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The role of human movement kinematics in internal state inference

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Thesis submitted to the Faculty of Science at the
University of London for the degree of Doctor of
Philosophy

I, Rosanna Edey, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

A handwritten signature in black ink, appearing to be 'RE', with a horizontal line extending to the right.

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Abstract

The kinematics of our movements reflect our internal (mental and affective) states. This thesis tests the hypothesis that these kinematic signals contribute to judgments about others' internal states through models based on our own actions. Chapter 1 details the theoretical background and previous literature that motivates this hypothesis.

Chapter 2 (typical adults) and 3 (typical adolescents) test the hypothesis that we use models of our own action kinematics to make judgments about others' affective states. Both experiments support the hypothesis by demonstrating that differences in one's own typical action kinematics determine the perceived intensity of affective states of observed point-light walkers.

Chapters 4, 5, and 6 examine the hypothesis that atypical movement kinematics in autism spectrum disorder (autism) contribute to social communication difficulties. Chapters 4 and 5 measure two basic skills required to make internal state judgments from observing others' actions: visual time perception and sensitivity to kinematic signals that describe 'natural' motion. Both studies find no deficits in the autism group compared to the typically developed group – and some enhanced abilities – suggesting that these basic skills are intact. However, Chapter 6 demonstrates that typically developed individuals are impaired at reading mental states from autistic actions, suggesting that atypical movement kinematics may be partly contributing to bi-directional communicative difficulties experienced between individuals with autism and their typical peers.

Chapter 7 investigates whether differences in movement kinematics early in development are associated with later social skills in a group of infants at high- or low-risk of developing autism. Indeed, movement kinematics at 10 months of age predicts social abilities at 14 months of age, demonstrating the value of kinematic markers for predicting social functioning and possibly disorder.

Chapter 8 summarises the studies presented in this thesis, which show support for the hypothesis that we judge others' internal states through models based on our own actions.

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Chapter 1: Introduction

1.1. Introduction

Our actions are our means to interact with the world around us. Through the exquisitely detailed coordination of our tongue and lips we are able to communicate; the effortless regulation of our legs enables us to travel to our intended destinations; and the precise sequencing of the movements of our arms, hands and fingers allows us to obtain and manipulate objects we desire.

The production of action is supported by a complex mechanism integrating efferent motoric signals, which move our muscles, with afferent sensory signals, which help us to accurately and effortlessly guide our movements (Wolpert, Doya, & Kawato, 2003) based on our perception of the world and items with which we interact (Fleming, Klatzky, & Behrmann, 2002; Jackson, Jackson, & Rosicky, 1995). Embedded within the time course of our movements there is therefore a wealth of information about our mental and affective ('internal', see Frith & Frith, 2006) states. For example, when lifting a box the low-level kinematic properties of our actions (e.g., the acceleration and duration of the lift phase of the movement) systematically vary depending on the perceived weight of the box (Auvray, Hoellinger, Hanneton, & Roby-Brami, 2011) as well as whether we are trying to deceive an observer about the weight of the box (Hamilton, Joyce, Flanagan, Frith, & Wolpert, 2007; Tidoni, Borgomaneri, di Pellegrino, & Avenanti, 2013).

There are commonalities in the way that people move, which support our ability to develop broad models for understanding others' internal states from these movement features. Some universality in the way internal states are expressed may stem from

evolutionarily advantageous functions to prepare the body for the most efficient course of action (de Gelder, 2006; Frijda, 2010) and communicate with others (Blair, 2003). For example, when experiencing fear we open our eyes widely, open up our nasal passageways (Susskind et al., 2008), and move more slowly (Roether, Omlor, & Giese, 2009b) which allows us to obtain more sensory information to make effective responses to the detected threat. Given these commonalities, we can read these cues in others as signals towards internal states and act accordingly – in this example, offer reassurance or act with caution when interacting with the potential threat oneself (Mineka & Cook, 1993; Olsson & Phelps, 2007).

Thus, our actions may facilitate our understanding of others by providing information about our ‘hidden’ internal states. Analogously to how specific facial configurations actuate attributions of a specific affective state, such as a frown signalling anger, recognition of particular kinematic cues may help us to attribute rapidly internal states to others’ behaviour, such as fast and accelerated movements also signalling anger. Detection of these signals may therefore be an initial step for a range of social-cognitive skills that facilitate fluid social understanding and interactions (Brown & Brüne, 2012; Klin, Jones, Schultz, & Volkmar, 2003; Lewkowicz, Quesque, Coello, & Delevoye-Turrell, 2015; Pavlova, 2012).

However, there are vast individual differences in how actions are produced. For instance, differences in movement kinematics may be generated from naturally occurring variability in the musculoskeletal structure, producing limbs of different lengths and weights, or atypicalities in motor function stemming from neurological disorders (e.g., cerebral palsy, or a range of neurodevelopmental disorders see Section 1.3). Therefore, despite some universality in how we convey our internal states there are likely nuances between individuals. Due to the volume of experience with our own

actions, the representations via which we understand others' internal states may be tuned to our own actions. Our interpretation of others' internal states from their actions would consequently be regulated by individualised representations, as opposed to a universal specification. To use the example outlined above, fast and accelerated movement has been previously associated with anger (Paterson, Pollick, & Sanford, 2001). However, it may be that we only perceive anger in others when they move with kinematics that we exhibit when angry, rather than when they move faster than some speed threshold which is commonly set in all perceivers. Therefore, our ability to accurately ascribe internal states to others we interact with may, in part, be determined by the similarity between the observed others' movements and our own.

This thesis tests the hypothesis that we judge the internal states of others from their action kinematics via models tuned to our own actions. To this end, I examine how variation in motor production kinematics can predict variation in internal state judgments from kinematic information, and thus investigate the relationship between two domains of functioning commonly studied independently – action control and social cognition.

This hypothesis is further detailed in the remainder of the introduction. Firstly, I describe the ways in which the kinematic properties of others' actions can convey crucial information about internal states, and outline evidence that experience tunes perceptual models. Secondly, I discuss how the atypical movement qualities that have recently been identified in individuals with autism spectrum disorders (a social communication disorder, American Psychiatric Association, 2013, hereafter autism) render this population ideal for testing the main hypothesis, and the specific implications of this hypothesis for those with autism. Finally, I outline in more detail the mechanisms that could feasibly support the acquisition of models tuned to one's

actions, before summarising the ways in which my thesis tests the current hypothesis empirically.

1.2. Perception of kinematic characteristics of biological movements

1.2.1. ‘Universal’ kinematic features of biological movements

Biological motion conforms to specific geometric and kinematic parameters (Dayan et al., 2007). A typical human movement between two points follows a bell-shaped velocity curve, such that the velocity increases towards the mid-point and decreases towards the turning points. The kinematic profile has been named the ‘minimum jerk’ profile (Viviani & Flash, 1995; Viviani & Stucchi, 1992) because the smooth changes in acceleration generate movements with low levels of jerk (the second derivative of velocity, or the change in acceleration), which are highly energy efficient (Viviani & Flash, 1995, see Figure 1.1). Despite the variability in the musculoskeletal restraints across the body this motion profile appears to be common to movements of different effectors (Atkeson & Hollerbach, 1985; de’Sperati & Viviani, 1997; Ostry, Cooke, & Munhall, 1987; Tasko & Westbury, 2004). Further, although children’s movements are generally more variable compared to adult movements (Schneiberg, Sveistrup, McFadyen, McKinley, & Levin, 2002) the kinematic structure complies with these general laws of motion (Berthier & Keen, 2006; Viviani & Schneider, 1991). The commonalities in kinematics across effectors and age groups are hypothesised to represent neuronal properties that govern motor codes and hence are thought to represent a typical feature of action production (de’Sperati & Viviani, 1997).

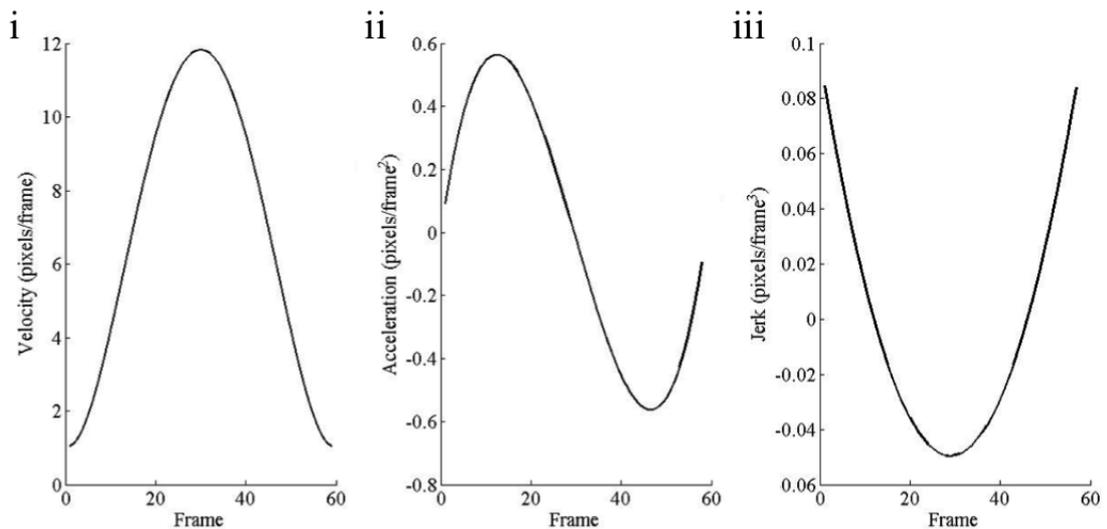


Figure 1.1: Graphical representation of the ‘minimum jerk profile’. Note the smooth increase in velocity to the mid-point of the trajectory and then decrease towards the end-point (i), which results in smooth changes in acceleration (ii) and minimal jerk (iii).

Effective perception of biological motion is a useful tool. For example, as an infant, being aware of the presence of a caregiver can signal imminent food, which may bring comfort. Furthermore, a bias to rapidly attend to others’ movements, such as following a pointing finger, eye gaze or turning body (Bedford et al., 2012; Charman, 2003; Yoon & Johnson, 2009) enables us to learn more about our environment and garner information about complex social concepts (Gergely & Watson, 1999). Preferential attention to others’ movements may be an adaptation that emerges through natural selection to enable us to learn from others (Bardi, Regolin, & Simion, 2011; Simion, Regolin, & Bulf, 2008), or may instead be an outcome of the high frequency with which infants are presented with biological movements early in life (Fausey, Jayaraman, & Smith, 2016; Rochat, 1998). Regardless of the origin or initial function, evidence indeed shows that early in infancy we exhibit high attention towards biological motion (Annaz, Campbell, Coleman, Milne, & Swettenham, 2011; Fox & McDaniel, 1982), which is likely beneficial for social development.

Standard stimuli used to test the ability to recognise different types of information from others' movements are point-light-displays (PLDs). Originally developed by Johansson (1973), these stimuli are created from videos of human actors performing various actions with infrared light sensors attached to each joint on their body. The videos are then manipulated so that only information captured from the point-lights remain. At a local level each of the points contains movements that conform to kinematic properties of human movements (i.e., minimum jerk) while at a global level the configuration properties are constrained to the structure of the human form (see Figure 1.2). These stimuli benefit from eliminating contextual cues, such as facial expressions (see Van den Stock, Righart, & de Gelder, 2007), and thus allow precise measurement of perception of specific kinematic and basic form cues (Blake & Shiffrar, 2007).



Figure 1.2: Example frames from a point-light display (PLD) stimulus of an actor walking. A light reflective point is attached to each joint of the actor's body (note in some versions of these stimuli the neck or head is also represented) while they perform an action. These stimuli are void of contextual information and isolate kinematic and basic form information that is expressed by the actor's movements.

There is vast evidence that the information in these simple stimuli is encoded rapidly, if not automatically. These stimuli appear to 'pop-out' to adult participants (Thornton, Rensink, & Shiffrar, 2002) and can distract from performance when they are irrelevant to the main task (van Boxtel & Lu, 2013). Human PLDs are easily distinguished from scrambled biological motion (point-light stimuli that are made by randomising the

spatial location of each of the points from a human PLD, thereby maintaining the local motion trajectories but scrambling the configuration or form resulting in ‘unnatural’ motion) by both typically developing children and adults (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Freire, Lewis, Maurer, & Blake, 2006). The perceptual models that enable rapid and robust encoding of biological motion information continue to be refined until adulthood, such that the ability to detect biological motion improves well into adolescence (Hadad, Schwartz, Maurer, & Lewis, 2015). The extensive experience one has with biological movements throughout one’s life may therefore improve perceptual representations that enable specialised encoding of this type of motion.

The specificity of these perceptual representations of biological motion is highlighted by the disruptive effects of subtle manipulations of the kinematic or basic form cues on perception. For example, replacing the local kinematic trajectories with constant velocity (an unnatural motion trajectory, Casile et al., 2009), altering the acceleration profile (Chang & Troje, 2009), or changing the temporal phase of the limb movements (Bertenthal & Pinto, 1994) causes perceptual disturbances. Similar encoding difficulties are observed when the local motion cues are biologically plausible, but the configuration is scrambled (Hirai, Watanabe, Honda, & Kakigi, 2009; Murphy, Brady, Fitzgerald, & Troje, 2009) or inverted (Atkinson, Tunstall, & Dittrich, 2007; Bertenthal & Pinto, 1994; Chang & Troje, 2009). The network that is employed to encode this type of information is therefore argued to be highly tuned to both the specific kinematic and basic form properties of human actions (Giese & Poggio, 2003; Jastorff & Orban, 2009; Ross, 2014).

1.2.2. Inferring others’ internal states from kinematic cues

Not only are individuals able to recognise a person from basic kinematic information accurately and rapidly, a large variety of movements can also be effortlessly identified.

For instance, one can discriminate different types of goal-directed or non-goal-directed actions from PLDs, such as classifying someone as walking or digging (Atkinson, Dittrich, Gemmell, & Young, 2004; Atkinson, 2009; Dittrich, 1993; Johansson, 1973), or inferring properties about objects with which the actor is interacting (Runeson & Frykholm, 1981). Additionally, other more complex social concepts are readily perceived through observation of these simple low-level signals, such as gender (Kozlowski & Cutting, 1977), identity (Loula, Prasad, Harber, & Shiffrar, 2005; Troje, Westhoff, & Lavrov, 2005), affective states (Atkinson et al., 2007; Atkinson, 2009; Bassili, 1976; Barliya, Omlor, Giese, Berthoz, & Flash, 2013; Nackaerts et al., 2012; Paterson et al., 2001; Pollick, Paterson, Bruderlin, & Sandord, 2001), and communicative intentions (Sebanz & Shiffrar, 2009). Complementary or synchronous actions – such as dancing or fighting sequences, or affective exchanges between two actors – are also easily detected from the kinematic and temporal cues within PLD stimuli, and more readily than actions that exhibit atypical sequential exchanges (Clarke, Bradshaw, Field, Hampson, & Rose, 2005; Manera, Schouten, Verfaillie, & Becchio, 2013; Neri, Luu, & Levi, 2006; von der Lühe et al., 2016).

Several studies using normal video recordings of actors performing actions have also identified distinct kinematic signatures which convey internal states. For instance, the speed at which a model moves towards a button when responding reflects how confident they feel, with higher velocity reflecting greater confidence (Macerollo, Bose, Ricciardi, Edwards, & Kilner, 2015; Patel, Fleming, & Kilner, 2012). Similarly, the speed of movements when performing a joint task can signal your partner's intention to cooperate (slower movements) or compete (faster movements, Georgiou, Becchio, Glover, & Castiello, 2007). Furthermore, the length of time it takes someone to form their face into a Duchenne-smile (where the cheek muscles form 'crow's feet') indicates authenticity (Krumhuber & Kappas, 2005), and movement pace is indicative of

affective state, e.g., fast movements denote anger and slow movements indicate sadness (Roether et al., 2009b; Roether, Omlor, Christensen, Giese, 2009a).

This wide range of studies demonstrates that the kinematic information embedded within actions are crucial cues that can be utilised to make an array of social judgments. Indeed, several studies have shown observers are sensitive to variations in these kinematic signals (Lewkowicz et al., 2015; Patel et al., 2012; Pollick et al., 2001; Roether, et al., 2009b), which can alter subsequent decisions about how observers choose to interact with others (Krumhuber et al., 2007; Georgiou et al., 2007). Evidence also suggests that when producing communicative movements the kinematic parameters of our actions are more exaggerated than non-communicative movements (Sartori, Becchio, Bara, & Castiello, 2009), and we are best at recognising others (Hill & Pollick, 2000) and their internal states (Atkinson et al., 2004) when the defining kinematic signatures are aggrandised. Thus, awareness and detection of these kinematic signals may facilitate social interactions (Endedijk, Meyer, Bekkering, Cillessen, & Hunnius, 2017; Jones et al., 2011; Lewkowicz et al., 2015), such that those who are more able to accurately perceive kinematic information from others' actions will be able to make more appropriate responses.

1.2.3. The role of visual-motor experience in action perception

The hypothesis tested in the present thesis states that our judgments about others' internal states from action cues are made via models of our own actions. This hypothesis originates from the assumption that action models are tuned through experience, and that we have intensive experience producing our own actions.

Consistent with this hypothesis, there is an array of evidence that we build models of the world through our sensory and motor experiences. For instance, it is unequivocal that infants are sensitive to statistically frequent sensory inputs within their

environments (Kirkham, Slemmer, & Johnson, 2002; Saffran, Aslin, & Newport, 1996; Hunnius & Bekkering, 2014) and appear to rapidly construct perceptual representations, or models, that assist fast and precise encoding of relevant and frequent sensory inputs (Kelly et al., 2009; Sangrigoli, Pallier, Argenti, Ventureyra, & De Schonen, 2005; Scott, Pascalis, & Nelson, 2007). Throughout our lives we are continuously presented with biological motion from observing and producing our own movements. Infants incessantly observe their own limbs (Rochat, 1998) and enjoy observing themselves in mirrors where they gain a third party perspective of their movements (Amsterdam, 1972). This continual observation supports the early integration and maturation of the motor and visual systems within the brain (de Klerk, Johnson, Heyes, & Southgate, 2015; Deoni et al., 2011; Gogtay et al., 2004; Paus, 2005), which enhances efficient motor control. Thus, in the same way we learn about any statistically frequent sensory signals in our environment, our own visual-motor experiences may specifically tune models of action (see Section 1.4.2 for a more detailed discussion on the possible neural mechanisms underlying this process).

Experts, such as professional sports players, have high levels of specific visual-motor experience. The role of visual-motor experience in tuning our mental models can therefore be examined by contrasting the perception of experts within their expertise domains with other observers. For example, Sebanz and Shiffrar (2009) asked expert and novice basketball players to identify fake from true passes when observing either PLDs of real basketball players, or static frames of the same action sequence. The expert players, with extensive visual and motoric experience producing fake and true passes, were significantly better at distinguishing the shots compared to the novices. Observation of the dynamic PLD stimuli also led to superior performance relative to the still frames, suggesting the kinematic structure of the passes was important for discrimination.

Similarly, Aglioti, Cesari, Romani, and Urgesi, (2008) found that expert basketball players made more accurate decisions earlier in the action sequence, relative to novice players and also expert watchers (e.g., basketball coaches). This finding suggests a possible specific function of motor input for enhancing perception, although the visual experience of an expert player may also differ between basketball players and coaches. Brault, Bideau, Kulpa, and Craig (2012) conducted a related study using virtual reality to measure the perceptual responses of expert and novice rugby players, and also their action responses when trying to intercept true or fake runs from a virtual attacking player. In line with the other findings, the experts were able to make more precisely targeted and timed responses compared to the novices, suggesting their visual analysis of the attacker's movement trajectory and their subsequent planned motor responses were more accurate. Professional ice-skaters also gave more precise estimates of the time-course of observed ice-skating performances that were partially covered by an occluder, compared to novices (Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012; Diersch et al., 2013). Additionally, these same effects, albeit slightly smaller, have been found in a group of retired professionals who still practiced ice-skating, but less frequently, compared to novice retirees (Diersch et al., 2012), suggesting the extensive visual-motor experience partially protects against some of the general declines in action perception in older age.

Comparable perceptual advantages have also been documented in infants, where there has often been greater control over the exposure to specific visual-motor experiences. For instance, using the 'sticky mittens' paradigm, infants – who have not developed the ability to reach and grasp objects they desire – can gain novel reach-and-grasp experiences by simply touching their Velcro covered mittens onto a Velcro covered toy. Following these experiences, infants show greater attentional biases towards novel goal-directed actions performed by an actor with the same mittens (Gerson & Woodward,

2014; Sommerville, Woodward, & Needham, 2005). In a similar paradigm, novel experience with an action was related to more anticipatory eye-gazes when observing others produce the same actions (Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012). Related evidence of anticipatory eye-gazes is found in adults when observing others produce actions with which one has had experience (Press & Kilner, 2013; Rotman, Troje, Johansson, & Flannagan, 2006). However, infants who merely observe another producing novel actions, or interact less specifically with novel objects (i.e., where they can reach to objects but cannot pick them up) do not show the same attentional bias towards the novel actions of others (Cannon et al., 2012; Gerson & Woodward, 2014; Somerville et al., 2005), suggesting a specific benefit of one's own visual-motor experiences when learning about the perceptual properties of actions. Equivalent perceptual advantages have been measured for other novel actions, such as crawling and walking (Stapel, Hunnius, Meyer, & Bekkering, 2016), as well as complementary neuroimaging evidence reporting similar effects (de Klerk et al., 2015; Gerson, Bekkering, & Hunnius, 2015).

A comparable line of experiments examining the role of biological motion cues for action perception suggests similar tuning according to one's own experiences. For instance, when participants judged the time-course of actions partially covered by an occluder, they were significantly more accurate when observing natural biological movements, relative to manipulated unnatural motion (Stadler, Springer, Parkinson, & Prinz, 2012; Stapel et al., 2016). Participants were also better able to identify a specific action when observing movements that they actually produced, and therefore have kinematic properties that are explicitly matched to their own motor repertoires (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Kandel, Orliaguet, & Viviani, 2000; Knoblich & Prinz, 2001; Loula et al., 2005, see also Abernethy, Zawi, & Jackson, 2008; Jackson, Warren, & Abernethy, 2006). These findings are consistent with the

notion that visual-motor experience of one's own actions (and action effects) increases perceptual sensitivity to specific kinematic parameters.

These studies emphasise the importance of our own visual-motor experiences for generating perceptual representations. Given that many internal states are associated with specific kinematic signatures (see Section 1.2.2), we might therefore predict that one's own models of the relationships between action kinematics and internal states develop through experience obtained when producing those actions. Specifically, although we all produce actions that contain similar kinematic properties (e.g., minimum jerk profiles), individual differences in the production of actions will forge idiosyncrasies. Thus, perception of others' actions will arguably be influenced by one's own visual-motor experiences and successful social communication might depend on the similarity of action models between ourselves and others with whom we interact.

Some initial research that is consistent with the current hypothesis has been provided by Patel et al. (2012). In this study participants made timed judgments about visually presented stimuli and then rated their confidence in their perceptual decision. The speed of their responses was found to correlate positively with levels of self-rated confidence, such that the participants moved faster when they were more confident in their response. Importantly, in a subsequent perception task, when participants were shown videos of others performing the original task, the perceived confidence of actors was calibrated to the participant's own confidence-speed relationship, rather than a universally defined velocity index for confidence. In other words, participants judged the actors' confidence relative to how confident they felt when they moved at the same speed, such that typically slower moving participants rated more movements as confident compared to participants who generally moved faster. These results suggest

that judgments about others' internal states may be calibrated to our own kinematic-internal state experiences when performing similar actions.

Chapters 2 and 3 will ask whether a similar mechanism for calibrating social judgments to one's own action kinematics operates for ascribing affective states to others' actions. By capitalising on individual differences in walking pace in adults (Chapter 2), and measuring developmental differences in motor production across adolescence (Chapter 3), it is predicted that differences in perception will be determined by quantifiable differences in the participants' own typical movement kinematics.

1.3. Autism: A case of atypical action models?

Autism is a neurodevelopmental disorder characterised by impairments in social and communication skills, as well as stereotypical and repetitive thoughts and behaviours (American Psychiatric Association, 2013). Importantly, individuals with this diagnosis frequently exhibit motor and co-ordination difficulties throughout development (Bhat, Landa, & Galloway, 2011; Cook, 2016; Green et al., 2009; Manjiviona & Prior, 1995; Teitelbaum, Teitelbaum, Nye, Fryman, & Maurer, 1998). A meta-analysis across 83 studies comparing motor abilities of typically developing individuals and those with autism found consistent abnormalities in motor production in those with autism (effect size = 1.2, Fournier, Hass, Naik, Lodha, & Cauraugh, 2010). Such strong evidence of motor impairments in autism has led some to argue that motor skills are a cardinal characteristic of the disorder (Anzulewicz, Sobota, & Delafield-Butt, 2016; Fournier et al., 2010), and intact motor ability might protect against greater social impairments (Sutera et al., 2007).

