	32	29	28	35	35	35	34	35	33	33	34	33	35	35	33	32		32	34	33	18	17	17	17	17	15	16	18	15	17	14	14	14	17
28	33	35	35	33	33	33	33	35	32	32	32	33	29	35	35	35	34	35	33	34	34	32	35	34	34	34	32		33	32	18	17	17	17	17	15	16	17	19	16	18	15	15	18
29	35	36	36	34	34	35	34	36	34	34	33	30	29	36	36	36	35	36	35	34	35	34	36	35	34	32	34	33		33	18	17	18	17	17	15	16	18	16	17	15	15	14	17
30	33	35	35	33	33	33	33	35	32	32	33	29	29	35	35	35	34	35	33	34	34	33	35	35	34	33	33	34	33		20	19	19	19	19	17	18	20	17	19	16	16	15	19
31	18	20	20	18	18	19	19	20	18	17	18	18	18	20	20	20	19	20	18	19	19	18	20	20	20	20	18	19	18	20		19	19	19	19	17	18	20	17	19	16	16	15	19
32	17	19	19	17	17	18	18	19	17	16	17	17	17	19	19	19	18	19	17	18	18	17	19	19	19	19	17	18	17	19	19		18	19	18	16	17	19	17	18	15	15	14	18
33	18	19	19	18	18	19	19	19	18	17	17	17	17	19	19	19	18	19	18	18	18	17	19	19	19	19	17	18	18	19	19	18		18	18	16	17	19	17	18	16	16	14	18
34	17	19	19	17	17	18	18	19	17	16	17	17	17	19	19	19	18	19	17	18	18	17	19	19	19	19	17	18	17	19	19	19	18		18	16	17	19	17	18	15	15	14	18
35	17	19	19	17	17	18	18	19	17	16	17	18	17	19	19	19	18	19	17	18	18	17	19	19	19	19	17	18	17	19	19	18	18	18		17	17	19	16	18	15	15	14	18
36	15	17	17	15	15	16	16	17	15	14	15	16	15	17	17	17	16	17	15	16	16	15	17	17	17	17	15	16	15	17	17	16	16	16	16		16	17	14	16	14	14	14	16
37	16	18	18	16	16	17	17	18	16	15	17	17	17	18	18	18	18	18	17	18	18	17	18	18	18	18	16	17	16	18	18	17	17	17	17	16		18	15	18	16	16	15	17
38	18	20	20	18	18	19	19	20	18	17	18	18	18	20	20	20	19	20	18	19	19	18	20	20	20	20	18	19	18	20	20	19	19	19	19	17	18		17	19	16	16	15	19
39	17	17	17	17	17	17	17	17	17	16	15	15	15	17	17	17	16	17	16	16	16	15	17	17	17	17	15	16	16	17	17	17	17	17	16	14	15	17		16	14	14	14	16
40	17	19	19	17	17	18	18	19	17	16	18	18	18	19	19	19	19	19	18	19	19	18	19	19	19	19	17	18	17	19	19	18	18	18	18	16	18	19	16		16	16	15	18
41	15	16	16	15	15	16	16	16	15	14	15	15	15	16	16	16	16	16	16	16	16	15	16	16	16	16	14	15	15	16	16	15	16	15	15	14	16	16	14	16		16	14	16
42	15	16	16	15	15	16	16	16	15	14	15	15	15	16	16	16	16	16	16	16	16	15	16	16	16	16	15	15	15	16	16	15	16	15	15	14	16	16	14	16	16		14	16
43	14	15	15	14	14	14	14	15	14	14	14	14	14	15	15	15	15	15	14	15	15	14	15	15	15	15	14	14	14	15	15	14	14	14	14	14	15	15	14	15	14	14		15
44	17	19	19	17	17	18	18	19	17	16	17	17	17	19	19	19	18	19	17	18	18	17	19	19	19	19	17	18	17	19	19	18	18	18	18	16	17	19	16	18	16	16	15	

Supplementary Table 11 Degrees of freedom related to the difference between Recognisers and Non-Recognisers in each connection. The channels added with the 44-channel configuration are highlighted in green.