The documented motor difficulties and atypicalities in both children and adults with autism are vast. The motor impairments include but are not limited to; atypical gait,

balance and posture (Gowen & Miall, 2007; Jansiewicz et al., 2006; Rinehart et al., 2006), difficulties with action sequencing and planning (Campione, Piazza, Villa, & Molteni, 2016; Cattaneo et al., 2007; Ekberg, Falck-Ytter, Bölte, Gredebäck, & the EASE Team, 2016; Fabbri-Destro, Cattaneo, Boria, & Rizzolatti, 2009; Forti et al., 2011; Glazebrook, Elliott, & Lyons, 2006; Mari, Castiello, Marks, Marraffa, & Prior, 2003; Martineau, Schmitz, Assaiante, Blanc, & Barthélémy, 2004; Rinehart, Bradshaw, Brereton, & Tonge, 2001), atypical eye movements (Schmitt, Cook, Sweeney, & Mosconi, 2014; Takarae, 2004), and atypical emotional facial expressions (Macdonald et al., 1989; Brewer et al., 2016).

The diversity of gross and fine motor difficulties suggests a global motor production deficit in those with autism. Atypical motor production could be a consequence of atypical neuropathology which affects the development of stored motor codes (e.g., cerebellar atypical pathology, Mostofsky et al., 2009; Rogers et al., 2013), poor connectivity of regions which are required for competent motor control (e.g., visual and motor regions, Gowen & Miall, 2007; Nebel et al., 2016; Villalobos, Mizuno, Dahl, Kemmotsu, & Miller, 2005), or alternatively a problem arising from more peripheral factors, such as abnormal muscle tone (Maurer and Damasio, 1982).

Importantly for the present thesis, it has been hypothesised recently that these production difficulties could be a function of atypical action kinematics. Cook, Blakemore and Press (2013) asked participants both with and without autism to produce simple sinusoidal arm movements. The analysis of the kinematic trajectories between the groups showed that the autistic participants produced movements that were higher in jerk, as well as acceleration and velocity, relative to the typical group. Complementary findings show greater use of sub-corrections (Forti et al., 2011) or micro-movements (Torres et al., 2013) within the trajectories of actions of those with autism, and also

greater force, and increased velocity when interacting with an object (Anzulewicz et al., 2016). These findings suggest that the movement kinematics of those with autism are quantifiably different from typical actions. Thus, it might not be that those with autism perform actions similarly to typically developed individuals but make a greater number of errors, but instead that they generally produce actions atypically which explains the greater errors.

As previously outlined, the production of one's actions is thought to be instrumental in building mental representations that can be used to interpret the actions of those with whom we interact. Given the wealth of evidence that autistic¹ actions are atypical, and more specifically follow atypical kinematic parameters relative to typical actions, we might predict that individuals with autism have models of actions that are distinct from typical models. Therefore, when individuals with autism interact with typically developed individuals, if both parties are using models of actions that are tuned to their own action experiences, we would expect to find bi-directional errors in action perception and understanding, which may consequently result in poor social communication between these groups.

1.3.1. Biological motion perception in autism

Consistent with the current hypothesis, across a range of experimental paradigms some studies report reduced ability to detect typical (i.e., not autistic) biological motion, as well as deficits in action recognition tasks, in those with autism compared to typical individuals (see Kaiser & Pelphrey, 2012 for review).

¹The term 'autistic people' is the preferred language of many individuals on the spectrum (see Sinclair, 2013). In this thesis, I use this term as well as person-first language (such as 'individuals with autism') to respect the wishes of all individuals on the spectrum.

For example, typically developing toddlers (from two-years-old, Klin, Lin, Gorrindo, Ramsay, & Jones, 2009) and children (Annaz et al., 2011) show preferences towards biological PLD stimuli versus comparison non-biological stimuli (e.g., a spinning top) or a configurally scrambled biological motion PLD. In contrast, matched toddlers and children with autism show the opposite preference or no preference (Annaz et al., 2011; Falck-Ytter, Rehnberg, & Bölte, 2013; Klin et al., 2009). Children with autism are also less able to differentiate these two types of motion stimuli (i.e., a person PLD and a configurally scrambled PLD, Blake et al., 2003), and children and adolescents with autism can tolerate fewer noise dots when identifying the direction of a point-light-walker (PLW, Kaiser, Delmolino, Tanaka, & Shiffrar, 2010; Koldewyn, Whitney, & Rivera, 2010). These studies suggest children with autism have impaired biological motion detection compared with matched typical children.

However, most studies testing biological motion perception in adults with autism find fewer differences, implying that they may ‘catch-up’ with their typically developing counterparts (Herrington et al., 2007; Freitag et al., 2008; McKay et al., 2012; Rutherford & Troje, 2011). These data could be interpreted as a delayed developmental trajectory and slower tuning of perceptual models due to a general reduction in early orienting to others (Annaz et al., 2011; Trevarthen & Delafield-Butt, 2013).

Alternatively, as some neuroimaging data suggests, biological PLD stimuli are encoded differently, via a compensatory mechanism (see Livingston & Happé, 2017 for discussion on compensatory mechanisms in autism) in those with autism but the computed representations often allow for comparable perception by adulthood.

Specifically, those with autism activate similar neural networks to those used when typical individuals encode inanimate, unfamiliar motion (Freitag et al., 2008; Herrington et al., 2007), making perception slower but in principle equivalent in accuracy. In line with this hypothesis, methodologies allowing for slower perception,

such as removing the time limits for responses (Freitag et al., 2008; Saygin, Cook, & Blakemore, 2010; McKay et al., 2012) report equal perceptual performance.

It is imperative to note that all of these previous studies have used stimuli where there are numerous cues for the presence of a biological agent, for example the form (global) as well as the specific kinematic information (local). Individuals with autism classically have greater difficulty generating global representations from static information, especially rapidly (Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015). Some argue this same difficulty is also evident when observing dynamic inanimate stimuli, and contributes to findings of poor biological motion perception (Dakin & Frith, 2005). Therefore, it is difficult to draw strong conclusions about the precise deficit those with autism have when processing biological motion, as performance could relate to perception of a number of these cues.

One study overcame this problem inherent in many of these studies by measuring perceptual sensitivity to kinematic information in isolation (Cook, Saygin, Swain, & Blakemore, 2009). In this paradigm participants were presented with two animations of either a hand or a ball moving with a profile combining different proportions of natural kinematics (minimum jerk or gravitational velocity, respectively) and constant velocity (which perturbed ‘naturalness’). When asked to judge which of the two movements was ‘less natural’ the typical participants were found to have significantly lower thresholds for detecting the natural hand movements compared with the autism group, suggesting that they were better at detecting natural kinematics of the hand. However, both groups were comparable in the gravitational ball condition. In a follow-up study Cook et al. (2013) correlated performance on a similar kinematics perception task with a measurement of participants’ own movement kinematics. Consistent with the current hypothesis, the participants with autism who moved with the most atypical kinematics

performed worst on the perceptual task. These results provide some preliminary evidence that perceptual differences identified in individuals with autism may stem from representations of natural biological motion that do not conform to typical kinematic parameters.

However, it is also possible that those with autism have underlying perceptual difficulties that mean their models of action are generally less precise than typical individuals. According to this account, perceptual differences are determined by different models of action, but not actually driven by differences in action production per se. Specifically, individuals with autism may be less able to represent the type of sub-second temporal information that is crucial for perceiving kinematic information, and thus forming representations of actions. Therefore, in Chapter 4, I will examine visual temporal resolution and visual-motor temporal mapping in adults with and without autism. This study will enable us to consider whether poor biological motion perception could originate from imprecise representations of the temporal qualities of others' actions, or irregularities in the mapping of visual and motor temporal information.

The results of the experiment in Chapter 4 show no impairment in representing sub-second visual temporal information in autism, and in fact some enhancements.

Therefore in Chapter 5 I will test the current hypothesis more explicitly by asking about perceptual sensitivity to both autistic and typical movement kinematics in both autistic and typical observers. Critically, the only previous study testing biological kinematic perception in autism used a mathematical representation of typical human motion (i.e., minimum jerk profile, Cook et al., 2009) and therefore presented motion that was not in fact 'natural'. Consequently the motion stimuli used in Chapter 5 will derive from real typical and autistic models. Using a variation on the Cook et al. (2009) paradigm,

participants will be asked to judge the naturalness of movements that follow autistic and typical kinematic trajectories. If those with autism have action models that are tuned to autistic kinematics (increased velocity, acceleration and jerk), it is predicted that they will have greater difficulties perceiving the information in the typical profile, but show enhanced perceptual sensitivity to the autistic movements. In contrast the typical participants, with typically tuned models, will show enhanced sensitivity to the typical movements. (NB. See Section 1.4.2 for discussion of different mechanisms and how these differences would only be predicted under a ‘sensitivity’ version of the present hypothesis).

1.3.3. Inferring internal states from movements in autism

It has been proposed that those with autism have great difficulty with tasks requiring a theory of mind, or mentalising (e.g., Baron-Cohen, Leslie, & Frith, 1985), such that those with autism do not spontaneously attribute internal states to others, or attribute incorrect internal states (Happé, 2015). Understanding of others’ internal states is tested through a variety of means (Turner & Felisberti, 2017). However, the most consistent deficits in mentalising are found in tasks where participants are required to make rapid or implicit decisions about subtle cues provided in others’ behaviours (Brewer, Young, & Barnett, 2017), where they are not able to explicitly and carefully think through possible solutions (see Livingston & Happé, 2017 for review).

Impairments in reading others’ internal states in autism, may, at least in part, reflect their atypical actions. Consistent with this hypothesis, one of the paradigms frequently used to test intention attribution gives all intention information via kinematic signals, and consistently reveals deficits in autistic individuals. This task was designed by Heider and Simmel (1944) and adapted by Frith and Happé (Abell, Happé, & Frith, 2000). The stimuli in this paradigm are short animations of inanimate objects (triangles

and circles) which represent different social scenarios (internal state animations).

During the task participants watch the animations and then describe what they thought happened. Importantly, to understand the social content of the sequence of movements of the shapes, the observer must firstly perceive the objects as animate, and then ascribe internal states to the movements, such that the interaction described between the shapes is intentional. For example, Figure 1.3 shows the sequence of movements for the coaxing animation, where the triangles represent a ‘mother’ and ‘child’. In this scene the larger ‘mother’ triangle is encouraging the smaller ‘child’ triangle, who is nervous, to come and explore the space outside of the central box. In a set of comparison stimuli, participants must again perceive the shapes as animate, but the same high-level reasoning about their internal states is not required in order to understand the interaction (e.g., one triangle following the other around the scene). In a third set of animations the movements of the shapes describe random trajectories, where there was no deliberate interaction between the objects (e.g., two triangles aimlessly bouncing).

Several studies using these stimuli have shown that both typical children and adults spontaneously ascribe accurate and appropriate internal states to the shapes (Abell et al., 2000; Castelli, Happé, Frith, & Frith, 2000). The frequency of intentional words also reduces from the internal state to the comparison animations, and is the lowest for the random animations. Similar results have been found cross-culturally (Barrett, Todd, Miller, & Blythe, 2005), suggesting, at least at some level, universal understanding of the social kinematic cues present in these stimuli. Individuals with autism however, frequently show atypical responses to these types of animations. Specifically, those with autism use more inappropriate intentional language to describe the internal state interactions, and more often assign internal states to the random movements (Abell et al., 2000; Bowler & Thommen, 2000; Castelli, Frith, Happé, & Frith, 2002; Jones et al., 2011; Klin, 2000; White, Coniston, Rogers, & Frith, 2011; Zwickel, White, Coniston,

Senju, Frith, 2011). Consistent with these behavioural findings, neuroimaging data shows individuals with autism activate classic ‘mentalising’ brain regions (e.g., medial prefrontal cortex, [mPFC] or superior temporal sulcus [STS], see Section 1.4.2 for more discussion on neural mechanisms supporting this process) less when observing the stimuli that requires attribution of mental states, compared to typical individuals, and also have reduced connectivity within this network (Castelli et al., 2002).

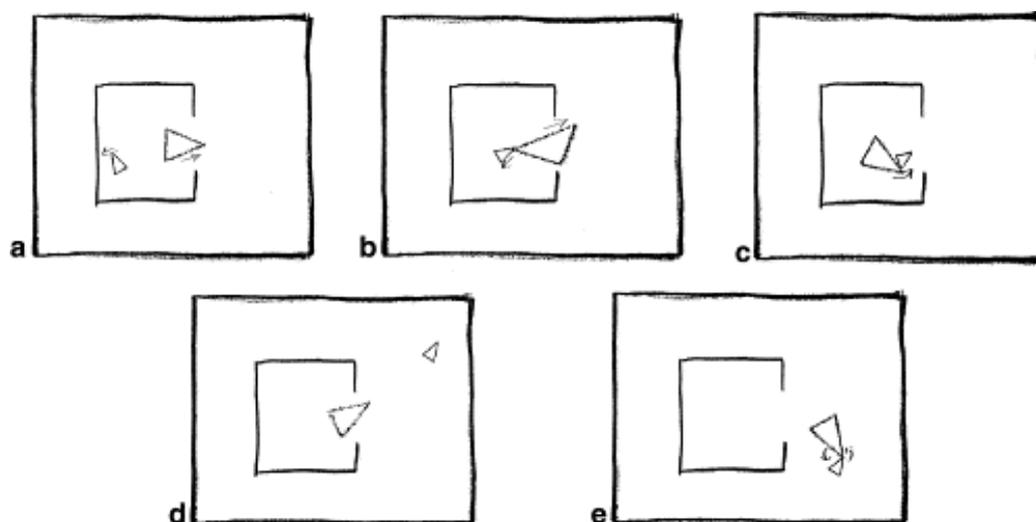


Figure 1.3: Example frames from the coaxing animation taken from Abell et al., 2000 where a mother (large triangle) and child (small triangle) are interacting. (a) The mother tries to interest the child in going outside (b) the child is reluctant to go outside and resists the mother’s pull (c) the mother gently nudges the child towards the door (d) child slowly explores outside (e) mother and child play happily together. (Script and image taken from Abell et al., 2000).

Variants on this paradigm show that those with autism do not have difficulties perceiving the objects as animate (Bowler & Thommen, 2000) or taking the shapes’ ‘visual’ perspective (Zwicker et al., 2011); both of which are prerequisite skills for mentalising. The eye-movements (Klein, Zwicker, Prinz, & Frith, 2009; Zwicker et al., 2011) and some aspects of brain activity of both typical (Castelli et al., 2000) and autistic (Castelli et al., 2002) observers when watching the internal state animations

suggest that both groups perceive the relative complexity (Kemner, van der Geest, Verbaten, & van Engeland, 2007) and greater unpredictability (Hillebrandt, Friston, & Blakemore, 2015) of the movements, compared to the comparison stimulus sets. For instance, both groups exhibit longer fixations on the shapes, and activate extrastriate visual regions of the brain more when watching the internal state animations, which are patterns associated with greater cognitive effort (Klein et al., 2009; van Gog, Kester, Nieuvelstein, Giesbers, & Paas, 2009). These studies suggest that the participants with autism are therefore able to recognise the intricacy of the kinematic properties within the action sequences. However, the two groups consistently provide different social descriptions of the movements, and those with autism are more likely attribute the ‘wrong’ internal states.

Under the current hypothesis differences in the production of actions could, in part, contribute towards differences in the perception of the kinematic features within others’ actions, which may result in incorrect understanding of others’ internal states. It could therefore be the case that individuals with autism, who move atypically, are less sensitive to typical kinematic features that signal others’ internal states, and therefore make more errors, or that different kinematic signatures represent different internal states to those with autism. For example, if those with autism move with different kinematics, then the kinematic profiles produced by typical individuals when expressing certain internal states will not be equivalent to profiles produced by autistic individuals when expressing the same internal state. This difference may partly explain the relatively consistent findings that individuals with autism exhibit impairments when asked to identify the internal states conveyed in typical actions (Atkinson, 2009; Brewer et al., 2017; Di Cesare et al., 2017; Hubert et al., 2006; Moore, Hobson, & Lee, 1997; Nackaerts et al., 2012; Parron et al., 2008). Those with autism however, may exhibit improved understanding when observing autistic actions. Importantly, the current

hypothesis would also predict that typical individuals exhibit impaired understanding of autistic actions, and thus impaired communication between autistic and typical individuals is a bi-directional understanding deficit rather than lying solely with the autistic individual.

Chapter 6 will therefore ask whether typical individuals are impaired at interpreting the movements produced by autistic, relative to typical individuals, as well as investigating the performance of individuals with autism when observing both groups' movements. To investigate this question I will use an adaptation of the Frith-Happé paradigm (Abell et al., 2000).

For a mechanism where the production of atypical kinematics interferes with the perception of others' actions it is informative to examine whether atypical movement kinematics first present early in life. If differences are present early, they may play an instrumental role in the development of social cognition atypicalities. Furthermore, reliable diagnosis of autism usually occurs at around age 2 or 3 years old (Baird, Cass, & Slonims, 2003), and often requires lengthy assessments in a range of settings (Charman et al., 2016). This delay is potentially detrimental to the lives of individuals with autism given that an intervention that starts earlier in life is believed to be the most effective (Eldevik et al., 2009; Howlin, Magiati, & Charman, 2009; Warren et al., 2011). Thus, identifying an early biomarker that is easily measured, such as movement kinematics, may inform the developmental trajectory of social difficulties and aid the design of interventions that can start earlier in development. Therefore, in Chapter 7 I will investigate whether kinematic differences in early action production (at 10 months) are associated with later social skills (at 14 months) in a group of infants who have either a high- or a low-risk of developing autism (due to familial risk factors).

1.4. The specific mechanisms underlying own action model calibration

1.4.1. Criterion setting or perceptual narrowing?

There are a variety of ways in which mechanisms identifying others' internal states may be tuned by our own actions. First, it is likely that the experience with our own action kinematics determines the criterion points at which we categorise others action kinematics as displaying specific internal states. For example, although we all will increase our speed when we express anger, the extent to which we perceive anger in others' movements may vary depending on individual differences in our own typical pace. More precisely, an individual who typically moves faster than the average person will move particularly quickly when they express intense anger. In contrast a typically slower walker will also increase their walking pace when they express intense anger, but this speed might still be slower than the fast mover's angry pace. Consequently – if these two individuals are using models with criteria set to their own kinematics – the slower walker might perceive the fast walker's typical pace to convey anger, when in fact they are not expressing any strong emotion. Similarly, when the slower walker expresses intense anger, the fast-moving observer might not perceive anger, as the velocity does not reach their criterion for anger. A more detailed explanation of this theory is described in Section 2.1 (see Figure 2.1). Evidence from other fields in psychology is consistent with this hypothesis suggesting that such 'criterion setting' may be a function of our experiences (see Pollak & Kistler, 2002; Pollak, Messner, Kistler, & Cohn, 2009).

Second, action may influence our perception and understanding of others through altering our sensitivity to the perceptual information within their actions. To use the previous example, a slow mover might not only be more likely to label fast movements as angry – because they are much faster than their own typical movement pace – but

they may also be less sensitive to subtle differences in fast movements because this represents information that they do not typically experience. A range of studies corroborate that experiences tune perceptual sensitivities. For instance, Hirsch and Spinelli (1970) reared newborn kittens such that they only had visual access to either horizontal or vertical lines. After such ‘training’, the trained stimulus type elicited greater activation in orientation-tuned neurons than untrained types. Similar evidence is found in the human developmental literature and is defined as ‘perceptual narrowing’ (Scott et al., 2007). For example, infants show greater sensitivity to faces of the racial group encountered most frequently during development (Kelly et al., 2009; Sangrigoli et al., 2005), as well as sounds specific to their environment (Benasich, Choudhury, Realpe-Bonilla, & Roesler, 2014; Werker & Tees, 1984).

Both of these influences of action on perception and understanding are possible and are consistent with the basic proposal of the current hypothesis. However, the criterion setting version is perhaps more likely with respect to internal state inferences. Different internal states have been found to have distinct kinematic signatures (see Section 1.2.2), therefore in order to distinguish them we must categorise kinematic information accordingly. The criterion setting version of the current hypothesis assumes that we establish our criteria based on our own movements when experiencing these internal states, and hence determine the internal states in others by assessing their movements against these criteria. In other words, it assumes that we all have sufficient experience of different kinematics to process the kinematic information but that it means different things to different people. In contrast, the sensitivity version assumes that we simply are unable to detect the kinematic information that is relevant to making judgments when observing others who move outside of our motor repertoire. Although the sensitivity version is plausible, differences in detection performance between individuals would likely depend on large individual differences in action kinematics such that the

distributions do not overlap and that perception is tuned almost exclusively to one's own actions (which is perhaps unlikely, Hunnis & Bekkering, 2014; see also Section 8.2 and 8.3 related to this point).

When considering individual differences between typically developing individuals I therefore designed experiments specifically to target the criterion setting prediction (Chapters 2 and 3). However, when examining differences between autistic and typical individuals, the large differences in kinematics (e.g., Cook et al., 2013) and reduction in early visual input from observing others (Jones, Gliga, Bedford, Charman, & Johnson, 2014; Klin et al., 2003) in autistic populations renders the sensitivity hypothesis more plausible. This sensitivity question is therefore addressed in Chapter 5, before examining mental state inferences in Chapter 6 with a task where both differential criterion setting and perceptual sensitivity would influence performance.

1.4.2. Neural mechanisms of action model tuning – motor and visual contributions

Our ability to ascribe internal states to others based on analysis of their movements with reference to our own kinematic models requires a neural network that incorporates higher-level (frontal executive, mPFC and integrative perceptual, temporoparietal junction and posterior STS, pSTS; Blakemore, 2008; Castelli et al., 2000; Grossman et al., 2000; Herrington, Nymberg, & Schultz, 2011; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Kaiser & Pelphrey, 2012; Van Overwalle & Baetens, 2009) and lower-level (visual and motor) systems. This high-level network likely supports the analysis and prediction of others' internal states from information from low-level inputs (Adolphs, 2003).

There is much debate about what neural processes are involved in encoding the low-level kinematic features of others' actions. For example, the discovery of so-called

'mirror neurons' (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004) offered a possible neural substrate by which the brain can match observed and produced actions. Mirror neurons were first discovered in macaques, and are visual-motor neurons that have unique firing patterns such that comparable activation is observed when a monkey produces an action and also when he observes another monkey making the same action. Although these neurons were originally identified in the premotor cortex (PMC; Gallese et al., 1996) and inferior parietal lobule (IPL; Fogassi, 2005) of the macaque, there is increasing evidence both through neural imaging and behavioural studies that human brains are also equipped with a similar system (Molenberghs, Cunnington, & Mattingley, 2012).

Activity in the motor system (or Mirror Neuron System, MNS) during action observation is argued to help us understand others' actions, and therefore, in relation to the current hypothesis, action models may be tuned within the motor system. For instance, following application of Transcranial Magnetic Stimulation (TMS) to the IPL, a technique that induces a virtual lesion, reductions in accuracy in labelling others' actions (van Kemenade, Muggleton, Walsh, & Saygin, 2012) and identifying their intentions (Tidoni et al., 2013) have been recorded. A range of studies also suggest that activity within the MNS specifies motion information that is within one's own motor repertoire (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2004; Calvo-Merino et al., 2006; Liew, Han, & Aziz-Zadeh, 2011; Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2015; Paulus, Hunnius, van Elk, & Bekkering, 2012), with evidence that the PMC is essential for discriminating actions that move with impossible and possible kinematics (Candidi, Urgesi, Ionta, & Aglioti, 2008) and configurations (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). The motor system may therefore be tuned to our own motor experiences, and during action observation these signals could directly influence perception of others' internal states by feeding information into higher-level

regions (de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Liew et al., 2011; Van Overwalle & Baetens, 2009).

However, visual regions are also important to consider for action model tuning as during action production we of course have lots of visual inputs from our actions (e.g., Rochat, 1998). The pSTS is a high-level perceptual region involved in synthesising a range of visual (and other sensory) inputs during observation of biological motion (Hillebrandt et al., 2015; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001) and parses the consolidated information into relevant temporal units (Redcay, 2008) and on to motor regions (Van Overwalle & Baetens, 2009). The pSTS also has direct connections with frontal regions relevant for inferring internal states from observing movements (Moessnang et al., 2017). Thus, the structure of the ‘mentalising’ network (including frontal, higher-level visual and motor regions) is such that low-level visual and motor signals can communicate and integrate rapidly (Sepulcre, 2014), and send information directly onto higher-level regions. Moreover, it is worth noting that the activity in the motor system during action perception originates from filtered information from the visual system. This arrangement enables the production of fluid visually guided movements (Wolpert et al., 2003), but importantly suggests the visual system is also highly tuned to our motoric experiences and thus the kinematical qualities of our actions. We may therefore generate perceptual models of actions that we use when observing and interpreting others’ actions without necessarily requiring any motor input.

Either of these mechanisms – direct motor models or indirect motor tuning of perceptual models – would generate effects whereby one’s motor experiences can alter judgments about others’ internal states from their actions. Of course, it is likely that both the visual and the motor system work in concert to aid perception and understanding of others’

actions and therefore that they both play a role in any own action calibration. This thesis will not attempt to disentangle these two possibilities, however it will provide novel experiments that examine whether variability in visual-motor experiences moulds ‘mental models’ that are unique to one’s experiences, and therefore can either help or hinder social understanding and communication depending on the similarity of one’s interaction partners’ movements to one’s own.

1.5. Summary

Under the main hypothesis it is predicted that individual differences in one’s own actions lead to idiosyncrasies in judgments of internal states from movement cues. Consequently, observing others performing actions that are more closely matched to one’s own actions will result in more accurate assessments about their internal states. This hypothesis will be tested in three ways. First, I will examine whether differences in action kinematics predict differences in emotion perception in typical development (adults: Chapter 2 and adolescents: Chapter 3). Second, I will consider the role of atypical action kinematics in the perceptual and social impairments found in adults with autism. I will verify that basic visual temporal perception skills required for these judgments are intact in autism (Chapter 4) before asking about the perceptual sensitivity to typical and autistic action kinematics in typical and autistic observers (Chapter 5). I will then measure how differences in action kinematics may generate differences in higher-level socio-cognitive skills (mentalising, Chapter 6). Finally, in Chapter 7, I will examine whether atypical kinematics are present early in development (10 months) and are associated with later social skills (14 months). In Chapter 8 I will summarise the findings, and provide some suggestions for future work to further the findings of this thesis.

Chapter 2: Our own action kinematics determine the perceived affective states of others

Our movement kinematics provide useful cues about our affective states. Given that our experiences furnish models that help us to interpret our environment, and that a rich source of action experience comes from our own movements, the present study examined whether we use models of our own action kinematics to make judgments about the affective states of others. For example, relative to one's typical kinematics, anger is associated with fast movements. Therefore, the extent to which we perceive anger in others may be determined by the degree to which their movements are faster than our own typical movements. We related participants' walking kinematics in a neutral context to their judgments of the affective states conveyed by observed PLWs. As predicted, we found a linear relationship between one's own walking kinematics and affective state judgments, such that faster participants rated slower emotions more intensely relative to their ratings for faster emotions. These findings suggest that perception of affective states in others is predicted by one's own movement kinematics, with important implications for perception of, and interaction with, those who move differently.

2.1. Introduction

Behavioural expressions of affective states are often automatic and exhibit many similarities across individuals (Frijda, 2010). These similarities allow recognition of affective states in others from a range of cultures (e.g., Sauter, Eisner, Ekman, & Scott, 2010). Various cues provide information about our affective states, such as facial expressions (Bassili, 1979; Ekman & Friesen, 1975), vocalisations and sign language (Hietanen, Leppänen, & Lehtonen, 2004; Scherer, 1995), touch (App, McIntosh, Reed, & Hertenstein, 2011; Hertenstein, Holmes, McCullough, & Keltner, 2009) and importantly, the way that we move (Dael, Mortillaro, & Scherer, 2012). In the same way that perception of a smile prompts the attribution of happiness, perception of fast movements can prompt the attribution of anger (Atkinson et al., 2007; Roether et al., 2009a; 2009b). The association of specific movement cues with specific affective states can provide a rapid route for the attribution of affective states to others, enabling fast and appropriate responses to others' behaviour (Brown & Brüne, 2012; Klin, et al., 2003; Sartori, Cavallo, Bucchioni, & Castiello, 2012).

As detailed in Chapter 1, our experiences with our own actions may generate action representations tuned to our own movements (e.g., Calvo-Merino, et al., 2006; Gerson et al., 2015; Hunnius & Bekkering, 2014; Paulus et al., 2012). Therefore, when observing the actions of others our attributions of their internal states may be calibrated to these mental models which are tuned to our own actions.

The present study tests whether participants' models of their own movements determine their interpretation of the affective states of others. Whereas anger is associated with fast and accelerated movement (Ada, Suda, & Ishii, 2003; Montepare, Goldstein, & Clausen, 1987; Roether, et al., 2009a), sadness is demonstrated through low velocity and reduced acceleration (Michalak et al., 2009; Pollick et al., 2001). Some (Ada et al.,

2003), but not all (Barliya et al., 2013; Ikeda & Watanabe, 2009), studies also find that happiness is associated with high velocity relative to a neutral affective state. It was therefore hypothesised that individual differences in participants' own typical movement kinematics would determine differences in the perception of others' affective states.

For example, we may all increase our velocity when we feel angry, and reduce our velocity when we feel sad. However, a 'fast mover' – who typically moves faster than an average person – will move particularly quickly when they are angry, but when feeling sad their speed might be more comparable to that of an average person who is not experiencing any strong emotional state (see Figure 2.1A). If this 'fast mover' is using a model of their own kinematics to interpret others' affective states, another's fast movements (conveying anger) are unlikely to be perceived as intensely angry (see Figure 2.1Aii) because they are comparable to the fast mover's own typical movements. However, this person will perceive sad (slow) movements as intensely sad because they are much slower than they would typically move and therefore reach their kinematic criterion for detecting sadness. Conversely, someone who moves slower than average would perceive fast (angry) movements as more intensely emotional relative to slow (sad) movements (see Figure 2.1Ai).

Variability in participants' typical kinematics was assessed by recording the velocity of their motion while walking in a neutral context. In addition, participants viewed emotional (angry, happy or sad) PLW stimuli (see Figure 2.1B). The kinematics of these stimuli were either affect-specific (e.g., high velocity for angry walkers), or manipulated to converge to neutral kinematics (see Figure 2.1C). Participants were asked to rate the extent to which the PLW appeared happy, angry and sad.

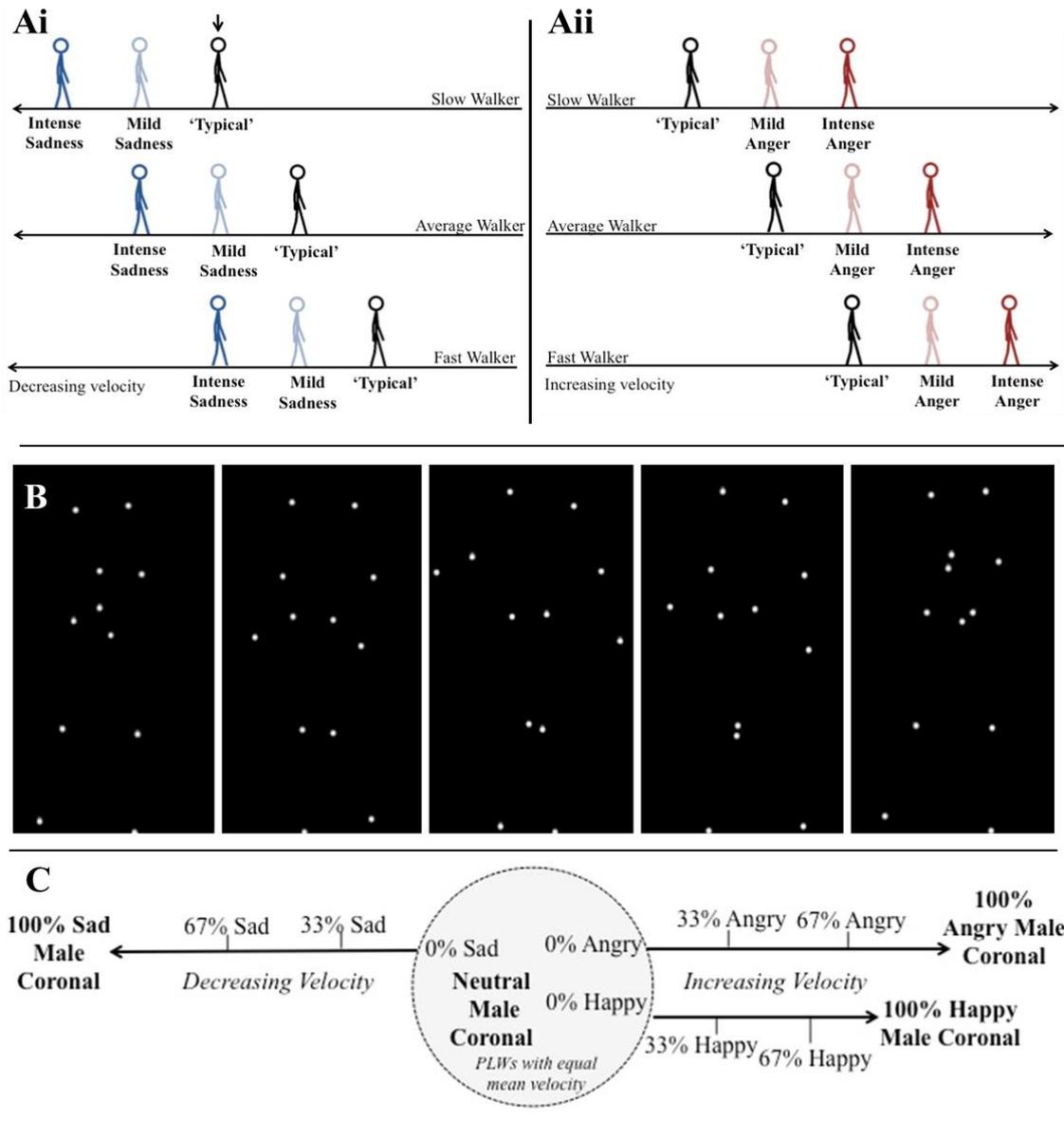


Figure 2.1: (A) Schematic diagram of the experimental hypothesis. The left panel (Ai) depicts the kinematics of fast, average, and slow walkers when sad. The right panel (Aii) depicts the kinematics of fast, average, and slow walkers when angry. Note that at the velocity highlighted by the arrow in the left panel, a slow walker is feeling no particular emotion, but a fast walker is feeling intensely sad. (B) Example frames taken from the happy intermediate (45°) male PLW. In these PLWs, 12 points reflect the motion at the important joints in the body (see <http://www.bbk.ac.uk/psychology/videos/CPress/> for example videos). (C) The velocity of the original (100%) animations was altered to assess the extent to which kinematic information is used to make affective state judgments. 0% stimuli exhibited velocities equal to the neutral stimuli (e.g. the 0% happy male coronal velocity was equal to that in the neutral male coronal animation), and 33% and 67% animations exhibited velocities between the neutral and 100% emotion stimuli.

It was predicted that there would be a linear relationship between one's own walking velocity and perception of others affective states, such that the faster participants would rate the slower emotions more intensely relative to the faster emotions. Findings of this nature would indicate that our perception of others' affective cues are determined by our own action models.

2.2. Method

2.2.1. Participants

This study was initially conducted with 41 participants (17 males, aged 20-43 years, $M=27.37$, $SEM=1.04$), however it was subsequently deemed prudent to increase the sample size (full sample $N=87$, 40 males, aged 18-62 years, $M=29.48$, $SEM=1.00$), to ensure that the initial effects were not due to sampling error. The effects reported below replicated in both sub-samples, but given that the precision of effect size estimation depends primarily on sample size (Maxwell, Kelley, & Rausch, 2008; Asendorpf et al., 2013) all participants were pooled in reported analyses for optimal sensitivity.

Participants were recruited through the local university database. All participants gave informed consent, procedures received ethical approval from the Birkbeck ethics committee and all data were collected in accordance with the guidelines laid out in the 1964 Declaration of Helsinki². There were no multivariate outliers.

2.2.2. Stimuli

The original stimuli were PLWs (Figure 2.1B) adapted from those developed by Nackaerts et al. (2012). These original PLWs depicted a male or female actor expressing happy, sad, angry or neutral affective states, in two different viewpoints

²Note this was the same protocol in all studies presented in this thesis.

(coronal [0°] and intermediate to coronal and sagittal [45°]). Stimuli were approximately 21° visual angle vertically, and 8–17° horizontally, when viewed at the typical distance of 40 cm.

The velocity of each original affective animation (original animations are referred to hereafter as 100% emotion stimuli) was manipulated to generate velocity-adapted animations (0%, 33% and 67% velocity, [NB. our algorithms were ineffective for generating kinematic adaptations of the original sagittal [90°] animations which is why the other two viewpoints were selected]).

To produce the kinematic adaptations, each of the 12 points were isolated using Adobe After Effects. The change in x and y position of each point was tracked across each frame by first order differentiation of the position vectors and averaged to calculate the mean velocity of each point. The overall mean velocity of each animation was then calculated across all 12 points. The ratio between the mean velocity of the 100% emotional animation and its corresponding neutral animation was calculated (i.e., the mean velocity for the neutral coronal male divided by the mean velocity for the happy coronal male). From this ratio, animation-specific constants were generated by multiplying by the desired velocity level (e.g., 33%), which was finally multiplied by the frame-rate of each of the 100% animations to speed up or slow down the animation accordingly.

Given that the affective stimuli varied in both length of animation and number of step cycles, two versions of the experiment were produced. All 100% animations were either cropped to the equivalent duration (2.04 seconds, N=17), or the same number of step-cycles (1.8 cycles; N=69). The findings did not differ according to the animation type used so analyses are reported collapsed across both versions.

Two random frames from each neutral walker frame-set were also selected, resulting in eight static control images which contained no affective information – postures were neutral and there was no kinematic information.

2.2.3. Procedure

All participants first completed the emotion perception task with the original PLWs, followed by the velocity adapted PLWs, and finally the static control images.

Participants subsequently performed the walking task and completed the questionnaire measures³.

2.2.3.1. Emotion perception tasks

Each task was run via Matlab® on a 24 inch screen computer. On each trial, the participants were presented with a PLW and asked to rate the extent to which the walker was expressing one of the three target emotions: happy, angry or sad. The rating scale ranged from ‘not at all (happy, angry, sad)’ to ‘very (happy, angry, sad)’. Participants clicked on a visual analogue scale, and responses were recorded on a 0-10 scale (to two decimal places; value not shown to participants). The initial position of the cursor was randomised for each trial. Participants could change their response until they pressed a key to continue. The affective state judgment to be made was blocked, resulting in three separate blocks (happy, angry and sad judgments). All stimuli were presented once in each block, and the order of the blocks was counterbalanced across participants. In addition, the order of presentation of the stimuli was randomised for each participant within each block. Before beginning the study the participants had three practice trials.

³A fixed order was selected to enable comparability between the testing conditions for all participants and allow the study of individual differences. It was deemed that the walking task should always be performed after the emotion perception tasks to minimise the risk that participants were primed to make explicit reference to their own walking pace during the perception tasks.

In each practice trial participants were asked to rate one of the three emotions and were shown a randomly selected 100% emotional sagittal PLW. For the static control images the procedure was also the same, however, on each trial within each of the three blocks, the image was presented for 2.04 seconds (mean duration of the animations). These stimuli were used to measure response bias (Greenleaf, 1992).

Participants were therefore asked to make a total of 48 ratings of the 100% emotion PLWs, then 108 ratings of the velocity adapted emotional PLWs, and 24 ratings of the static control images. The emotion perception tasks took approximately 35 minutes to complete with breaks between each task.

2.2.3.2. Walking task and questionnaires

Participants were instructed to walk continuously between two cones (10 metres apart) at their own typical walking pace and that they would be told when to stop (after 120 seconds). An iPhone 5c was attached to the medial side of the participants' right ankle using a running strap, and an identical band was attached to the left ankle with an equivalent weight to the iPhone. The internal accelerometer of the iPhone was used to track the precise time taken and distance travelled for each participant, via the Sensor Kinetics Pro© application. To calculate mean walking velocity, each participant's data was cropped to the beginning and end of the last full lap of the walking period by visual inspection. The distance walked (metres) was calculated from the accelerometer data as the number of full laps, again identified by visual inspection of the data, multiplied by 10 (one lap corresponded to 10 meters). The duration was calculated as the difference between the time at final and first timestamp for the cropped data (deduced from Sensor Kinetics Pro© timestamps). Mean velocity was calculated as the distance travelled divided by the time taken.

It is worth noting that the participants' own walking kinematics could not be precisely compared to those of the PLWs for several reasons, such as the fact that the kinematics of the animations were two-dimensional. This limitation precludes the possibility of determining absolute differences between the kinematics of the observed PLWs and one's own walking pace. Nevertheless, regardless of the precise equivalence point, the important point for the analyses is that the affect-specific kinematics in the animations will have been lower /higher relative to the typical kinematics of the fast /slow participants.

Mood has previously been shown to bias perception when making affective judgments, such that one's own affective state influences perception of a range of affective stimuli (Forgas, 1995; Fiedler, Nickel, Muehlfriedel, & Unkelbach, 2001; Mayer, Gaschke, Braverman, & Evans, 1992). Therefore, at the end of the experiment, to assess response biases associated with mood all participants were asked to think carefully about how they felt during the whole experimental session and rate their current mood (happy, angry and sad) using the same scale as that used in the emotion tasks, from 'not at all (happy, angry, sad)' to 'very (happy, angry, sad)'. Sixty-six of the participants also completed the Positive and Negative Affect Schedule-Expanded form (PANAS-X, Watson & Clark, 1994) to assess trait General Positive and General Negative Affect.

2.3. Results

Greenhouse-Geisser corrections have been applied where necessary, and all multiple comparisons are reported with Bonferroni corrected *p* values.

2.3.1. Control measures

2.3.1.1. Static control ratings

To test for response biases from using the different emotional rating scales, a One-Way ANOVA was conducted on the three emotional ratings from the static control task. There was a main effect of emotion scale ($F(1.84,158.11)=44.12, p<.001, \eta_p^2=.339$), with follow-up simple comparisons revealing higher ‘happy’ ratings for the neutral static images ($M=5.28, SEM=.12$) compared to both ‘sad’ ($M=3.82, SEM=.13, p<.001, 95\% CI [1.52, 2.83], d=.87$) and ‘angry’ ratings ($M=4.19, SEM=.15, p<.001, 95\% CI [1.12, 2.13], d=.84$), with no difference between the ‘angry’ and ‘sad’ ratings ($p=.080, 95\% [-.046, 1.14], d=.24$). This effect is indicative of a ‘happy’ response bias, as is commonly found in emotion perception studies, and it is important to assess its influence on the primary result (see Section 2.3.3).

2.3.1.2. Mood ratings

Due to technical error mood ratings data was lost for one participant. To test for differences in mood ratings a One-Way ANOVA was performed using the participants’ mood ratings (happy, sad, angry). There was a main effect of emotion ($F(2,170)=127.66, p<.001, \eta_p^2=.600$). Follow-up comparison tests showed a happy mood bias, such that participants rated themselves as happier ($M=6.46, SEM=.21$), than angry ($M=1.40, SEM=.25, p<.001, 95\% CI [4.15, 5.98], d=1.46$) or sad ($M=1.90, SEM=.24, p<.001, 95\% CI [3.61, 5.52], d=1.26$), but no differently on the sad and angry scales ($p=.206, 95\% CI [-1.16, .16], d=.12$).

To test for differences in participants’ trait mood measures a paired t-test was conducted comparing participants’ General Negativity and Positivity scores for the subsample who completed the PANAS-X. There was again a ‘happy trait bias’ ($t(65)=9.95, p<.001$,

95% CI [16.12, 10.73], $d=1.23$), such that participants scored higher on the positivity (M=30.03, SEM=1.06) relative to the negativity scale (M=16.61, SEM=.79).

These mood biases could influence participants' walking pace, as well as emotion perception ratings, therefore it is important to assess the influence of participants' mood on the primary analysis (see Section 2.3.3).

2.3.2. Emotion perception ratings for the velocity adapted animations

From the participants' judgments 'emotional intensity scores' (EIS) were calculated for each emotion and velocity level (3 emotions x 4 levels). These measures were calculated as the mean rating on the modelled emotion scale (e.g., angry for the 0%, 33%, and 67% angry stimuli) minus the mean of the two ratings on the non-modelled emotion scales (happy and sad in this case). This subtraction was performed to isolate participants' rating of the modelled emotion from the non-modelled emotions, akin to a measure of precision. This measure distinguished participants who rated highly on all emotional scales for any given PLW, from those who correctly differentiated the modelled from the non-modelled emotions. High EIS therefore indicates that participants judged the PLW as intensely expressing the modelled emotion, while low (or negative) scores indicate that the PLW is judged as weakly expressing the modelled emotion or expressing a non-modelled emotion.

To test whether participants across the whole group were using the kinematic information in the animations to make their emotion intensity judgments a 3x4 ANOVA was conducted, with emotion (happy, angry and sad) and velocity level (0%, 33%, 67% and 100%) as within-participant factors. As expected, there was a strong linear trend across velocity level ($F(1,86)=290.71$, $p<.001$, $\eta_p^2=.772$), suggesting that as the affect-

specific velocity information was removed, intensity ratings for the modelled emotion decreased (see Figure 2.2).

There was also a main effect of emotion ($F(2,172)=16.87, p<.001, \eta_p^2=.164$) and a linear interaction between level and emotion ($F(1,86)=28.27, p<.001, \eta_p^2=.248$). To examine this interaction separate ANOVAs were performed for each of the three emotions with velocity level as the within-participant factor. For all three analyses there was a linear trend across velocity level (sad: $F(1,86)=230.67, p<.001, \eta_p^2=.728$; happy: $F(1,86)=29.98, p<.001, \eta_p^2=.239$; angry: $F(1,86)=86.23, p<.001, \eta_p^2=.501$).

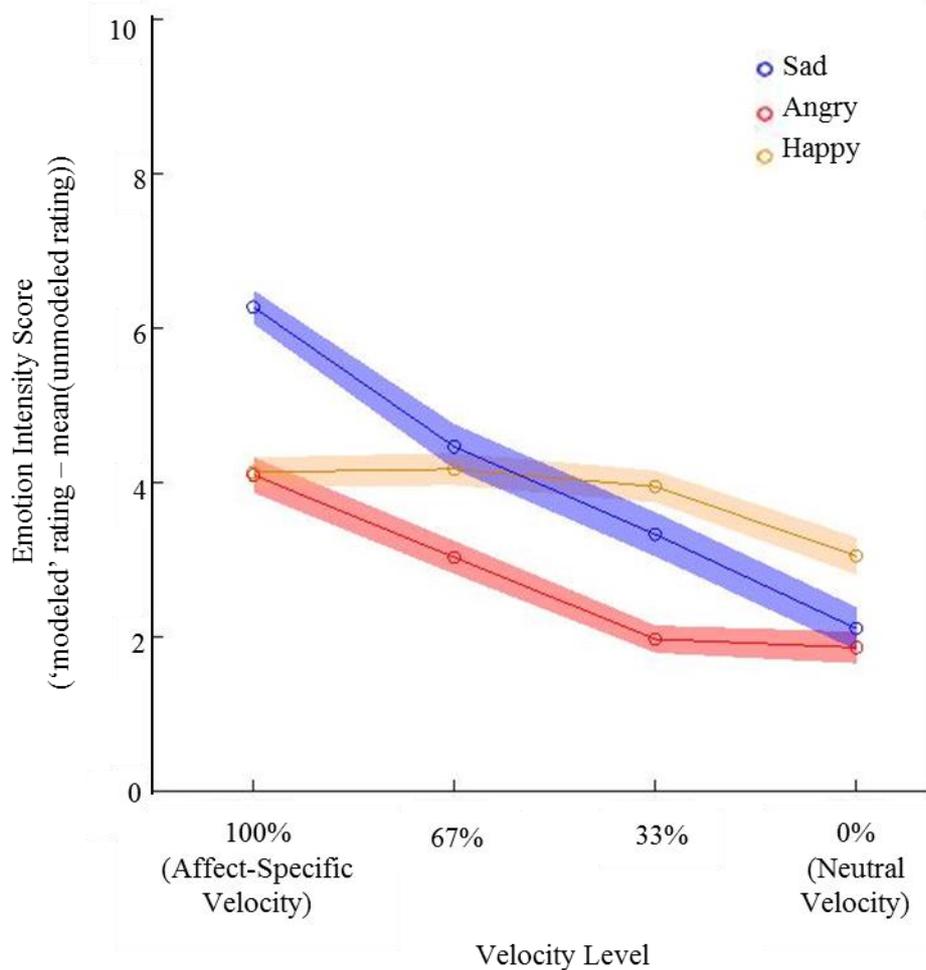


Figure 2.2: Emotional intensity scores (EIS) across the four velocity levels for the three emotions. Shaded areas represent the SEM.

These analyses suggest that the kinematic cues are important for detecting all three emotions, with the interaction driven by lesser use for happy emotions (see Figure 2.2). These results therefore extend previous findings that kinematic information is a crucial cue for the perception of emotion (Atkinson et al., 2007; Roether et al., 2009a; 2009b) by demonstrating that removal of affect-specific kinematic cues is associated with a decrease in the intensity of the perceived emotion.

2.3.3. Relationship between walking kinematics and emotion perception (EIBS)

To assess the primary hypothesis concerning the relationship between participants' walking speed and emotion perception a composite emotional intensity rating was calculated. These 'emotional intensity beta scores' (EIBS) represent the linear relationship in intensity scores from the slowest (sad) to the fastest (angry) emotions (via happy). This score was calculated by modelling the regression slope (β) between animation kinematics and EIS, such that the predictor values were the mean velocity of the PLWs' right ankle for each of the three modelled emotions in the 100% emotion stimuli (see Figure 2.3A), and the dependent values were the corresponding EIS. A positive EIBS denotes higher intensity ratings for the faster relative to the slower emotions and a negative score represents higher intensity ratings for the slower emotions.

A Pearson Product Moment Correlation was performed to examine whether individual differences in walking velocity were related to emotion perception, measured by the 100% EIBS. In line with the hypothesis, there was a negative relationship ($r=-.310$, $N=87$, $p=.003$, 95% CI [-.489, -.106]; see Figure 2.3B) such that participants whose walking kinematics were faster rated the slower emotions more intensely, relative to the faster emotions.

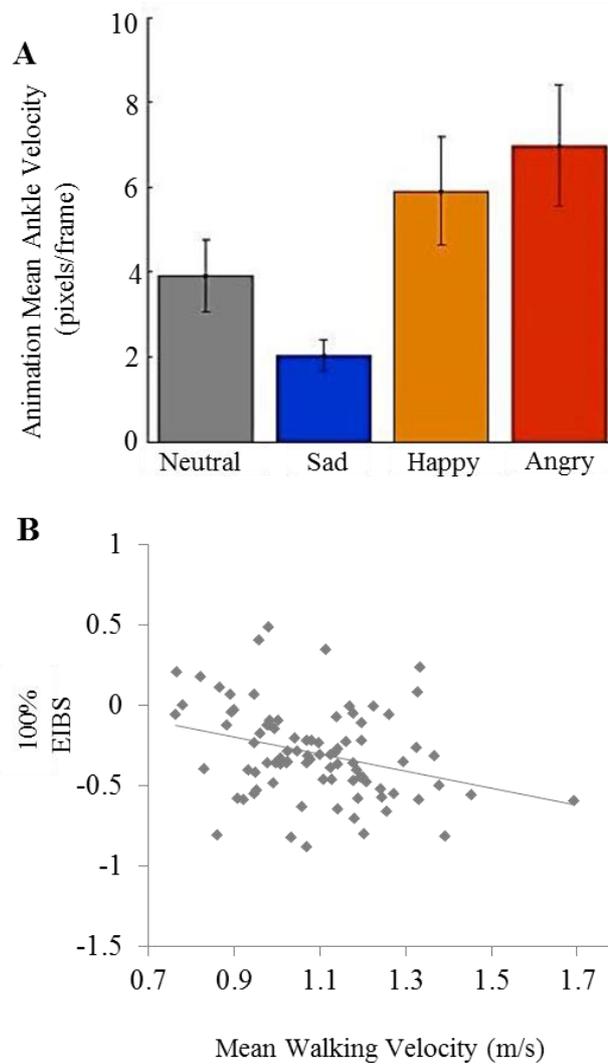


Figure 2.3: (A) Mean ankle velocity for animations in each affective category. Error bars represent SEM in both panels. (B) Scatter plot of the negative correlation between the 100% EIBS and the participants' own walking velocity. A high 100% EIBS represents participants rating the faster emotions (anger) as more intense relative to the slower emotions (sadness).

To control for the 'happy response bias' identified from the results of the static control task (see Section 3.1) a happy bias score was calculated. This score represented the extent to which participants rated control stimuli higher on the 'happy', relative to the 'sad' and 'angry' static scales (i.e., happy static ratings – mean of the sad and angry static ratings). A measure of the participants' 'happy mood bias' was also calculated from their state mood ratings by subtracting the mean of their sad and angry mood ratings from their happy mood rating. To ensure neither bias mediated the observed relationship between walking kinematics and emotional perception, a partial correlation

was performed controlling for variability relating to both happy rating and happy mood biases. This control analysis showed the same negative correlation as reported above ($r=-.312$, $N=86$, $p=.004$, 95% CI $[-.406, -.212]$).

The same result was also found when controlling for trait happy mood bias (i.e., participants general positivity scores – general negativity scores calculated from the PANAS-X questionnaire), in the sub-sample for whom scores were obtained ($r=-.332$, $N=66$, $p=.007$, 95% CI $[-.533, -.090]$).

2.3.4. Relationship between walking kinematics and individual emotion ratings (EIS)

To examine the individual contribution of each emotion to the relationship found between walking velocity and emotion perception (as measured by the 100% EIBS), three follow-up correlations were calculated between participants' walking velocity and each of the three individual 100% EIS (which made up the 100% EIBS). As expected, the angry EIS showed a negative relationship with velocity ($r=-.243$, $N=87$, $p=.023$, 95% CI $[-.038, -.429]$), and the sad EIS showed a small numerical, but non-significant positive relationship ($r=.126$, $N=87$, $p=.245$, 95% CI $[-.325, -.083]$). There was no sign of a relationship between the happy EIS and velocity ($r=.062$, $N=87$, $p=.570$, 95% CI $[-.266, .147]$; see Figure 2.4). While one would have predicted that any unique relationship between happy ratings and walking velocity would have been negative – given findings that happiness is sometimes associated with high velocity (Ada et al., 2003) – the absence of a relationship may be unsurprising given the inconsistencies in this finding (Barliya et al., 2013; Ikeda & Watanabe, 2009). Furthermore, although the relationship between sad EIS and walking velocity did not approach statistical significance the numerical relationship was in the positive direction that would be expected (see Figure 2.4A).

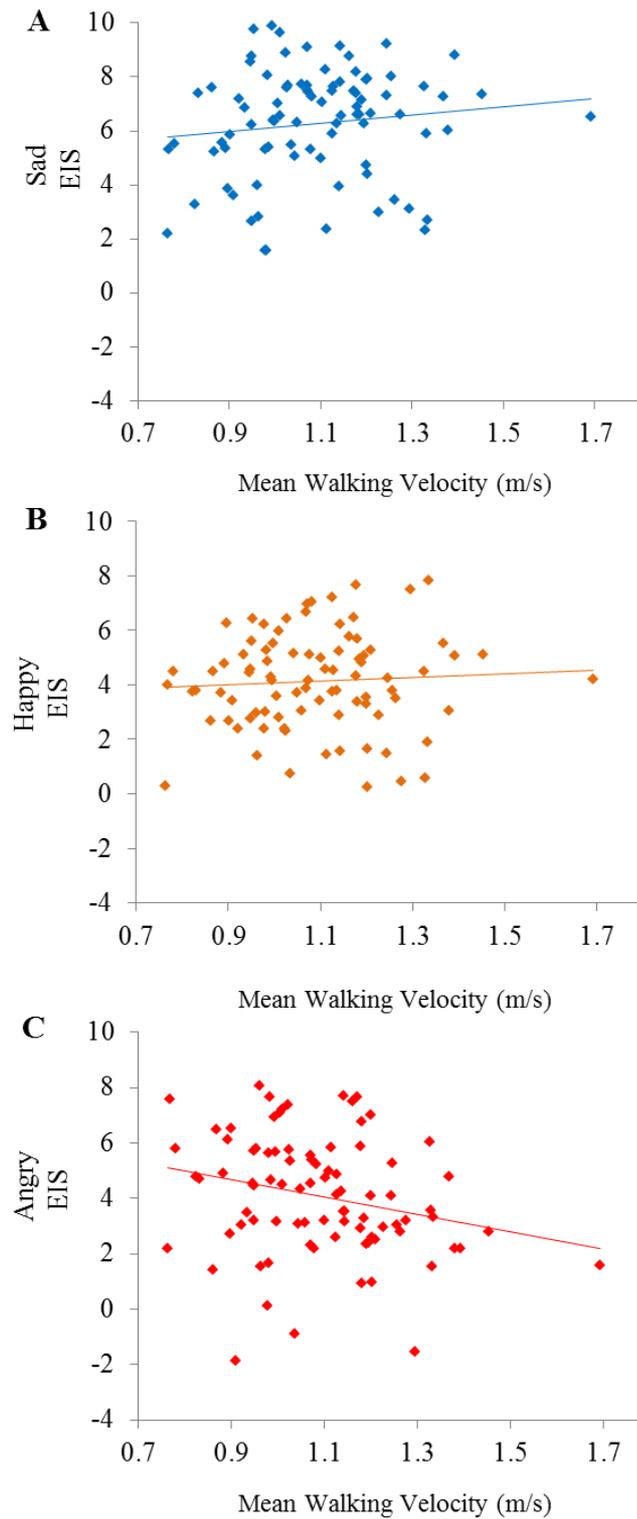


Figure 2.4: Scatterplots showing correlations between participants' walking velocity and 100% EIS (A) Sad EIS showing a non-significant correlation trending in a positive direction, (B) Happy EIS showing no correlation and (C) Angry EIS showing a negative correlation.

The non-significance of this relationship is perhaps related to the reduced variability in the sad EIS (see Figure 2.4). It is worth noting that the aim of the present study was to look for overall relationships between the EIBS (participants' relative intensity ratings across the three emotions) and walking velocity and therefore one should be cautious in drawing emotion-specific inferences from the present findings.

2.4. Discussion

This study examined whether an individual's own movement kinematics predict their perception of others' affective states. In line with this hypothesis, participants who walked with greater speed were found to rate the high velocity (angry) emotions as less intense relative to low velocity (sad) emotions, this association could not be explained by variance related to participants' response bias, state or trait mood. Such findings provide novel evidence that attributions about others' covert affective states are calibrated to one's own action experiences. Observation of walking may therefore be assumed to activate codes used when walking at that velocity oneself and attribution of an affective state to the observed other may be determined by the speed of these codes relative to one's own typical pace.

The present findings have important implications for our understanding of affect perception between different populations. The current study predicts that social interactions should be most successful between interaction partners who move similarly, as greater understanding of others' internal states is likely to result in more successful social interactions. For example, differences in the production of actions may impact cross-cultural affect perception (Hareli, Kafetsios, & Hess, 2015; Matsumoto, Seung Hee Yoo, & Fontaine, 2008; Quiros-Ramirez & Onisawa, 2015). Indeed, Japanese participants rate animated emotional body expressions with a smaller range of movement as more intense compared to both Sri Lankan and American participants

(Kleinsmith, De Silva, & Bianchi-Berthouze, 2006), and such results could be interpreted as reflecting the smaller range of movements used to express emotions in Japanese culture. Thus, it is important to consider how movement differences between cultures may contribute to impaired cross-cultural understanding (Hareli, Kafetsios, & Hess, 2015; Quiros-Ramirez & Onisawa, 2015), specifically for more subtle cues.

In conclusion, the present results suggest that we use models of our own movement kinematics to make affective judgments about others. This finding may have important implications for those with whom we choose to interact, and also how well we interact with them.

Chapter 3: Developmental differences in action kinematics across adolescence determine emotion perception

Chapter 2 demonstrated that – in adults – perception of affective states was determined by individual differences in kinematics during action production. A prediction from this study is that groups who move differently will show comparable differences in perceiving affect in others. Adolescence is a pivotal stage of social, cognitive and physical development, which also frequently coincides with an increase in conflicts with caregivers. There are likely numerous factors that contribute to this change in relationship; however, one important factor could be differences in how each group moves, given that adolescents are likely to move differently from adults as they learn to control their changing body. To test this hypothesis, the same experiment as described in Chapter 2 was conducted with three groups of adolescents; Early (11-12 years old), Middle (13-14 years old) and Late (16-18 years old) Adolescence. As predicted, we found differences in walking kinematics between the groups. Specifically, there was a linear relationship between age group and walking kinematics, such that as the groups got older they moved more slowly. Importantly, measures of emotion perception also followed a linear trajectory across age groups, as was anticipated on the basis of the key hypothesis. Namely, as the groups got slower (i.e., older) they rated the slower emotions less intensely relative to their ratings for faster emotions. Social communication difficulties between adolescents and caregivers could therefore, in part, stem from misattributions concerning internal states.

3.1. Introduction

The transition from childhood to adulthood is a gradual evolution defined by a succession of important social and biological events (Spear, 2000). During adolescence (for the purposes of this chapter defined as 11-18 years old, see Spear, 2000) one learns to cope with the greater level of independence, making more decisions, and dealing with increasingly complex social demands and novel experiences. This pivotal part of development is marked by changes in brain structure and function (Paus, 2005; Dumontheil, 2016; Peters, Vlamings, & Kemner, 2013), which support the maturation of the socio-cognitive skills (Batty & Taylor, 2006; Burnett & Blakemore, 2009; Crone & Steinbeis, 2017; Dumontheil, Apperly, & Blakemore, 2010; Heller & Casey, 2016; Moore et al., 2012; Steinberg, 2005; Taylor, Barker, Heavey, & McHale, 2013; Vink, Derks, Hoogendam, Hillegers, & Kahn, 2014) required for an autonomous adult life (Tonks, Williams, Frampton, Yates, & Slater, 2007).

Adolescence is a time notorious for conflicts with caregivers (Flannery, Montemayor, Eberly, & Torquati, 1993) as well as a high incidence of mood disorders (Merikangas et al., 2010; Ormel et al., 2015). A meta-analysis shows the number of conflicts peaks in early adolescence, but the emotional intensity of conflicts continues to increase until mid-adolescence, and eventually declines towards the end of adolescence (Laursen, Coy, & Collins, 1998). There are likely a multitude of contributing factors to caregiver-adolescent conflict, for instance both poor emotional regulation (Heller & Casey, 2016; Pfeifer et al., 2011) and reduced inhibition (Blakemore & Choudhury, 2006; Steinberg, 2005) in adolescents likely play major roles, as well as more general socio-cultural factors related to the content of the conflicts.

However, one possibly important factor that has received little empirical attention is bilateral misinterpretation of the internal states experienced by adults and adolescents.

Perception of others' affective states across adolescence has been examined in a handful of studies using facial expressions. Most studies show identification accuracy and sensitivity to emotion specific signals continues to improve well into adolescence, with small improvements observed between younger children (~8 years) and early adolescents, then a steep linear trajectory between mid and late adolescence (~13-18 years old; Herba, Landau, Russell, Ecker, & Phillips, 2006; Johnston et al., 2011; Kolb, Wilson, & Taylor, 1992; Thomas, De Bellis, Graham, & LaBar, 2007). Despite body movements being an equally important emotional signal (de Gelder, 2006), the change in the perception of emotion from body movements has not been examined across adolescence (NB. Ross, Polson, & Grosbras, 2012 included adolescents in their sample of children but had insufficient power to compare effects across this developmental period).

As well as changes to social relationships and related cognitive functions in adolescence, there are also vast changes to the physical shape and size of the body (Rogol, Clark, & Roemmich, 2000; Tanner, Whitehouse, & Takahashi, 1966). Changes to the neuromuscular system and musculoskeletal growth in this period result in continued refinement of motor repertoires during adolescence, with differences in performance and movement kinematics between adolescence and adults observed in a range of motor tasks (Davies & Rose, 2000; Largo et al., 2001; Quatman-Yates, Quatman, Meszaros, Paterno, & Hewett, 2012; Rueckriegel et al., 2008; Visser, Geuze, & Kalverboer, 1998; Wilson & Hyde, 2013), including walking (Froehle, Nahhas, Sherwood, & Duren, 2013; Sutherland, 1997). Given the findings in Chapter 2, it is predicted that differences in action production between adults and adolescents would result in different tuning of action representations, and thus divergent calibration of internal state judgments from kinematic cues.

One's 'spontaneous' speed of movements (McAuley, Jones, Holub, Johnston, & Miller, 2006) and 'preferred' walking pace (Oberg, Karsznia, & Oberg, 1993) has been documented to slow across development and into old age. Therefore it is predicted that adolescents will exhibit an elevated baseline speed relative to adults, and thus adolescent affective state judgments from others' kinematic cues will be different from those of adults. For example, an adolescent's expression of anger will be much faster than a typical adult's expression of anger. Differences in the production of actions between adults and adolescents may lead to incorrect attributions of internal states. More precisely, an adult expression of intense anger (speed increase relative to baseline) may not be perceived as an intense expression of anger to an adolescent observer because it corresponds to an adolescent's typical movement pace. Misattributions of others' affective states could therefore contribute to conflicts between caregivers and their adolescent children.

The present experiment tests the hypothesis that adolescents interpret affective states from movement cues differently from adults, in a way that would be predicted on the basis of their own movement kinematics. Three groups of adolescents were tested (Early, Middle and Late Adolescence), and the same methodology described in Chapter 2 was used to measure walking velocity, individual 'emotion intensity scores' (EIS), and the composite emotion perception scores (EIBS) across three target emotions (sad, happy and angry).

There were two hypotheses. First, it was predicted that there would be differences in walking velocity between adults and adolescents. Specifically, given that our preferred speed of movements tends to slow as we age (Oberg et al., 1993; McAuley et al., 2006), walking speed was predicted to decrease linearly as the groups got older. In line with the findings reported in Chapter 2, the second prediction was that the decrease in

walking speed (across the age groups) would determine the trend of emotion perception ratings across groups. To date no previous studies have tested whether adolescent observers are able to use affect-specific kinematic cues. Therefore before assessing the second hypothesis it was necessary to confirm that adolescents use kinematic information in others' actions to make affective judgments by comparing ratings across 0, 33, 67 and 100% velocity levels. Having confirmed that they indeed use these cues, it was examined whether the youngest (fastest) group rate the slower emotions (sadness) more intensely than faster emotions (anger), with the pattern decreasing or reversing across age, as walking speed decreased.

3.2. Method

3.2.1. Participants

Adolescent participants were recruited from two schools (one in London and one in Sussex, both were state funded mixed secondary schools with attached sixth-form colleges). Three age groups (11-12; 13-14; and 16-18 years old) were chosen to be representative of distinct stages of adolescent development (Early, Middle and Late Adolescence), which have previously been defined in the developmental literature (Spear, 2000). Forty randomly selected adolescents from each age range (20 of each gender) were invited to participate in the study. All of those who self-consented, and for all children under 16-years-old also obtained consent from their legal guardian were tested. This method of opportunity sampling resulted in 35 adolescents in the Early Adolescence Group (19 males), 30 in the Middle Adolescence Group (9 males), and 30 in the Late Adolescence Group (13 males).

These adolescent groups were compared against the adult group reported in Chapter 2 (N=86, 20-62 years old, 39 males⁴). There was no difference in the ratio of male to female participants across the four groups ($\chi^2(3)=3.95, p=.267$). To confirm that gender did not contribute to any of the effects found, gender was added as a fixed factor in each of the analyses reported below and no interactions with gender were found.

Demographic data for all the participants are shown in Table 3.1.

Table 3.1: Demographic data for the three Adolescence and Adulthood groups

	Age Mean (SEM)	Gender (N=male)
Early Adolescence (N=35)	11.83 (.06)	19
Middle Adolescence (N=30)	13.90 (.06)	9
Late Adolescence (N=30)	16.67 (.10)	13
Adulthood (N=86)	29.62 (1.00)	39

3.2.2. Procedure

The stimuli and procedure were identical to that reported in Chapter 2. In summary, participants were asked to make emotional judgments (happy, angry and sad) after observing 100% and velocity-adapted animations (67, 33 and 0% affect-specific velocity) of actors expressing happiness, anger, sadness and a neutral affective state,

⁴Please note that one adult was excluded from the sample reported in the current experiment because they were 18-years-old, but they were included in the adult sample in Chapter 2 as they were recruited through the same means as the other adults. Also note that 17 of the adult participants performed a different version of the experiment whereby they rated animations that had been matched for duration and not number of step cycles. No differences were found between participants who performed the two variations and the results reported in the current experiment were the same when excluding these participants.

and static control stimuli (see Section 2.2.2 for further details). Participants then performed the walking task and finally completed a state-mood questionnaire (described in Section 2.2.3.2). Adolescent participants were tested in a quiet room at their school during a lesson in the school day and the ‘walkway’ in the walking task was an isolated corridor in the school or playground.

3.3. Results

Greenhouse-Geisser corrections have been applied where necessary, and all multiple comparisons within and between groups are reported with Bonferroni corrected p values.

3.3.1. Control measures

3.3.1.1. Group differences in static control ratings

Before testing the main hypotheses, group differences in response biases were assessed by analysing the static control scores when observing the static control stimuli. A 4x3 Mixed ANOVA was conducted with age group (Early, Middle, Late Adolescence, and Adulthood) as a between-participant factor, and emotion (happy, angry, sad) as a within-participant factor. There was no main effect of age group ($F(3, 177)=1.31$, $p=.273$, $\eta_p^2=.022$). As in the experiment reported in Chapter 2, there was a main effect of emotion ($F(1.91, 337.46)=37.09$, $p<.001$, $\eta_p^2=.173$), and there was also an interaction between emotion and age group ($F(5.72, 337.46)=2.73$, $p=.015$, $\eta_p^2=.044$).

The same ‘happy bias’ was identified in the Middle ($F(1.56, 45.29)=4.21$, $p<.030$, $\eta_p^2=.127$) and Late Adolescence ($F(2,58)=13.83$, $p<.001$, $\eta_p^2=.323$) groups, as previously found for the Adulthood group ($F(1.84, 156.54)=44.05$, $p<.001$, $\eta_p^2=.341$), although the simple effects were significant only in the Late Adolescence group. The

pattern in the data demonstrated that the static control images were rated as more happy than sad (Middle Adolescence: $p=.084$, 95% CI [.09, 1.53], $d=.42$; Late Adolescence: $p<.001$, 95% CI [.81, 1.87], $d=.95$) or angry (Middle Adolescence: $p=.125$, 95% CI [.02, 1.03], $d=.39$; Late Adolescence: $p<.001$, 95% CI [.72, 1.80], $d=.88$) but with no differences between sad and angry ratings (Middle Adolescence: $p=.726$, 95% CI [.09, 1.53], $d=.22$; Late Adolescence: $p=1.0$, 95% CI [-.76, .60], $d=.04$). This bias was not evident for the Early Adolescence group ($F(1.62, 55.09)=1.76$, $p=.187$, $\eta_p^2=.049$), where participants rated equally across the three scales (Happy vs. Sad: $p=1.0$, 95% CI [-.18, .97], $d=.23$; Happy vs. Angry: $p=.726$, 95% CI [-.15, 1.02], $d=.26$; Sad vs. Angry: $p=1.00$, 95% CI [-.33, .42], $d=.04$). Overall these results suggest that the three older groups used the three emotional scales similarly, with a ‘happy bias’, but the Early Adolescence group tended to be less biased in their responses (see Table 3.2). To account for any variance in emotion perception scores between the groups that is attributable to differences in response bias the main emotion perception analyses were also conducted with the ‘happy bias’ scores (happy static ratings – mean[sad, angry static ratings]) added as a covariate.

Table 3.2: Mean affective ratings for the four age groups for the static control task

	Mean Sad Static Rating (SEM)	Mean Happy Static Rating (SEM)	Mean Angry Static Rating (SEM)
Early Adolescence (N=35)	4.57 (.16)	4.95 (.17)	4.52 (.19)
Middle Adolescence (N=30)	4.15 (.28)	4.96 (.22)*	4.44 (.16)
Late Adolescence (N=30)	3.83 (.23)	5.17 (.15)**	3.91 (.27)
Adulthood (N=86)	3.82 (.14)	5.29 (.12)**	4.20 (.15)*

Note. ** $p<.001$ (difference from sad and angry ratings), * $p<.10$ (difference from sad ratings)

3.3.1.2. Group differences in mood ratings

Due to technical error, mood ratings were lost for one Late Adolescence participant and one Adulthood participant.

A 3x4 Mixed ANOVA was conducted to test for group differences in mood ratings, with age group as a between-participant factor, and mood rating (sad, happy and angry) as a within-participant factor. There was a main effect of emotion ($F(1.65, 289.28)=292.27, p<.001, \eta_p^2=.625$), but importantly no main effect of age group ($F(1, 175)=712, p=.546, \eta_p^2=.012$) or interaction between age group and emotion ($F(4.96, 289.28)=1.35, p=.236, \eta_p^2=.023$). The main effect of emotion was driven by all participants rating themselves as happier ($M=6.45, SEM=.15$) relative to angry ($M=1.24, SEM=.18, p<.001, 95\% CI [4.77, 5.67], d=1.71$) and sad ($M=1.67, SEM=.18, p<.001, 95\% CI [4.26, 5.25], d=1.40$), with no difference seen between sad and angry ratings ($p=.060, 95\% CI [-.79, -.14], d=-.21$).

Table 3.3: Mean mood ratings for the four age groups

	Happy Mood Rating (SEM)	Sad Mood Rating (SEM)	Angry Mood Rating (SEM)
Early Adolescence (N=35)	7.11 (.25)	1.17 (.31)	1.24 (.41)
Middle Adolescence (N=30)	5.91 (.40)	1.74 (.43)	.93 (.33)
Late Adolescence (N=30)	6.30 (.32)	1.86 (.44)	1.51 (.41)
Adulthood (N=86)	6.48 (.21)	1.90 (.24)	1.30 (.23)

A 'happy mood bias' was calculated (happy mood rating – mean[sad and angry mood ratings]) and again, the emotion perception analyses were also conducted with this measure added as a covariate.

3.3.2. Walking kinematic analysis

Kinematic data was lost due to technical error for one Late, four Middle, and eight Early Adolescence participants, which resulted in N=29 Late, N=26 Middle, and N=27 Early Adolescence participants data being including in the walking kinematic analysis.

To test for linear effects of walking pace across the groups a One-Way ANOVA was conducted comparing mean walking velocity. This analysis identified a linear trend across age groups ($F(1, 164)=36.40, p<.001, \eta_p^2=.140$). In line with the prediction, the direction of the linear trend was such that the groups walked more slowly as age increased, with the Early Adolescence group walking the fastest and the Adulthood group walking the slowest (see Figure 3.2A).

3.3.3. Group differences in emotion perception for the velocity adapted animations

The emotion perception data was pre-processed using the same method detailed in Chapter 2 (Section 2.3.2). To reiterate, high EIS scores indicate that participants judged the PLW as intensely expressing the modelled emotion while low (or negative) scores indicate that the PLW is judged as weakly expressing the modelled emotion or expressing a non-modelled emotion.

Before examining the main hypothesis, it was necessary to confirm whether the adolescent groups used the variation of the kinematic information in the animations to the same extent as the adults. A 3x4x4 Mixed ANOVA was therefore performed, with emotion (happy, angry and sad) and velocity level (0%, 33%, 67% and 100%) as within-participant factors, and age group as a between-participant factor (Early, Middle, Late Adolescence, and Adulthood).

Similarly to the effect reported in Chapter 2, there was a linear trend across the four velocity levels ($F(1,177)=548.38, p<.001, \eta_p^2=.756$), which importantly showed no linear interaction with age group ($F(3,177)=1.00, p=.392, \eta_p^2=.017$). Again, as found in Chapter 2 there was a linear interaction between level and emotion ($F(1,177)=12.73, p<.001, \eta_p^2=.067$), but notably no three way interaction between this effect and age group ($F(3,177)=1.49, p=.219, \eta_p^2=.025$). These results demonstrate that all age groups used the kinematic cues in animations to identify the modelled emotion, such that the perceived intensity of the emotion reduced as the kinematic signal decreased. Again, the effect of kinematic cues was larger for affective states that are more robustly associated with specific kinematic signatures (sad and angry; Barliya et al., 2013). See Figure 3.1 for a summary of the main effect of level across the four age groups.

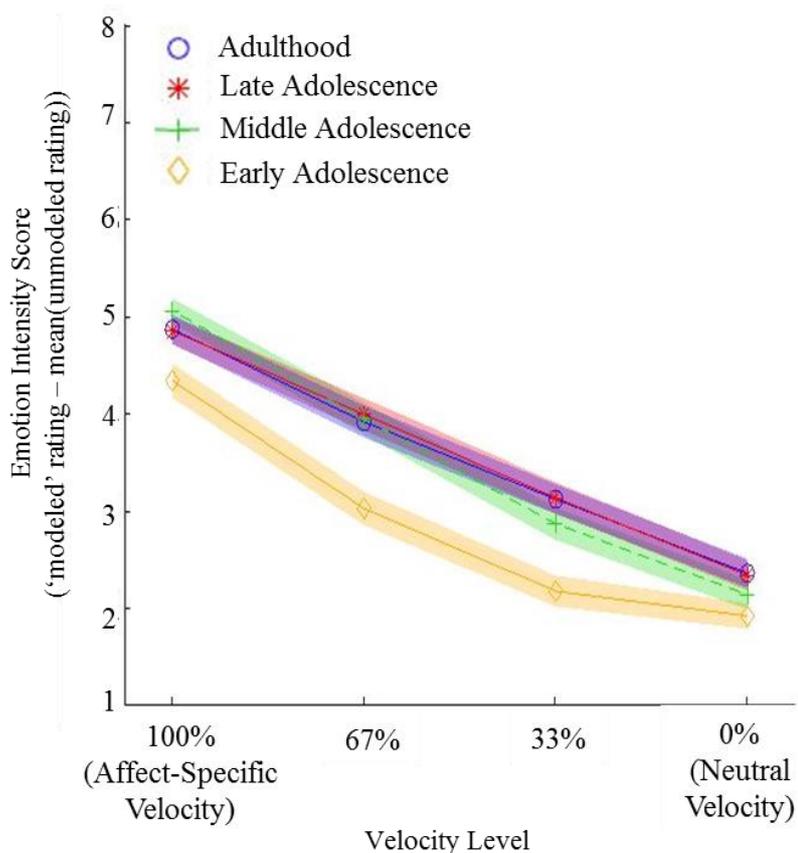


Figure 3.1: Emotional intensity scores (EIS) across the four velocity levels for the four age groups. Shaded areas represent the SEM.

To control for the differences between the groups in ‘happy rating bias’ measured from the static control task, and ‘happy mood bias’, the same analysis was conducted with these measures as covariates. All effects remained the same. The linear trend across level remained significant ($F(1,173)=136.761, p<.001, \eta_p^2=.442$), and the linear interaction with age group was non-significant ($F(3,173)=1.04, p=.377, \eta_p^2=.018$). Therefore differences in scale use or mood could not account for the effects found.

3.3.4. Emotion perception linear analysis (EIBS)

Like in Chapter 2, composite EIBS were calculated for the 100% animations, which represented the linear relationship in intensity scores from the fastest (angry) to the slowest (sad) emotions (via happy). A high score denotes higher intensity ratings for the faster relative to the slower emotions and a low score represents higher intensity ratings for the slower emotions.

Based on the results from Chapter 2 it was predicted that the 100% EIBS scores would follow an opposite linear trend across age groups to that found for walking velocity. Specifically, in line with the results from the kinematic analysis the fastest group (Early Adolescence) are predicted to have the lowest 100% EIBS and the scores will increase as the groups get older. To test this prediction a One-Way ANOVA was performed between age groups for 100% EIBS scores. Critically, there was a linear trend across age group that followed the predicted trajectory ($F(1,177)=4.84, p=.029$; see Figure 3.2B). The identical linear effects were found when controlling for ‘happy mood bias’ and ‘happy response bias’ ($r=-.095, N=179, p=.046, 95\% \text{ CI } [-.185, -.004]$). This pattern of results shows that the fastest walking group (Early Adolescence) rated the slowest emotion (sadness) higher relative to the fastest emotion (anger) and this relationship decreased as the own walking speed within the groups decreased.

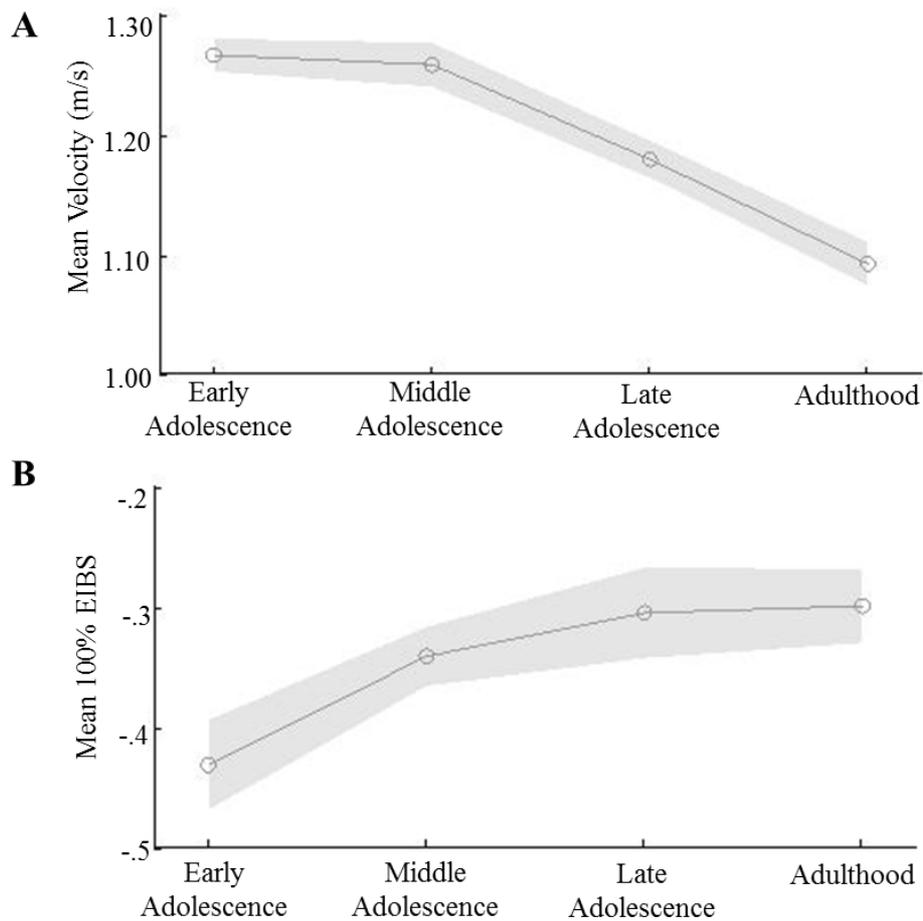


Figure 3.2: (A) Mean walking velocity demonstrating the linear effect across age groups (B) Mean 100% EIBS showing the opposite linear trend to walking velocity across groups. A low EIBS represents participants rating the slower emotions (sad) as more intense relative to the faster emotions (anger). Shaded areas represent SEM.

3.3.5. Individual emotion ratings linear analysis (EIS)

As in Chapter 2 the specific contribution of each emotion generating the linear effect across the 100% EIBS was examined in follow-up One-Way ANOVAs across age groups for each emotion.

The 100% EIS analyses revealed no significant linear effect across the sad ($F(1,177)=.365, p=1.00$), happy ($F(1,177)=4.46, p=.108$), or angry ($F(1,177)=2.67, p=.312$) scores. Although most effects did not survive Bonferroni corrections the directions of the effects went in the predicted directions based on the speed of the groups. In other words, the sad ratings tended to decrease as the groups got older (i.e.,

slower) whereas the happy and angry ratings increased (see Figure 3.3; please also note that the aim of the present study was to look at the relationship between the EIBS, i.e., the relative relationship between the participants different affective state ratings, and group differences in walking pace).

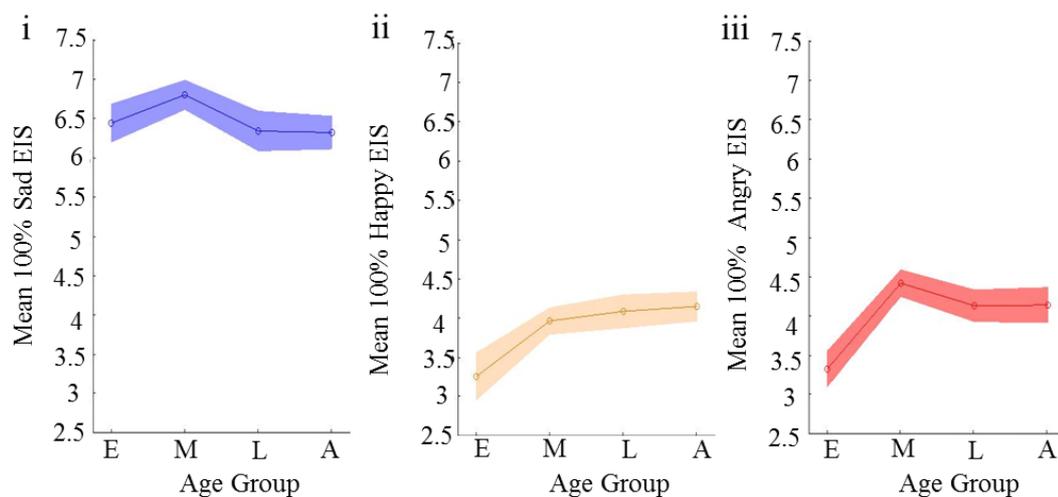


Figure 3.3: 100% EIS across the four age groups. A high EIS shows participants rated the modelled emotion as more intense than the unmodelled emotion (i) Sad (ii) Happy and (iii) Angry. Note for the faster emotions (angry and happy) the linear trends are positive, such that the faster groups have lower ratings relative to the slower groups, whereas the slow emotion (sad) trends in the opposite direction. E= Early Adolescence; M= Middle Adolescence; L=Late Adolescence; A=Adulthood. Shaded areas represent SEM

3.4. Discussion

The present study asked whether group differences in walking kinematics between different stages of adolescence (Early, Middle, and Late Adolescence and Adulthood) were associated with differences in affect perception. As predicted, there was a linear effect of walking velocity across the age groups, such that as participants got older they walked more slowly. Adolescent participants were also able to use the kinematic information in others' actions to make appropriate affective judgments, as evidenced by the analysis with the velocity-adapted animations. However, consistent with the main

hypothesis, an opposite linear trend to that found for walking velocity was found across age groups for the composite affect perception measure. Specifically, the extent to which the participants rated the slowest animations (sad) as more intense relative to the fastest animations (angry) also changed across age groups, in the way that would be predicted based on their walking kinematics. Differences in response biases and state mood bias did not account for these differences in affect perception scores between the groups.

The current findings suggest that although adolescents are able use the kinematic information within others' actions to make affective judgments, they might misrepresent the intensity of their caregiver's expressed internal states. Misattributions of others' internal states due to differences in how one moves could therefore contribute to the increase in conflicts between caregivers and their adolescent children (Flannery et al., 1993; Laursen et al., 1998). Emotional socialisation can also be influenced by how caregivers and adolescents recognise and respond to each other's internal states (Halberstadt, 1986; Meyer, Raikes, Virmani, Waters, & Thompson, 2014; Sanders, Zeman, Poon, & Miller, 2015; Zeman, Cassano, & Adrian, 2013), and errors in identifying others' internal states could disrupt normal socialisation as well as the relationships between caregivers and their adolescent children.

Moreover, the current results could help to explain some behavioural preferences in adolescence. For instance, as children enter adolescence they show a large preference for spending their time interacting with their peers, rather than adults (Brown, 2013; Spear, 2000). This shift in preference may be partially related to a desire to spend more time with those who they understand better and who also understand them more. The positive feedback following these more successful interactions, which may partly stem from similarity in movements as well as possibly other social signals such as

similarities in facial cues (Rhodes & Anastasi, 2012), may drive adolescents to spend increasingly more time with their peers.

It is assumed, from the current data, that adults will also be more likely to attribute erroneous affective states to adolescent actions, as they would be kinematically different from adult expressions. For example, adolescents who are not expressing any strong emotion may be perceived as angry by an adult observer, and expressions of sadness will be more frequently missed. The same predictions could extend to other internal states that are expressed by specific kinematic signatures. The perception of others' self-confidence (Patel et al., 2012), competitiveness (Georgiou, et al., 2007) or trustworthiness (Krumhuber & Kappas, 2005) may also be incorrectly attributed between adults and adolescents who move differently. To fully explore the bi-directionality of communication difficulties between adolescents and their caregivers, future work could look to replicate the current experiment but using adolescent actors, as well as actions expressing other internal states.

When examining developmental effects it is often the case that individuals simply improve with age and there could be a range of factors that explain such improvements. However, this generalised improvement is unlikely to explain the current results. It is first important to note that the EIBSs are relative rating scores. Therefore a high or low score represents the participants' tendency to rate higher on the slow or fast emotions, with higher values representing a greater disparity across the affective ratings. This measure does not represent accuracy or better performance per se. Furthermore, the adolescence groups do not show a comparable change across all three affective states. The differences in affective ratings were in line with perceptual differences due to walking pace (i.e., the adolescents tended to rate lower than the adults on the two faster emotions, but had comparable and often higher ratings on the sad animations). This

imbalanced performance, where the younger group performed ‘best’ on sadness, but ‘worse’ on happiness and angry would not be consistent with a general developmental improvement effect, or any performance effect related to the valance of affective states (as the two ‘fast’ emotions were opposite valances).

The current study examined developmental differences according to age. However, there will likely be within age group differences with respect to stages of pubertal development. Puberty typically occurs between ~11-16 years old, but can be much earlier and later (Tanner et al., 1966). During this time there are large changes in the hormonal, physical and neurological processes, which might contribute to changes in movement kinematics, but importantly also socialisation processes such as learning to self-regulate affective states (Blakemore & Choudhury, 2006) and gaining greater perspective taking or mentalising skills (Dumontheil et al., 2010). Development of these more complex social-cognitive skills will improve judgments about others’ internal states, which could be related to refinement of kinematic models of internal states. Interestingly, some evidence suggests puberty onset can disrupt some social-cognitive functions (e.g., McGivern, Andersen, Byrd, Mutter, & Reilly, 2002) and pubertal development has dissociable effects of maturation of neuronal networks recruited during social tasks from those related to chronological age (Goddings, Burnett Heyes, Bird, Viner, & Blakemore, 2012). Therefore, further work may look to examine whether the relationship between typical movement kinematics and affect perception changes when assessing group differences based on pubertal development, particularly for more complex internal states expressed by others.

In conclusion, these results suggest that adolescents are sensitive to the same cues as adults that signal others’ internal states from body movements. However, and most importantly for the present thesis, the linear difference in typical walking velocity

across the age groups is consistent with the observed linear changes in affect perception ratings, suggesting that use of own action models to interpret others in adolescents leads to different models relative to adults. These differences in perception could contribute towards breakdowns in social communication between these differently moving developmental groups.

Chapter 4: Adults with autism spectrum disorder show no deficits in visual time perception and enhanced visual-motor coordination

This thesis tests whether we use models of our own actions to help us understand others' internal states. In the case of those with autism it is predicted that the problems with social understanding and communication are partly due to *different* models of action and associated internal states relative to typical individuals, which are a result of differences in action production. Before examining this hypothesis it is essential to investigate whether the basic skills required for modelling others' actions are impaired in those with autism. Specifically, to generate and use models of one's own actions one must accurately represent temporal information. A general difficulty representing this type of information would mean that social functions relying on action models are impaired due to inherently deficient rather than *different* models. In the present Chapter, adult participants with autism and matched typically developed adults performed two visual time perception tasks with sub-second stimuli. The first was a purely perceptual task, whereas the second required integration of visual and motor time codes. The participants with autism performed similarly to typical controls for measures of time perception, and they outperformed their typical counterparts on measures of visual-motor temporal integration. The basic time perception abilities required for understanding of others' actions therefore appear to be intact in individuals with autism.

4.1. Introduction

Precise representation of temporal information is important for a host of social cognitive skills. For example, to understand spoken words and sentences one must accurately represent the duration of specific elements of the speech sounds and the silent intervals between sounds (Bhatara, Babikian, Laugeson, Tachdjian, & Sininger, 2013; Grossberg & Myers, 2000; Repp, Liberman, Eccardt, & Pesetsky, 1978). Similarly, during non-verbal communication, measuring the duration of an interactant's movements enables us to make social judgments, such as the extent to which their smile is genuine (Krumhuber et al., 2007) or whether they are trying to be deceptive (Hamilton et al., 2007). Monitoring the duration of joint actions, like eye contact, can also make interactions feel more successful (Binetti, Harrison, Coutrot, Johnston, & Mareschal, 2016). Importantly for the hypothesis examined in the present thesis, the representation of time is also a prerequisite for making more complex assessments about the kinematic features of others' actions (e.g., calculating velocity, acceleration and jerk, Dayan et al., 2016), which can provide significant social signals (Krishnan-Barman, Forbes, & Hamilton, 2017).

As outlined in Chapter 1, autism is characterised by difficulties with social understanding and communication. Given the importance of temporal information for a host of social-cognitive skills (Bartlett & Bartlett, 1959; Gergely & Watson, 1999; Falter & Noreika, 2011; Fawcett & Tuncgenc, 2017; Neri et al., 2006; Shepherd, 2010; von der Lühne et al., 2016; White & Schlosberg, 1952), many of the impairments exhibited by those with autism could in principle stem from problems representing this type of information (Falter & Noreika, 2011; Wimpory, Nicholas, & Nash, 2002). In relation to the current hypothesis, inaccuracies in representing the temporal information in others' actions could generate erroneous estimates of kinematic signals, which could

result in unreliable kinematic models and thus incorrect attributions of others' internal states. To give an example, when assessing whether someone is reaching towards an object in an aggressive or calm manner we must measure the speed of their movement. If our temporal estimate for duration of their movement was inaccurate we might make the wrong judgment about their internal state, or generally be unsure as to what state they are expressing (Di Cesare et al., 2017). This suggestion would be in line with consistent findings that individuals with autism make a greater number of inaccurate internal state judgments when observing dynamic social stimuli (Atkinson, 2009; Brewer et al., 2017; Castelli et al., 2002; Livingston & Happé, 2017; Nackaerts et al., 2012). Errors in representing temporal information could also lead to miscalculations of the duration and kinematic parameters of one's own movements, and may therefore lie at the heart of atypical action kinematics in autism (Anzulewicz et al., 2016; Cattaneo et al., 2007; Cook et al., 2013; Fabbri-Destro et al., 2009; Fitzpatrick et al., 2016; Forti et al., 2011).

There have been a handful of studies that have tested time perception in individuals with autism and these have found mixed results. Some studies show that autistic children and adolescents indeed have reduced sensitivity to temporal information (Allman, DeLeon, & Wearden, 2011; Karaminis et al., 2016), and also perform in a pattern that is indicative of an immature or developmentally delayed timing mechanism (Allman et al., 2011; Brenner et al., 2015; Falter, Noreika, Wearden, & Bailey, 2012a; Karaminis et al., 2016). Some studies find mixed results across the durations tested, with those with autism performing worse on some test durations – either the longer durations in the test set (Allman et al., 2011; Karaminis et al., 2016; Martin, Poirier, & Bowler, 2010) or the longest and shortest durations (Maister & Plaisted-Grant, 2011; Szelag, Kowalska, Galkowski, & Pöppel, 2004). In contrast other studies find no differences between children and adolescents with autism and matched typical groups

(Gil, Chambres, Hyvert, Fanget, & Droit-Volet, 2012; Mostofsky, Goldberg, Landa, & Denckla, 2000; Wallace & Happé, 2008).

Different neural mechanisms are recruited when encoding durations of different lengths (Grondin, 2010; Meck, 2005). For example perception of durations less than ~1 second is thought to rely heavily on automatic mechanisms centred in sensory and motor regions, such as the cerebellum (Ivry & Spencer, 2004; Schubotz, Friederici, & Yves von Cramon, 2000). In contrast, perception of longer durations is hypothesised to require greater cognitive representation, with an important role of sustained attention and working memory (Ivry & Schlerf, 2008; Mangels, Ivry, & Shimizu, 1998).

Consequently, temporal representation of longer durations could be affected by atypicalities in a number of cognitive processes. Most previous studies examining temporal perception in autism have tested durations greater than 1 second. Thus, discrepancies across studies of temporal perception may be a result of differential executive requirements, and not necessarily an indication of a specific timing deficit.

Representation of sub-second temporal information is arguably most essential for a number of social skills, such as accurately following and anticipating others' movements (Rosenbaum, 1975; Viviani & Stucchi, 1992) and contingency learning (Bartlett & Bartlett, 1959; Gergely & Watson, 1999; White & Schlosberg, 1952). Most importantly for the present thesis, temporal encoding required for representing the kinematic information in others' action likely relies upon processing sub-second temporal intervals. Only a handful of studies have examined perception of sub-second intervals in individuals with autism, with the majority using auditory stimuli and findings are inconclusive (Falter et al., 2012a; Gil et al., 2012; Gowen & Miall, 2005; Jones et al., 2009; Mostofsky, et al., 2000). There is evidence that different mechanisms operate for encoding temporal information in different sensory modalities (Grondin,

1993; Grondin, Meilleur-Wells, Ouellette, & Macar, 1998). For the current hypothesis concerning assessment of the kinematics of others' actions it is most important to test whether perception of temporal information that is presented visually is atypical in individuals with autism, and therefore the present study assessed perception of visually presented sub-second intervals.

Additionally, to generate and utilise action models one must be able to precisely map visual temporal codes onto motor codes. For example, if we cannot map the temporal information between motor and visual systems then the action models we generate of our own internal states will be grounded on unreliable kinematic information. Thus, even if we are able to perceive accurately the temporal information when observing others' actions we might make inconsistent attributions about others' internal states due to deficient visuo-motor mapping. Therefore, it is also imperative to examine the ability to coordinate and synchronise visual and motor temporal information. Temporal auditory-motor coordination has been previously measured by Gowen and Miall (2005). In this study adults with and without autism were asked to tap their finger in time with tones. The participants with autism produced actions with a greater absolute error with respect to the timing of the tones (interval 400- 800 ms apart). These findings would be in line with a prediction that individuals with autism have difficulty mapping sensory and motor temporal information. However, as outlined above, there is evidence that visual and auditory temporal processing may be different (Grondin, 1993; Grondin, et al., 1998). Therefore it is important to measure whether the same deficits are found in visual-motor temporal perception.

The aim of the current study was to determine whether adults with autism have deficits in perceiving durations of visually presented sub-second intervals, as well as deficits producing accurately timed motor responses to such stimuli. The design was based upon

the Gowen and Miall (2005) study, but presented visual rather than auditory events for coordination, and an additional task with no coordination requirements but where participants must simply judge the intervals between the events.

4.2. Methods

4.2.1. Participants

Twenty-five typical adults and 26 adults with autism were recruited from the local research volunteer database. An opportunity sample was used – all those registered on the database were contacted and all who volunteered were tested. The Birkbeck ethics committee approved the study, and all participants gave informed consent.

Two participants with autism were excluded because they gave insufficient responses on the visual-motor task (> 20% missed trials). Four participants with autism and one typical participant were excluded because their responses on the visual-motor task were three standard deviations above the group mean. Excluded participants were removed from all analyses, but it should be noted that the results for the perception task were identical regardless of whether these participants were included or not. These exclusions resulted in a final sample of 24 typical participants and 20 participants with autism.

An independent clinician diagnosed participants in the autism group according to DSM-IV criteria (American Psychiatric Association, 1994), and the Autism Diagnostic Observation Schedule -2 (ADOS-2, Lord et al., 2012) was administered to confirm participants' current level of social functioning. Two participants' total ADOS score was below the required cut off (score < 7) for classification of an autism spectrum disorder. These participants were indistinguishable from the other participants on all measures therefore data from all participants in the autism group is reported, however, the same pattern of results was found when excluding those who did not reach the total

score criterion⁵.

The two groups were matched on Full-Scale IQ (FSIQ), as measured by the Wechsler Abbreviated Scale of Intelligence (WASI, Wechsler, 1999; $t(42)=.948$, $p=.331$, $d=.30$), age (autism 18-69 years, typical 19-50 years, $t(42)=.417$, $p=.679$, $d=.13$) and gender (Fisher's Exact Test, $p=.316$), but, as expected, there was a significant difference between the groups in Autism Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) scores ($t(42)=6.68$, $p<.001$, $d=2.02$; see Table 4.1).

Table 4.1: Demographic information for the autism and typical group

	FSIQ Mean (SEM)	Age Mean (SEM)	Gender (N=male)	AQ Mean (SEM)	ADOS Mean (SEM)
Autism Group (n=20)	114.05 (3.05)	35.15 (3.16)	17	35.05 (2.00)**	9.45 (.77)
Typical Group (n=24)	110.04 (2.71)	33.67 (1.91)	23	18.67 (1.54)	-

** $p<.001$

4.2.2. Procedure

The experiment consisted of two temporal tasks – one visual perception and one visual-motor coordination task – the order of which was counterbalanced across participants. The stimulus for both tasks was a white dot presented (for 100 ms) in the centre of a black screen (13 inches), 3° diameter visual angle when viewed at the typical distance of 40 cm. On each trial the dot stimulus was shown four times with a fixed inter-stimulus interval (300, 400, 500, 600, 700, 800, or 900 ms). Each test duration was

⁵Note this protocol was used for all experiments in this thesis that included participants with autism, see participant sections Chapters 5 and 6.

presented in a random order six times in each task, resulting in a total of 42 trials per task.

Verbal instructions for both tasks were provided before the testing session began. Once the experiment began, the participant was made aware of the task they would be completing first via computerised instructions. As part of the onscreen instructions, examples of the shortest (300 ms) and longest (900 ms) durations were presented, and the participants completed two practice trials – one at the slowest and one at the fastest speed. No performance feedback was given during the practice trials, or the actual experiment.

4.2.2.1. Perception task

Participants were instructed that on each trial four white dots would flash on the screen, each separated by a constant interval that was either long or short. Following observation of the four dots, participants were asked to make a judgment about the speed at which the dots were presented. Responses were made by pressing a key on a scale that ranged from 1 (slow) to 7 (fast) and there was no time limit for responses. After the participant had made their response a fixation cross appeared in the centre of the screen for 500 ms to indicate the start of the next trial.

For each trial the participants' deviation from the correct interval duration was calculated by subtracting their response from the correct response (i.e., for a 900 ms trial the correct response would be 1, therefore a response of 2 would result in a deviation of 1).

Absolute mean errors were calculated by averaging across these values for each of the seven test durations⁶.

4.2.2.2. Visual-motor task

Like in the perception task, participants were instructed that on each trial four white dots would flash on the screen, separated by a constant duration. Participants were instructed to assess the duration between the first and second events, and to tap the spacebar in time with the third and fourth. After the fourth dot, a fixation cross appeared for 500 ms to signal the start of the next trial. If the participant failed to respond on one or both of the required responses within a trial, the trial was omitted from analysis (total omitted trials did not differ between groups $t(42)=-.873$, $p=.387$, 95% CI [-1.269, .502], $d=.29$ autism: $M=.45/42$ trials, $SEM=.20$, typical: $M=.83/42$ trials, $SEM=.36$).

Visual-motor coordination deviation was defined as the absolute deviation between the time of the first and second response and the onset of the third and fourth dot stimuli, respectively. The deviations were averaged to generate an overall mean deviation score (please note no significant main effect or interaction was found when the two responses were entered separately in the analysis).

For all measures on both tasks scores closer to zero indicated more accurate performance.

4.3. Results

Greenhouse-Geisser corrections were applied where necessary, and all multiple

⁶Note that the shortest (300 ms) and longest (900 ms) test durations could only have errors in one direction as they were at the end of the scale, and deviations could have greater range as the duration became closest to the central value. However, analyses excluding the more extreme responses and equalising the range of possible deviations yielded results in line with those reported, therefore the skewed scale measure was not thought to contribute to the effects found.

comparisons are reported with Bonferroni Corrections.

4.3.1. Perception task

To test for group differences in visual time perception a 2x7 Mixed ANOVA was performed with test duration (300-900 ms) as a within-participant factor and group (autism or typical) as a between-participant factor. Crucially, there was no main effect of group ($F(1,42)=.002, p=.964, \eta_p^2<.001$), or interaction between duration and group ($F(6, 252)=1.613, p=.144, \eta_p^2=.037$). There was, however, a main effect of duration ($F(6,252)=6.36, p<.001, \eta_p^2=.136$). From visual inspection of the pattern of results in Figure 4.1A, the main effect of duration appears to be driven by participants making most errors when judging the longest durations relative to the shortest. Consistent with this observation there was a linear trend across duration ($F(1,42)=19.90, p<.001, \eta_p^2=.332$). These results suggest that both groups have similar perceptual sensitivity to differences in visually presented sub-second intervals.

4.3.2. Visual-motor task

To examine group differences in visual-motor coordination a 2x7 Mixed ANOVA was performed on the visual-motor deviation scores, with test duration (300-900 ms) as a within-participant factor, and group (autism or typical) as a between-participant factor. There was a main effect of group ($F(1,42)=7.35, p=.010, \eta_p^2=.149$), which was driven by the autism group producing responses that were more accurate ($M=82.93$ ms, $SEM=7.37$) compared to the typical group ($M=110.01$ ms, $SEM=6.73$). There was no main effect of test duration ($F(4.56,191.65)=1.20, p=.310, \eta_p^2=.028$), but there was a trend towards an interaction between group and duration ($F(4.56,191.65)=2.31, p=.052, \eta_p^2=.052$). This trend appears to reflect the fact that participants with autism outperformed the typical group to the greatest extent on the longest duration (see Figure

4.1B).

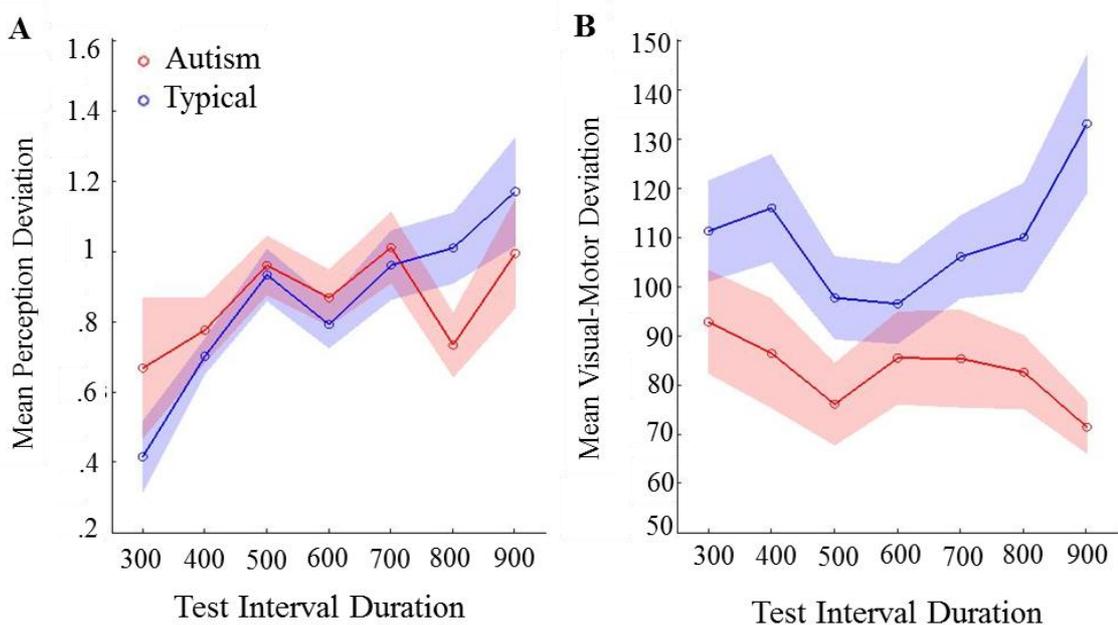


Figure 4.1: (A) Mean Perception Deviation scores calculated as the absolute mean error for each test duration in the perception rating task. (B) Mean Visual-Motor Deviation scores calculated as the absolute mean deviation error of both motor responses from the visual stimulus in the visual-motor task. On both scales scores closer to zero are more accurate. Shaded areas represent the SEM.

4.4. Discussion

The current experiment measured the performance of participants with and without autism on two visual temporal tasks. No differences in performance were found between the groups on the perception task, where participants were required to judge the speed of visually presented intervals. In the visual-motor temporal perception task, where participants had to tap in time with a visually presented stimulus, the autistic participants were more accurate than the typical group, particularly for the longest test duration. The data from the current study therefore suggests that those with autism are unimpaired in their visual perception of sub-second intervals, and exhibit enhanced abilities in performing a motor response in time with these temporal signals. Therefore, difficulties observed in social cognitive tasks that may require precise temporal

representations, such as perceiving the subtle kinematic cues within others' actions or accurately mapping visual and motor temporal codes to generate models of action, are unlikely to be a function of deficient time perception, as some have previously theorised (Falter & Noreika, 2011; Wimpory, et al., 2002).

The finding of enhanced visual-motor coordination performance in the autism group may be speculatively due to a detail focused cognitive style (Happé & Frith, 2006; see also Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012). This style of processing has previously been emphasised in spatial encoding (Happé & Frith, 2006; Van der Hallen et al., 2015) but could possibly also apply to processing of visual detail over time (Dakin & Frith, 2005; Falter, Elliott, & Bailey, 2012b). More accurate detection of the onset and offset of the visual targets could result in more precise temporal resolution (Ivry & Schlerf, 2008) and thus improved visual-motor coordination. One study supports this hypothesis, by showing that visual simultaneity thresholds – measured by asking participants to judge the synchronicity of two grey bars – are significantly lower in those with autism, such that autistic participants have a lower tolerance for asynchrony in simultaneity judgments (Falter et al., 2012b).

The group performance may have differed between the perception and visual-motor task due to differences in the sensitivity of the measures. Specifically, the inter-stimulus interval increased by 100 ms across each of the seven test durations, however this manipulation resulted in global difference of 300 ms for each test duration (e.g., the 400 ms test trial lasted 1600 ms, whereas the 500 ms test trial lasted 1900 ms). The coarser difference in the length of each trial may have made the perception task easier and hence the groups performed more equally. Additionally, ratings only differed on a 1-7 scale in the perception task whereas the dependent variable could vary more in the

visuo-motor task. Therefore, speculatively the visual-motor measure might be a more reliable estimate of the two groups' temporal resolution.

In conclusion, adults with autism were found to have no deficit in representing sub-second temporal information, relative to a group of matched typical adults in a temporal perception task. Performance was superior in the autism group in a visual-motor temporal task, which is speculated to relate to a detail focussed processing style. The current results rule out the possibility that those with autism have difficulty representing sub-second temporal information, and hence the possibility that problems making social judgments from observing others' actions stems from an inability to generate temporal models of action. In the next chapter I will therefore investigate the main hypothesis more explicitly, by asking whether the two groups differ in terms of their sensitivity to autistic and typical kinematics.

Chapter 5: Adults with autism are sensitive to the kinematic information that defines typical and autistic motion profiles

Chapter 4 suggested that it is unlikely that a visual timing deficit contributes to atypical action perception in autism. It is therefore possible that *different* models of action contribute to social and communicative difficulties in autism. Under the ‘sensitivity’ version of this hypothesis (see Chapter 1 Section 1.4.1), individuals with autism may exhibit enhanced perceptual sensitivity for autistic relative to typical action kinematics. Additionally, typical individuals may exhibit poor sensitivity for autistic relative to typical actions. To test this hypothesis in the current study, adults with autism and matched typical adults were presented with two animations of a moving hand and asked to identify which was the ‘less natural’. One animation always moved with parameters that reflected typical or autistic kinematics, and the other was a linear combination of the same profile combined with constant velocity. The participants’ sensitivity to perturbations of both natural movement profiles (typical and autistic models) was measured through a staircase procedure. There was an interaction between observer group and modelled profile, but it was driven by the typical participants demonstrating greater sensitivity to the *autistic* relative to typical movements and equally good sensitivity to both profiles in the autism group. These findings therefore provide no support for the sensitivity hypothesis.

5.1. Introduction

The main hypothesis tested in this thesis posits that extensive experience producing actions generates mental representations tuned to one's own action kinematics, which are used to aid perception and understanding of others' actions. As outlined in Chapter 1, one possible mechanism by which action models are tuned is through a process akin to 'perceptual narrowing' (Scott et al., 2007). Under this version of the hypothesis the concentrated experience with one's own action kinematics generates models that are highly sensitive to similar kinematic features, but poor sensitivity to kinematic information that is different, or infrequently experienced. In the case of individuals with autism – who have consistently been found to produce movements with atypical kinematics (Cook, 2016; Fournier et al., 2010; Gowen & Hamilton, 2013) compared to typical individuals – this sensitivity account would predict that perception of typical movement kinematics should be impaired, yet perception of atypical autistic kinematics should be enhanced. Importantly, the converse prediction can be made of typical individuals, where their perceptual sensitivity to typical kinematics should be enhanced relative to that of autistic movements.

Findings of insensitivity to kinematic information from others' actions in those with autism could contribute towards social understanding and communicative deficits in this population. For instance, if individuals with autism fail to perceive information within typical others' actions they will not be able to learn from and about others' movements in the same way as typically developing individuals (Klin et al., 2003). In the same vein, insensitivity in typical individuals to autistic individuals' actions could also contribute towards diagnostic deficits within autism by influencing communication efficacy for individuals with autism. More precisely, if typical individuals are unable to perceive the information in autistic actions accurately they may make more errors in their

attributions of internal states and miscommunicate with autistic individuals.

Inappropriate and /or inconsistent responses of typical individuals to autistic individuals may also obstruct how those with autism learn about typical social exchanges (Gergely & Watson, 1999) which could hinder their social development.

The previous literature examining action perception in those with autism finds conflicting results (see Chapter 1 and Kaiser & Pelphrey, 2012 for review). There are numerous potential methodological reasons for the discrepancies in these findings, which make it difficult to draw firm conclusions about biological motion perception abilities in individuals with autism. For example, most previous studies have used stimuli where it is difficult to tease apart perceptual abilities that might be related to kinematic encoding of biological movements and those related to computing the structural form or posture of the body from the perceptual.

However, as outlined in Chapter 1, one study has tested exclusively perceptual sensitivity to kinematic information in typical biological movements. Cook et al. (2009) asked participants with and without autism to identify which of two vertical sinusoidal hand movements was less natural. One movement was programmed to move following the minimum jerk profile (thought to characterise biological movement; Todorov, & Jordan, 1998, see Figure 5.1), while the other moved with a linear combination of this profile and constant velocity (CV or unnatural movement). In line with the sensitivity hypothesis the typical participants showed enhanced sensitivity to this profile compared to the participants with autism. Furthermore, in a follow-up study, Cook et al. (2013) found a positive relationship in an autism group between a bias to label natural motion as unnatural and the extent to which their own movements were kinematically atypical (high acceleration and jerk). In other words, the autistic participants who moved most atypically perceived the objectively 'natural' movement to be more unnatural.

However, to date no studies have fully tested the bi-directionality of the current hypothesis. Specifically, no studies have used ‘autistic’ models to test perception in either typical or autistic observers. The current study therefore modified the paradigm employed in Cook et al. (2009) by displaying both typical and autistic motion profiles. Additionally, the profiles for the current study were generated using the average profiles of the real hand movements of typical and autistic participants collected by Cook et al. (2013). Thus, as well as testing the bi-directionality of the hypothesis, the stimuli presented motion that was in fact natural. The previous study addressing kinematic perception in autism used stimuli generated from the mathematical formula representing minimum jerk (Todorov, & Jordan, 1998). The mathematically generated stimuli differ from natural profiles of real movements in that they have less kinematic noise (see Figure 5.1). In principle autistic participants may simply be less willing to label this computationally-derived profile as natural – especially if their sub-second temporal perception is enhanced (Chapter 4) – and therefore previous findings may not be driven by lower sensitivity to typical human motion in autism but the fact that the profile used was not in fact natural.

The sensitivity hypothesis would predict that participants with autism would show enhanced performance on the autistic profile, compared to the typical profile, as this movement trajectory would be better matched to their own atypical representation of natural movement. This account would also predict that the typical participants would show enhanced performance on the typical profile relative to the autistic movements. In contrast, if one’s own action does not influence action models through perceptual narrowing, no such differences would be found.

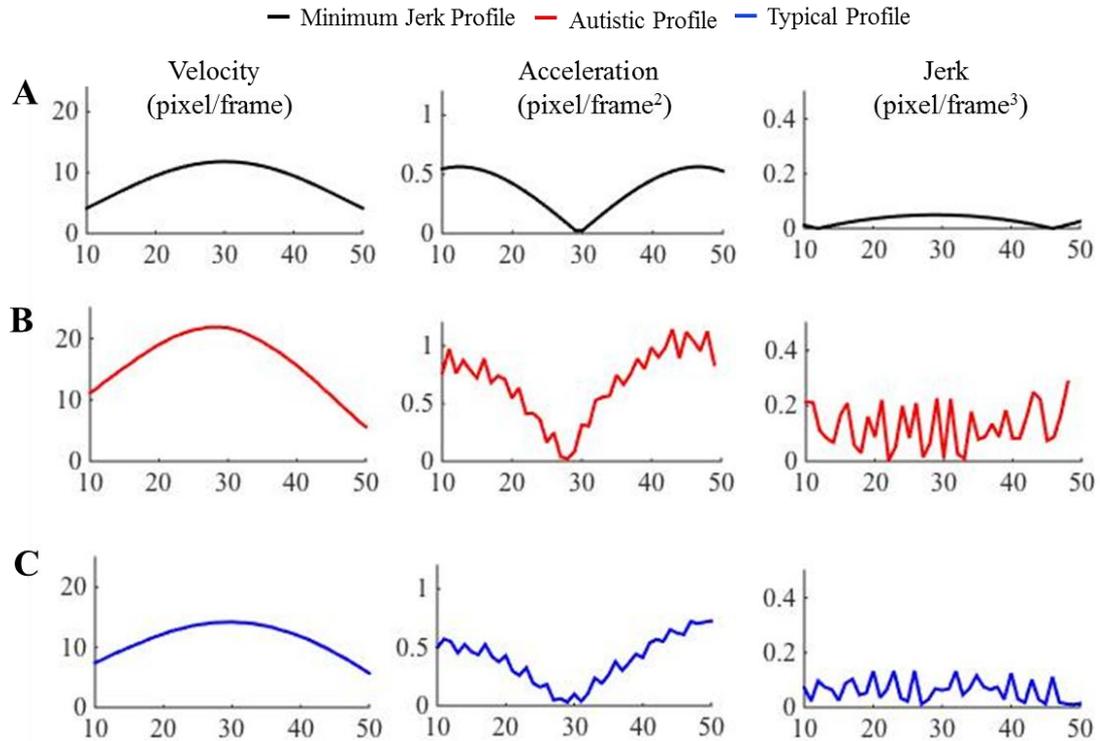


Figure 5.1: Example kinematic trajectories for one direction of movement used by Cook et al. (2009) (A) and the current experiment (B = autistic profile, C = typical profile). The first column denotes the velocity (pixels/frame) within each reference profile, the middle column acceleration (pixels/frame²), and the last column jerk (pixels/frame³). Note the typical and autistic profiles, generated from real actors, follow a profile that generally complies with the minimum jerk profile (increase and decrease in velocity) but the signal is more noisy i.e., less superficially smooth.

5.2. Methods

5.2.1. Participants

Thirty-one typical adults and 25 adults with autism were recruited from the local research volunteer database. Seven participants from the typical group and three participants from the autism group were excluded because their data for one (autism N=2, typical N=2) or more (autism N=1, typical N=5) of the four test staircases did not reach criteria to produce robust perceptual threshold estimations (see section 5.2.4).

These exclusions resulted in a final sample of 24 (23 males) typical and 22 (18 males)

participants with autism. An independent clinician diagnosed participants in the autism group, and the ADOS-2 (Lord et al., 2012) was additionally administered to confirm participants' current level of functioning. Three participants did not meet all ADOS-2 criteria for classification of an autism spectrum disorder. In line with the other autism chapters, data from all autistic participants are reported, but the same pattern of results was found regardless of their inclusion. The participants were matched on FSIQ, as measured by the WASI (Wechsler, 1999; $t(44)=1.34, p=.186, d=.40$), age ($t(32.86)=1.63, p=.121, d=.48$), and gender (Fisher's Exact Test, $p=.178$), but, as expected, there was a significant difference between the groups in AQ (Baron-Cohen et al., 2001) scores ($t(44)=6.79, p<.001, d=2.00$; see Table 5.1).

Table 5.1: Demographic information for the autism and typical groups

	FSIQ mean (SEM)	Age mean (SEM)	Gender (N=male)	AQ mean (SEM)	ADOS mean (SEM)
Autism Group (n =22)	111.18 (3.27)	36.77 (3.02)	18	32.77 (1.91)**	9.86 (.782)
Typical Group (n =24)	105.46 (2.77)	31.21 (1.68)	23	17.58 (1.41)	-

** $p<.001$

5.2.2. Stimulus generation

The stimuli for the experiment were created using Matlab® Cogent. An image of a hand was manipulated to move across the horizontal plane of a computer screen with varying movement kinematics. The movement trajectories for the stimuli were generated using data collected in a previous study where participants either with or without autism performed a sinusoidal horizontal hand movement (Cook et al., 2013). For each profile

(autism or typical), the mean x and y displacements of the actor groups' hand movements were used as the x and y co-ordinates at which to present the image of the hand on the computer screen. This process therefore generated two distinct animated profiles that represented the mean of the two previous autistic and typical actor groups' natural kinematic trajectories. These animations were the 'reference' (100% natural) stimuli. Each animation lasted approximately 2 seconds.

The 'target' stimuli presented a linear combination of reference stimuli and a CV (unnatural) profile. The velocity morphs were calculated using the formula:

$$\text{Velocity Morph} = p_1(\text{Natural Movement}) + p_2(\text{Unnatural Movement})$$

where the p_1 weight determines the proportion of 'natural' movement in the trajectory, and the p_2 weight determines the proportion of the 'unnatural' movement profile. The initial target stimulus at the beginning of each block contained a weighing of 1 unnatural motion, and 0 natural (typical or autism) such that it was highly distinguishable from the reference stimulus. The weighting of the subsequent target stimulus on each trial was calculated according to the participant's performance on the preceding trial (see section 5.2.4).

5.2.3. Procedure

The experiment was run via Matlab® on a 24 inch screen computer. The experiment consisted of a forced choice paradigm, where on each trial the participant was presented with a target and a reference animation, which were presented in a random order and separated by a black blank screen for 1500 ms. Following the two animations, participants were asked to choose which of the two hand movements was 'less natural' (see Figure 5.1A for schematic diagram of an example trial). Responses were made by pressing a key to indicate the first or second animation; and there was no time limit for

the participant's response.

Before the experiment, the experimenter read instructions to the participant, where natural movement was defined as how a person would typically move when moving their arm, without expressing any emotion; and unnatural movement was defined as odd or mechanical movement. To familiarise participants with the procedure and the stimuli they completed two practice mini-blocks of five trials for each condition, which were randomised across participants. No feedback was given. Next, the participants began the testing session, which consisted of six blocks for each condition. Each block contained 17 trials (total of 204 trials), and lasted approximately two minutes. The conditions of the blocks were interleaved and randomised in pairs, such that participants never completed more than two blocks of the same condition in a row. The duration of the whole experiment was approximately 30 minutes.

5.2.4. Sensitivity threshold calculation

To measure each participant's sensitivity to the two types of 'natural' movement their psychophysical threshold was calculated using a two-interval forced-choice adaptive staircase procedure. The ratio between natural and unnatural motion within the target stimulus decreased linearly throughout the staircasing procedure (see morphing formula above, and Figure 5.1B), according to the participant's performance. The weighting of the target stimulus was determined on a trial-by-trial basis, using a 'three-down, one up' adaptive technique. In this procedure three correct responses resulted in a step down the staircase (decrease in threshold, the unnatural weighting decreased and the natural weighting increased, thus the target and reference became more physically similar). One incorrect response resulted in a step up the staircase (increase in threshold, the unnatural weighting increased and the natural weighting decreased, thus target and reference became more perceptually distinct). This method aims to identify the 79.4% correct

point on a psychometric function. In a two-choice method, the probability of moving down or up the staircase must be equal. Therefore, if the probability of moving up the staircase is p , then the probability of moving down must be equal $p * p * p$, or .5, and hence the target probability of getting a correct response $\sqrt[3]{.5} = .794$ (Kingdom & Prins, 2010).

Initially, the weighting changes for either three successive correct, or one incorrect response was 20% (hereafter a ‘jump’). Given that the proportion of ‘unnatural’ movement could never exceed 100%, incorrect responses at this level resulted in the subsequent trial continuing to display the target with full CV. Note that the lowest level of CV movement was capped at 16% (again, if participants reached this threshold, and continued to get the responses correct then the target would continue to be shown at 16% unnatural motion). After four turning-points on the staircase, these weighting ‘jumps’ were reduced to smaller ‘steps’ (step size = 2.5%) to allow for a finer estimation of the participants threshold. A lower psychophysical threshold therefore represents greater sensitivity to the specific movement cues that define natural motion.

Each staircase consisted of three experimental blocks (51 trials) for each condition and a psychophysical threshold estimate was calculated for each. The threshold was calculated as the mean proportion of unnatural movement present across all step turning-points. The estimates from the two staircases for each condition (autistic or typical models) were then averaged to obtain one estimate per condition. When staircase number (first or second) was included in the analysis as an additional within-participant factor the pattern of results was the same, and there was no main effect of staircase number, or interactions with any of the other variables. Participants who failed to transition from ‘jumps’ to ‘steps’ (i.e., had fewer than 4 turning-points) on any staircase were excluded as it was not possible to generate a robust threshold for their data

(Kingdom & Prins, 2010; see Participants section 5.2.1).

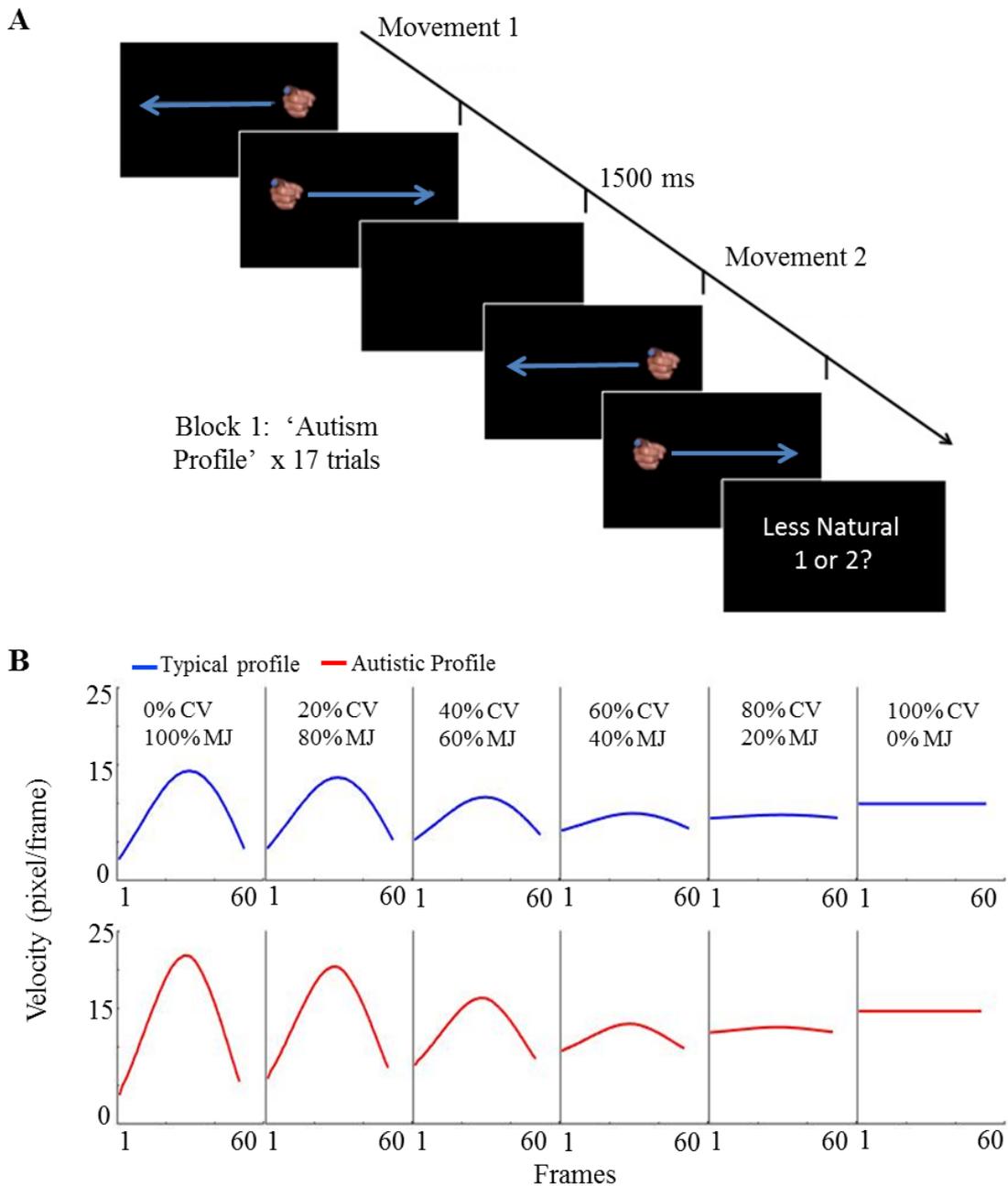


Figure 5.2: (A) Schematic diagram of an experimental trial. Within each trial participants were presented with two animations of a hand moving across the screen and were asked to judge which was less natural. Blocks were randomised in pairs, such that participants never completed more than two blocks of the same condition in a row. (B) Examples of the velocity profiles for the first half the sinusoidal motion (e.g., from left to right on the computer screen), both profiles show a general bell shaped curve (blue lines represent the typical velocity profile, red lines represent the autistic velocity profile), with the reference stimuli in the first panels on the left of the figure, initial targets in the last panels on the right, and examples of some of the possible linear combinations shown in the middle panels.

5.3. Results

A 2x2 Mixed ANOVA was performed on the sensitivity threshold data, with group (autism or typical observer) as a between-participant factor, and model (autistic or typical movement trajectory) as a within-participant factor. There was no main effect of group ($F(1,44)=0.81, p=.778, \eta_p^2=.002$) or of model ($F(1,44)=1.33, p=.255, \eta_p^2=.029$). As predicted under the sensitivity hypothesis, there was an interaction between model and group ($F(1,44)=4.08, p=.049, \eta_p^2=.085$). However, unexpectedly the simple effects revealed that this interaction was driven by the typical group showing greater sensitivity to the autistic than typical model (autistic model: $M=.68, SEM=.06$, typical model: $M=.75, SEM=.05, p=.027, 95\% CI [.008, .126], d=.42$) and the autism group showing equivalent, and relatively good, performance with both profiles (autistic model: $M=.70, SEM=.06$, typical model: $M=.68, SEM=.05$), $p=.551, 95\% CI [-.027, .065], d=.11$, see Figure 5.3).

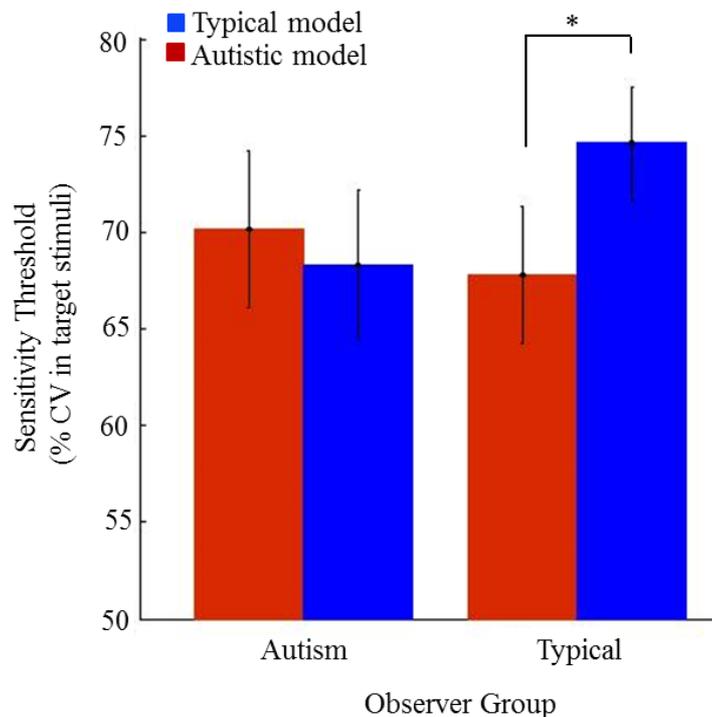


Figure 5.3: Perceptual sensitivity thresholds (79.4% accuracy) for the autism and typical observers for the autistic and typical movement conditions. Lower thresholds indicate that participants have greater sensitivity to perturbations in the natural kinematics. Error bars represent the SEM. * $p<.05$

5.4. Discussion

Perceptual sensitivity to biological motion, where the motion stimuli were generated from motion profiles obtained from autistic and typical actors (Cook et al., 2013), was measured in a group of matched typical and autistic adults. The sensitivity version of the own action hypothesis proposes that the intensity of experience with one's own action kinematics generates models that are highly sensitive to similar kinematic features, but with poor sensitivity to kinematic information that is different, or infrequently experienced. Therefore, under this theory it was hypothesised that participants would show greatest perceptual sensitivity to their own group's natural movement exemplars. However, the results did not support this hypothesis; the typical group showed greater sensitivity to the autistic, relative to the typical profile, yet the autism group showed similarly strong performance for both profile types.

Given that the present findings did not provide support for the sensitivity hypothesis, one possibility is that both groups have frequent experience of both movement profiles. Notably, the kinematic qualities of our movements can vary dramatically depending on our internal states. Thus, although individuals with autism might generally move faster, and with greater acceleration and jerk, they may frequently also produce movements that follow a more typical kinematic profile in some circumstances (e.g., when underconfident; Patel et al., 2012). Likewise, a typical individual may also occasionally produce movement kinematics that comply with an autistic profile (e.g., when in a state of greater social uncertainty typical individuals produce jerkier movements; Quesque et al., 2013). Therefore general differences in how typical and autistic individuals move may correspond to different internal state-kinematic models but due to the variability in action experiences across a range of settings perceptual sensitivity to kinematic features that fall within both exemplar profiles might be equal.

Nevertheless, it must also be considered that the typical group were *superior* when observing the autistic profile. Of relevance here is that the autistic motion was in fact more physically distinct from the unnatural (CV) profile (see Figure 5.2B), and therefore perhaps it is easier to distinguish from the unnatural profile compared to the typical profile. Interestingly, the autism group did not show the same enhancement (in fact their performance was comparable to the typical performance with the autistic profile such that they generally showed good performance on the task, regardless of profile).

One potential explanation could be the lesser influence of context on perceptual judgments in the autism group, which has been theorised to explain differences in perceptual processing styles in autism (Lawson et al., 2014; Pellicano & Burr, 2012). The participants with autism may have made their judgments on a trial-by-trial basis, always identifying the action out of the two comparison stimuli that they saw to have the greater kinematic variants (i.e., greater changes in velocity and acceleration) as more natural (Bowler & Thommen, 2000; Tremoulet & Feldman, 2000). However, the typical participants might have been considering the range of other profiles they had been shown throughout the experiment and making comparisons against these, such that the less kinematically distinct typical profile became harder to detect. Therefore in the context of the current experiment the autistic profile, with greater kinematic variants, was labelled as more natural than the typical profile by the typical participants.

It should also be noted that the results of the present experiment may require a reinterpretation of the findings of Cook et al. (2009), where the autistic participants performed more poorly than the typical group on a similar motion perception task. A crucial difference between the current study and Cook et al. (2009) are the stimuli. Cook et al. (2009) used computer-generated movements that followed the mathematical

formula for human movements, while the current study used kinematic trajectories of real movements. The computer-generated movements, which follow a perfectly smooth trajectory, may have been devoid of vital kinematic ‘noise’ that provides a better cue for naturalness. Consequently, the computer-generated stimuli may in fact be too artificially smooth (see Figure 5.1), which might have had greatest impact on the autistic group who may be more sensitive to sub-second kinematic information (Chapter 4).

In conclusion, the current study found no evidence for impaired perceptual sensitivity to natural typical movements in adults with autism, or improved sensitivity to typical relative to autistic movements in matched typical adults. Previous findings suggestive of such differences in sensitivity may therefore be generated by use of stimuli that were computationally derived rather than natural. The current results suggest that any differences in internal state understanding and communication in autism generated through different action models are therefore more likely to result from differences in models concerning the relationships between actions and their associated mental states – differences in ‘criterion setting’ not ‘sensitivity’.

Chapter 6: Interaction takes two: typical individuals show mindblindness towards those with autism

The experiments in Chapters 4 and 5 found evidence that the basic perceptual skills required for interpreting the actions of others – visual temporal perception and perceptual sensitivity to kinematic information – in adults with autism are intact. The atypicalities in internal state inference and communication may therefore result from bilateral difficulties between those with autism and typical others in interpreting the internal states of others from their kinematics (cf. Chapters 2 and 3). Specifically, some of the social impairments exhibited by individuals with autism may, at least in part, be a product of a failure to infer internal states from the movements of those who move differently, and therefore autistic individuals may infer incorrectly the internal states of typical others. Similarly, communicative difficulties may emerge from typical individuals misreading internal states from autistic movements. To test this hypothesis, in the current experiment, individuals with autism and matched typical adults manually directed two triangles to generate animations depicting mental state interactions. Replicating previous findings, kinematic analysis of the generated animations demonstrated that the participants with autism moved atypically, specifically with increased jerk, compared to the typical participants. In confirmation of the primary hypothesis, typical individuals were better able to identify the mental state portrayed in the animations produced by typical, relative to autistic individuals. The participants with autism did not show this ‘same group’ advantage, demonstrating comparable performance for the two sets of animations. These results suggest that differences in the kinematic qualities of the movements constrain typical individual’s ability to understand internal states of those with autism, which may contribute to communication difficulties between autistic and typical individuals.

6.1. Introduction

As discussed in Chapter 1, there is vast evidence that our interactions with the world enable us to develop models that facilitate our interpretation of others' behaviour. For example, greater experience of executing a particular action leads to more accurate judgments about the underlying intentions of other individuals performing that action (Abernethy et al., 2008; Aglioti et al., 2008; Sebanz & Shiffrar, 2009). Therefore, the way in which we execute actions is likely to have dramatic implications for our understanding of others' internal states, such that we may be better placed to understand and interact with those who move most like us (see Chapters 2 and 3 for evidence supporting this hypothesis in typically developing individuals).

Given that individuals with autism move in a quantifiably different way from typical adults (Cook et al., 2013) it is predicted that those with autism will have distinct representations of action compared to typical individuals, which might affect social interaction between these two groups. The two experiments presented in Chapter 4 and 5 demonstrate that individuals with autism are able to 1) perceive temporal differences in visually presented information, 2) modulate their actions to accurately co-ordinate a motor response with a visual cue and, 3) are sensitive to the kinematic features that define natural motion. Therefore, those with autism appear to have at least some of the basic perceptual skills that are required to encode the complex kinematic cues that provide informative signals for a whole host of socio-cognitive processes, such as ascribing internal states to others actions or mentalising.

One possible explanation for the difficulty those with autism have in interpreting others actions (Abell et al., 2000; Atkinson, 2009; Bowler & Thommen, 2000; Castelli et al., 2002; Jones et al., 2011; Klin, 2000; Nackaerts et al., 2012; White et al., 2011; Zwickel et al., 2011) concerns a mismatch between autistic and typical individuals in models of

the relationship between kinematics and internal states. In other words, because those with autism have experience producing actions that are atypically jerky, their representations of which kinematic signal exemplify which mental state may be distinct from those of typical individuals. When observing typical actions the kinematic properties will not signal the same information to an autistic observer, leading to erroneous ascriptions. For example, faster, jerkier movement is associated with angry affective states in typical individuals but similar movement may be produced by individuals with autism when they feel relatively calm. Autistic individuals may therefore fail to perceive anger in typical others, and conversely typical others may interpret autistic calm movements as reflecting anger.

Therefore, it was hypothesised that typical individuals will be impaired at reading internal states from kinematic cues in autistic actions, and autistic individuals will be impaired when interpreting typical actions. Critically, under this hypothesis, communication difficulties experienced by individuals with autism may not solely be due to understanding and behavioural impairments solely in the autistic individual. Individuals with autism may frequently attempt to communicate their desires, intentions and affective states, yet typically developing individuals may not interpret them correctly. Therefore, social communication difficulties between these two groups may, at least partly, be a manifestation of inaccuracies of both parties.

To test this hypothesis, the current study used an adaptation of the Frith-Happé animation task to test online mentalising. In an initial ‘Generation Phase’, participants with and without autism were asked to direct hand-held triangular magnets on a table top to depict the same mental state verbs as used in the standard version of the task (coaxing, mocking, seducing and surprising). In a subsequent ‘Perception Phase’, participants watched the animations and rated the extent to which they depicted each of

these target mental states (note that participants never observed their own generated animations). The accuracy of ratings in the ‘Perception Phase’ was compared when typical and autistic participants observed both typical and autistic animations to investigate whether individuals with autism show improved intention attribution when interpreting the movements of others with autism relative to typical movements, and vice versa for the typical group.

6.2. Generation phase

To test the main research question it was necessary to record animations generated by autistic and typical individuals, and verify that there were kinematic differences between them.

6.2.1. Method

6.2.1.1. Participants

Fifteen typically developed adults and 16 adults with autism were recruited via the same method used in Chapters 4 and 5. An independent clinician diagnosed participants in the autism group according to DSM IV criteria (American Psychiatric Association, 1994), and the ADOS-2 (Lord et al., 2012) was administered to confirm participants’ current level of social functioning. Two participants did not meet all ADOS-2 criteria for a classification of autism spectrum disorder. Like in Chapters 4 and 5, these participants were indistinguishable from the other participants on all measures and therefore the data are reported across all participants, but the same pattern of results was found when excluding them. The two groups did not differ on FSIQ, as measured by the WASI (Wechsler, 1999, $t(29)=2.00$, $p=.054$, $d=.72$), age ($t(29)=1.69$, $p=.102$, $d=.61$), or gender (Fisher’s exact test, $p>.99$), but as expected the autism group had significantly higher scores on the AQ (Baron-Cohen et al., 2001, $t(23.34)=6.15$, $p<.001$, $d=2.19$), see Table

6.1).

Table 6.1: Demographic information for the participants who generated the animations

	FSIQ Mean (SEM)	Age Mean (SEM)	Gender (N=male)	AQ Mean (SEM)	ADOS Mean (SEM)
Autism Generator Group (n =16)	116.00 (3.04)	42.06 (2.96)	14	30.44 (2.24)**	9.63 (.96)
Typical Generator Group (n =15)	105.53 (4.32)	34.80 (3.12)	13	14.67 (1.25)	-

** $p < .001$

6.2.1.2. Animation generation

The setting for the animations was based on the stimuli used in the Frith-Happé paradigm (Abell et al., 2000). A white table with a black enclosure was used as the background for the animations (see Figure 6.1A). A large red and a small blue triangle made from coloured card were attached to two magnets; the opposite pole of the magnet was attached below the table to enable manual operation of each triangle. Participants were given time to practise operating the magnets to manoeuvre the triangles, and had two practice trials (see Figure 6.1A; note that participants could see their action effects in the form of the triangle movements). A video camera (Panasonic SDR-S50) was positioned directly above the table to film the participants' animations at a rate of 25 frames /second.

The four target mental state words (coaxing, mocking, seducing and surprising – the same as used in Abell et al., 2000) were presented to participants in a random order. On each trial the participants were asked: 'How will you represent (coaxing, mocking,

seducing, surprising) with the two triangles?’ Participants were instructed that their animations should last ~30 seconds, and given one minute to think before providing a verbal response of how they would animate the mental state word. Participants were directed to the dictionary definition if they were unsure of the word’s meaning, and no further guidance was given. Following the verbal response the participants performed their animation. Each animation was edited to make size and colours consistent using Adobe After Effects (see Figure 6.1B). Any items that appeared on the screen, other than the triangles, were edited out (e.g. participants’ heads).

The animations were analysed using Matlab® to extract the kinematics (jerk, acceleration and velocity) of both triangles. First, every pixel (720 x 576 pixels) within each frame was coded for the presence of red or blue and saved as a colour-coded frame set. The following analysis was run twice to code the location of the red and blue triangle separately.

The colour-coded frame sets were scanned, starting at each corner of the background of the animation (top, bottom, left and right), to locate the four most extreme points of the triangles. Two of these points related to the same corner of the triangle, and therefore one was removed. From the remaining three points, the ‘nose’ of the triangle was located by identifying the adjoining point at the end of the two longest sides. The ‘tail’ was the mid-point between the other two points. This procedure resulted in location markers for the nose and tail of the red and blue triangle on each frame. The change in x and y position was tracked between each frame by first order differentiation of the position vectors. These vectors were low-pass Butterworth filtered at 2 Hz to remove noise associated with the imperfect localization of the x and y values on some frames due to occasional poor contrast in the animations. The velocity was calculated as the square root of the summed squared x and y displacement per frame. The velocity values

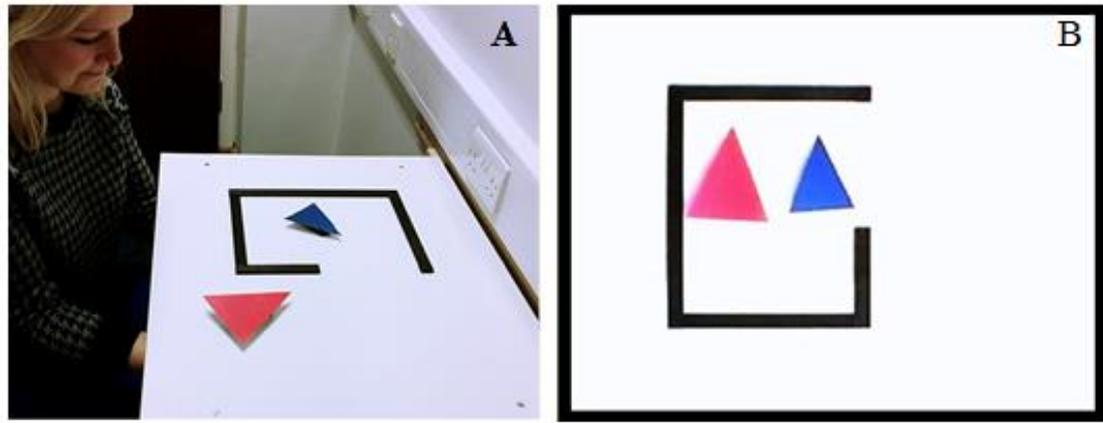


Figure 6.1: (A) Participants generated animations by manually directing triangles on a table top with magnets to represent the target mental state words (coaxing, mocking, seducing and surprising). (B) Edited example stimulus that was displayed to participants as a ~30 second animation

were then low-pass Butterworth filtered at 3 Hz to remove noise due to the imperfect measure of displacement of the nose / tail owing to occasional flickers in the animations due to extreme exposure in some of the frames. It was verified manually that filters were optimal in both preserving the movement information and removing noise. Visual inspection determined that frames with velocity values below 1 pixel / frame were periods of no movement, and were removed from further calculations. Acceleration was calculated as the absolute first order differential of the velocity vectors, and jerk was calculated as the absolute second order differential. The mean velocity, acceleration and jerk was calculated from these absolute values, and transformed from pixels / frame to mm / second.

6.2.2. Results

6.2.2.1. Animation kinematic analysis

To verify that the animations generated by the two groups differed in their kinematics, a 2x4 Mixed ANOVA was performed for each kinematic measure with group (autism or typical) as a between-participant factor, and mental state (coaxing, mocking, seducing

or surprising) as a within-participant factor.

Most importantly, there was a main effect of group for the jerk measure ($F(1,29)=4.89$, $p=.035$, $\eta_p^2=.144$). This effect was a result of the autism group moving with higher jerk relative to the typical group (see Figure 6.2), therefore replicating previous findings of jerkier movements in autistic individuals.

There was a main effect of mental state animation on jerk ($F(3,87)=8.74$, $p<.001$, $\eta_p^2=.232$), but there was no interaction between mental state animation and group ($F(3,87)=.132$, $p=.941$, $\eta_p^2=.005$). Follow-up pairwise comparisons to examine the main effect of mental state revealed the mocking animations ($M=6.52$ mm/s³, $SEM=.33$) had higher mean jerk than the coaxing ($M=4.46$ mm/s³, $SEM=.34$; $p=.003$, 95% CI [.55, 3.56], $d=.71$) and seducing animations ($M=4.57$ mm/s³, $SEM=.34$; $p=.002$, 95% CI [.57, 3.32], $d=.73$), and the surprising animations ($M=5.57$ mm/s³, $SEM=.32$) had higher mean jerk than the coaxing animations ($p=.016$, 95% CI [.151, 2.07], $d=.60$). The lack of interaction between mental state animation and group— and therefore comparable pattern of kinematics across the four mental state animations (see Figure 6.2B) — suggests that both groups modulated the kinematic features of their movements to represent different mental states in a similar fashion. This result suggests that both groups possessed a similar understanding of the different mental states (see also Verbal task, section 6.4).

There was no main effect of group for the acceleration data ($F(1,29)=1.62$, $p=.213$, $\eta_p^2=.053$). There was also no interaction between mental state animation and group ($F(3,87)=.33$, $p=.806$, $\eta_p^2=.011$), but again, there was a main effect of animation ($F(3,87)=9.73$, $p<.001$, $\eta_p^2=.251$). Follow-up pairwise comparisons revealed the same pattern as the jerk measure; the mocking animations ($M=15.36$ mm/s², $SEM=1.05$) had higher mean acceleration than the coaxing ($M=10.71$ mm/s², $SEM=.83$; $p=.003$, 95% CI

[1.31, 7.99], $d=.72$) and seducing animations ($M=11.06$ mm/s², $SEM=.69$; $p=.003$, 95% CI [1.20, 7.40], $d=.70$), the surprising animations ($M=13.94$ mm/s², $SEM=.74$) had higher mean acceleration than the coaxing animations ($p=.001$, 95% CI [1.13, 5.33], $d=.79$), and the surprising animations had higher mean acceleration than the seducing animations ($p=.038$, 95% CI [.12, 5.65], $d=.53$).

Finally, there was no main effect of group for the velocity measure ($F(1,29)=.027$, $p=.870$, $\eta_p^2=.001$). There was also no interaction between mental state animation and group ($F(3,87)=.38$, $p=.766$, $\eta_p^2=.013$), but there was a main effect of mental state animation ($F(3,87)=9.08$, $p<.001$, $\eta_p^2=.238$). Follow-up pairwise comparisons demonstrated the same pattern as in the acceleration and jerk analyses. The mocking animations ($M=109.05$ mm/s, $SEM=7.23$) had higher mean velocity than the coaxing ($M=80.77$ mm/s, $SEM=4.57$; $p=.003$, 95% CI [7.84, 48.73], $d=.71$) and seducing ($M=83.62$ mm/s, $SEM=4.53$; $p=.015$, 95% CI [3.61, 47.26], $d=.59$) animations, the surprising animations ($M=101.29$ mm/s, $SEM=5.12$) had higher velocity than the coaxing animations ($p=.001$, 95% CI [7.74, 33.31], $d=.83$), and the surprising animations had higher mean velocity than the seducing animations ($p=.050$, 95% CI [.02, 35.33], $d=.52$).

These results indicate that the animations produced by the participants with autism had different kinematic properties, specifically increased jerk relative to the typical generators. This confirmed our hypothesis and replicated the previous results, showing individuals with autism move with atypical kinematics (Cook et al., 2013).

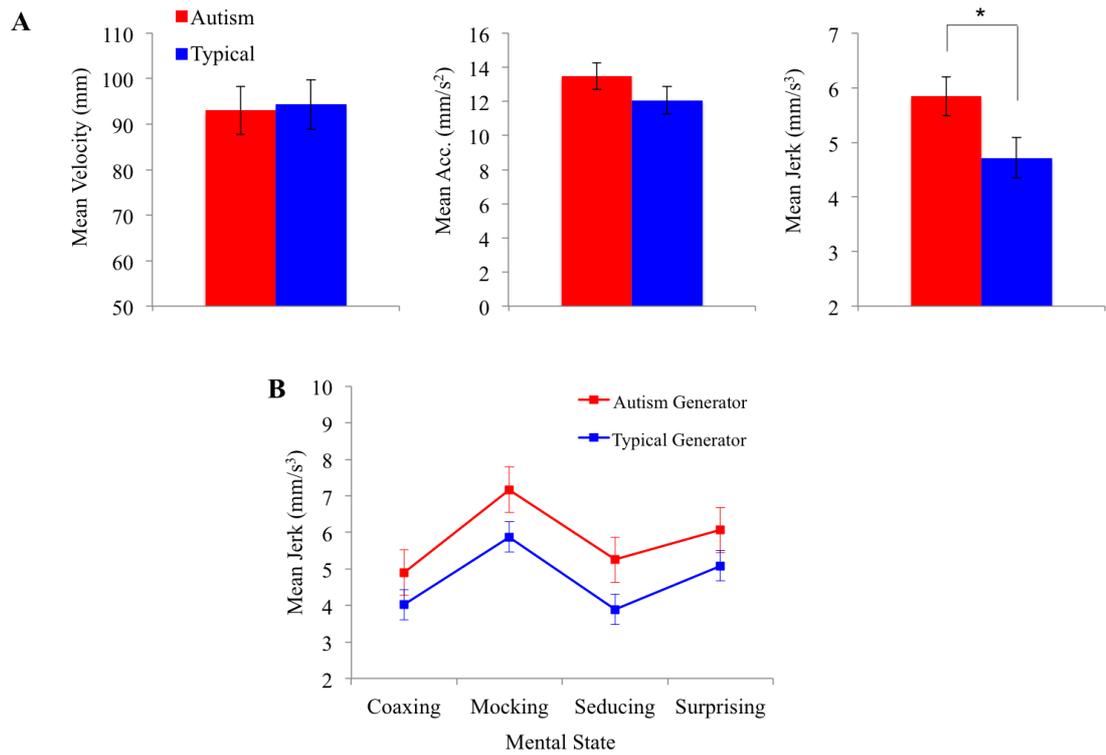


Figure 6.2: (A) Mean velocity, acceleration and jerk for the autism and typical animations. (B) Mean jerk for the four mental states for the typical and autistic animations. It can be seen that the jerk effect did not interact with mental state, such that both groups modulated their kinematics comparably according to the different mental states. Error bars represent the SEM. * $p < .05$

6.3. Perception task

6.3.1. Methods

6.3.1.1. Participants

Twenty-five typical adults and 23 adults with autism were recruited via the same method of recruitment for the typical and autistic participants described in the generation phase methods (Section 6.1.1, see Section 6.3.1.2 for information relating to those participants who also participated in both the generation and perception phase of the experiment).

Three participants did not meet all ADOS-2 criteria for a classification of autism

spectrum disorder. These participants were included in the main analyses reported, but the pattern of results was the same when excluding these three participants. Two participants (one participant from each group) were excluded from the analysis as their verbal responses suggested that they did not understand the task demands. The remaining participants were matched on FSIQ ($t(44)=-.05, p=.964, d=.01$), age ($t(44)=.63, p=.531, d=.19$) and gender (Fisher’s exact test, $p=.702$), and as expected, the groups differed in AQ scores ($t(44)=5.98, p<.001, d=1.85$; see Table 6.2).

Table 6.2: Demographic information for autistic and typical participants in the perceptual task and those who took part in the verbal descriptions experiment

	FSIQ Mean (SEM)	Age Mean (SEM)	Gender (N=male)	AQ Mean (SEM)	ADOS Mean (SEM)
Autism Perceiver Group (n =22)	111.05 (3.62)	38.50 (2.97)	19	32.82 (2.11)**	9.77 (.79)
Typical Perceiver Group (n=24)	111.25 (2.69)	36.08 (2.45)	19	17.29 (1.56)	-
Typical Verbal Experiment Group (n=24)	-	35.46 (2.98)	18	-	-

** $p<.001$

6.3.1.2. Animation selection

Six autism and six typical animations of each of the four mental state words were presented in the perception task, resulting in 48 animations. This number of animations was selected to ensure that the task, on average, took no longer than an hour to complete and therefore reduce possible fatigue effects.

From the usable animations each stimulus was selected for inclusion based on two

criteria. First, two animations above and two below the mean jerk value for that group (e.g. autism) and target mental state (e.g. mocking) were selected, all within one standard deviation of the mean, and two animations greater than one standard deviation from the mean (one above and one below the mean). This criterion was employed to match the jerk of the selected stimulus set to the distribution of the full sample of generated animations (see Table 6.3). Second, a maximum of three animations created by any given participant were included. This criterion was employed to ensure that any one participant's animations did not dominate the stimulus set.

Table 6.3: Mean jerk measures (mm/s³) for the two groups for all the animations in the generation phase, and for the selected animations to be shown in perception phase

	Coaxing		Mocking		Seducing		Surprising	
	Autism	Typical	Autism	Typical	Autism	Typical	Autism	Typical
Total Jerk mean (sd)	5.16 (2.53)	3.94 (1.50)	7.10 (3.48)	5.73 (2.40)	5.41 (2.04)	3.55 (1.20)	6.00 (1.86)	4.84 (1.55)
Six Selected Stimuli Jerk mean (sd)	4.9 (2.71)	4.27 (1.77)	7.44 (3.00)	6.03 (2.11)	5.13 (2.79)	3.60 (1.35)	6.07 (1.58)	4.78 (1.37)

Note: units mm/s³

Thirteen of the autism group and eight of the typical group also participated in the main perceptual task. There were approximately nine months between the animation generation and perceptual task. Participants who took part in both animation generation and the main perceptual task were not shown their own animations. Their animations were substituted with another exhibiting the closest jerk value for that animation (e.g., mocking) within their group (autism/ typical).

6.3.1.3. Procedure

The experiment was run via Matlab® on a 24 inch computer screen. An initial practice trial familiarised participants with the procedure and task requirements. On each trial, after viewing the animation, participants were asked to describe verbally what happened in the animation, to ensure that they had attended to the whole animation. Following the verbal response, they were asked to rate on a visual analogue scale (ranging from 1 [not at all] to 50 [a lot]) the extent to which the animation depicted the four target mental state words: coaxing, mocking, seducing, and surprising. Participants were able to choose the order in which they rated the four target mental state words, and they could change their responses at any point. It was not possible to go onto the following trial until all scales had a rating. The participant pressed a key when they were ready to begin the next trial. No feedback was given on their performance.

6.3.2. Results

Participants' ratings were scored for accuracy. This measure was calculated by subtracting the average of the three 'incorrect' ratings, from the 'correct' rating on each trial (e.g., the coaxing rating minus the mean rating of mocking, seducing and surprising when viewing a coaxing animation). A higher score indicates a greater match to the intended representation, and any score below zero indicates that the participants were unable to identify correctly the intended mental state verb.

Both the autism ($M=5.63$, $SEM=.70$; $t(21)=8.05$, $p<.001$, 95% CI [4.18, 7.09], $d=1.76$) and typical ($M=6.96$, $SEM=.62$; $t(23)=11.29$, $p<.001$, 95% CI [5.68, 8.23], $d=2.30$) perceiver groups' overall mean accuracy was significantly higher than zero, indicating that both groups could do the task effectively. Additionally, the mean accuracy for the animations generated by the autism ($M=5.48$, $SEM=.48$; $t(45)=11.48$, $p<.001$, 95% CI [4.51, 6.44], $d=1.28$) and typical ($M=7.19$, $SEM=.63$; $t(45)=11.45$, $p<.001$, 95% CI

[5.93, 8.46], $d=2.56$) participants was higher than zero, demonstrating significant signal present in the animations generated by both groups.

To test for differences in perception between the two perceiver groups a 2x2x4 Mixed ANOVA was performed with perceiver group (autism or typical observer) as a between-participants factor, and generator group (autism or typical generator) and mental state (coaxing, mocking, seducing or surprising) as within-participants factors.

There was a main effect of mental state animation ($F(3,132)=43.13, p<.001, \eta_p^2=.496$), which did not interact with perceiver group ($F(3,132)=1.70, p=.171, \eta_p^2=.037$) but did interact with generator group ($F(3,132)=7.10, p<.001, \eta_p^2=.139$). There was no three way interaction between generator group, perceiver group and mental state animations ($F(3,132)=2.04, p=.111, \eta_p^2=.044$). Follow-up t-tests indicated that the interaction between generator group and mental state animation was driven by better performance on the typical ($M=6.16, SEM=.61$) relative to autism surprising animations ($M=-1.16, SEM=.48; p<.001, 95\% CI [4.43, 10.21], d=.73$), without a generator group difference for the other mental state animations.

The main effect of perceiver group was not significant ($F(1,44)=2.04, p=.160, \eta_p^2=.044$), yet there was a main effect of generator group, with better rating accuracy when participants observed the typical ($M=7.14, SEM=.61$) compared to the autism animations ($M=5.45, SEM=.48; F(1,44)=8.53, p=.006, \eta_p^2=.162$). However, most importantly, this effect was qualified by an interaction with perceiver group ($F(1,44)=4.32, p=.044, \eta_p^2=.089$). Simple effects analysis showed the typical perceivers were significantly better at rating the typical animations than the autism animations ($p=.001, 95\% CI [1.23, 4.48], d=.66$), but the autism perceivers performed equally for the autism and typical animations ($p=.563, 95\% CI [-1.22, 2.18], d=.14$; see Figure 6.3). These results indicate that the typical group was able to identify the intended mental

state in the typical generated animations to a greater extent than for the autism-generated animations, while the autism group performed comparably on both groups' animations.

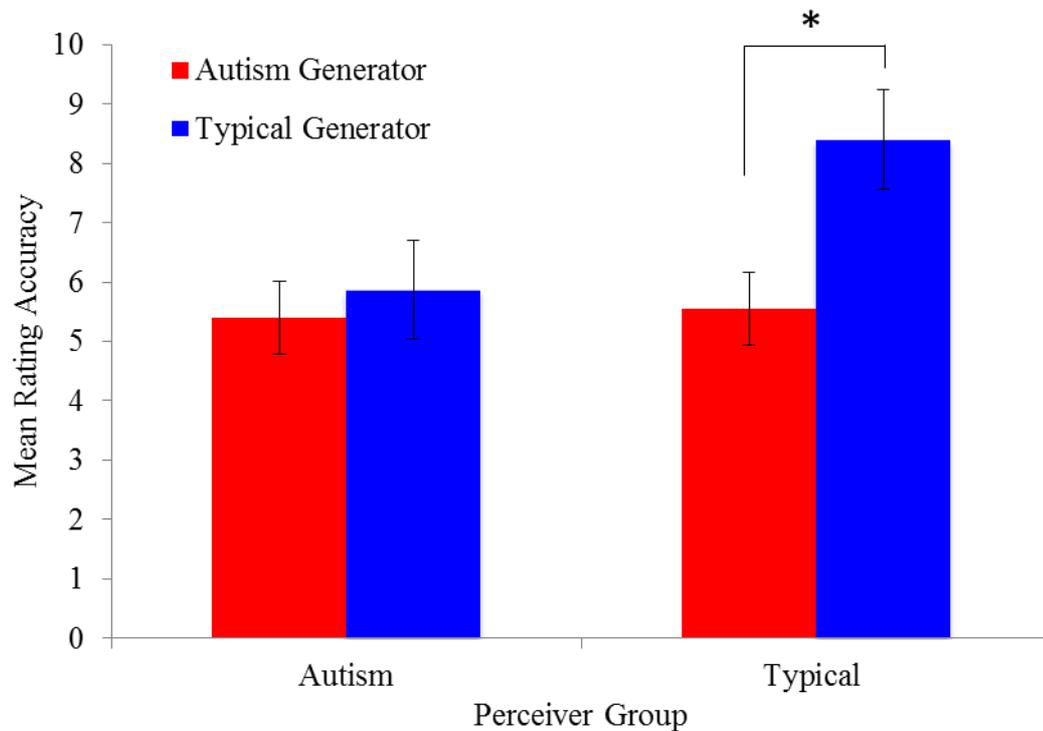


Figure 6.3: Mean rating accuracy for the autism and typical groups when rating the autism and typical generated animations. Error bars represent the SEM. $*p=.001$

6.4. Verbal Task

It was deemed prudent to verify that both generator groups had sufficient understanding of the mental state concepts. A follow-up study was conducted using the verbal descriptions provided by the generator participants prior to the production of their animations, to test whether the descriptions from both groups portrayed the intended mental states.

6.4.1. Method

6.4.1.1. Participants

For this study an independent group of typically developed participants (N=24) were recruited. They were matched for age (23 – 67 years, $t(46)=.16$, $p=.872$, $d=.73$) and gender ($\chi^2(2)=.12$, $p=.731$) to the typically developed participants in the perception task (see Table 6.2).

6.4.1.2. Stimulus selection and procedure

The stimuli for this task were based on the verbal descriptions the ‘generators’ gave prior to producing their animations (see section 6.2.1.2). From the descriptions of animations used in the perception task only those that did not use the target verb were included for possible selection as stimuli in the current task. From the remaining descriptions items were chosen at random to equate the number of autistic and typical descriptions for each mental state verb. This method resulted in three surprising and mocking, and four coaxing and seducing descriptions from each group, totalling 28 descriptions.

On each trial participants were presented, in a random order, with a verbal description, and rated out of 50 the extent to which the description represented each of the four target mental states (coaxing, mocking, seducing, and surprising). This method was designed to match closely the method employed in the perception task.

6.4.2. Results

Exactly as in the perception task, participants’ ratings of each of the verbal descriptions were scored for accuracy. To recap, accuracy was calculated by averaging the ratings of

the three ‘incorrect’ mental states (e.g. the mean rating of mocking, seducing and surprising when reading a coaxing description) and subtracting this number from the ‘correct’ rating. A score above zero therefore indicates that the participants rated the intended mental state verb more highly than the other verbs, with higher scores indicating a greater match to the intended representation.

Firstly, to verify that both generator groups had similar conceptual understanding of the mental state verbs included in the task the mean accuracy ratings for the autism and typical verbal descriptions were tested against zero. Both the autism and typical descriptions ratings were found to be significantly greater than zero (autism $t(23)=15.89, p<.001, 95\% \text{ CI } [19.46, 25.29], d=3.24$; typical $t(23)=22.65, p<.001, 95\% \text{ CI } [18.95, 22.76], d=4.62$), indicating that both generator groups understood the concepts. Moreover, a paired t-test revealed no difference between ratings for the two groups’ responses ($t(23)=1.24, p=.226, 95\% \text{ CI } [-1.01, 4.06], d=.25$; autism $M=22.38, SEM=1.41$; typical: $M=20.85, SEM=.92$).

The absence of this effect demonstrates that the verbal descriptions provided by each group were equally comprehensible, thereby suggesting that both generator groups had equal understanding of the social concepts. Thus, the failure of the typically developed observers to understand the autistic animations is unlikely to be due to the autism group producing animations based on ‘inaccurate’ conceptual representations of the intended mental states.

6.5. Discussion

The present experiment required individuals with autism and matched typical adults to generate animations depicting mental states. The animations generated by the movements of the participants with autism were found to have greater jerk than their

typical counterparts. In a subsequent perceptual task, the typical participants demonstrated an enhanced ability to attribute the intended mental state to the animations produced by other typical participants, relative to those produced by participants with autism. In contrast, individuals with autism exhibited no difference in assigning the intended mental state to animations produced by autistic and typical individuals. A secondary verbal task demonstrated that both generator groups had similar conceptual understanding of the mental state verbs therefore the perceptual differences are likely reflective of differences in the kinematic properties within the animations.

Differences in movement kinematics between the groups replicate previous findings of increased jerk when adults with autism make simple horizontal arm movements (Cook et al., 2013). The current findings extend this work by showing that these atypical kinematics are evident when those with autism produce complex, object-based actions. A lack of typical kinematics might be a consequence of peripheral factors such as abnormal muscle tone (Maurer & Damasio, 1982; Todorov, 2004), or central nervous system factors, such as poor anticipation of the subsequent part of a motor sequence (Cattaneo et al., 2007; Fabbri-Destro et al., 2009), or potentially relatedly, cerebellar neuropathology (Mostofsky et al., 2009; Rogers et al., 2013). Interestingly, Cook et al. (2013) also found group differences in velocity and acceleration, which were dependent upon the phase of the movement (turning-point or midpoint; see also Forti et al., 2011; Glazebrook et al., 2006). The phase effects are likely greater for larger magnitude movements (e.g., full length arm movements), therefore the absence of group differences in velocity and acceleration in the present study may be due to the relatively small magnitude of movements (hand and wrist gestures) which may have reduced differences pertaining to the phases of the movements.

Enhanced perception of typical, relative to autistic actions in the typical perceiver group is consistent with previous work that suggests we interpret others' actions according to models built through experience with our own actions (e.g. Sebanz & Shiffrar, 2009, see also Chapters 2 and 3 in the current thesis). The present study adds to these findings by showing that we are better at making higher-level mental state inferences (e.g., coaxing) from actions that look like our own⁷. These results therefore support the current hypothesis suggesting that our understanding of others' actions may be determined by our own action experiences.

These findings have important implications for interaction difficulties between autistic and non-autistic individuals. Successful interactions depend on accurate anticipation and prediction of others' movements, allowing us to attribute affective states, intentions and goals to our interaction partner so that we can adjust our behaviour accordingly (Behrends, Müller, & Dziobek, 2012). Therefore, if typical action models are not effective for interpreting the movements of individuals with autism, then the 'social impairments' exhibited by individuals with autism may, at least in part, be a product of a failure by typical individuals to infer correctly the affective states, desires and intentions of autistic individuals. Repeated inappropriate and /or inconsistent feedback from typical interactants following misunderstanding of autistic actions could subsequently obstruct learning about typical social interaction in those with autism, adding to social communication difficulties.

⁷It is important to note that all mental state information must have been derived from movement kinematics in the current study because there were no facial expressions, postures or language in the animations. However, despite the fact that jerk is an important cue concerning mental states (e.g. Pollick et al., 2001), other kinematic cues (such as the correlation between the movements of the two triangles) that were not measured in the current animations may also have contributed to inferences.

Crucially, incorrect interpretation of the movements of individuals with autism by typical individuals could also have important implications for clinical diagnosis. Autism is diagnosed following observation-based behavioural assessments of social functioning by a qualified clinician. On the basis of the current findings, and some recent similar work (Brewer et al., 2016; Sheppard et al., 2016) we might predict that social expressions by individuals with autism are more frequently incorrectly labelled. Therefore, these individuals may be assessed as lacking social understanding or expression by non-autistic clinicians, whereas in reality they simply have models incompatible with those of the assessor. Similarly, other assessments, which evaluate an individual's internal state, may fail to do so correctly when performed with autistic individuals, impacting on sentencing, medical support and treatments. Further study of how typical individuals could learn to interpret atypical expressions could improve intervention strategies and also reduce frustration, social anxiety and mood problems in individuals with autism (Simonoff et al., 2012), who may express their internal states but be frequently misunderstood.

Despite performing the task at a reasonable level, with comparable performance to the typical group when observing 'other' group animations, the autism group did not show the same benefit from observing 'same' group animations – performance when observing autistic animations was comparable in the two observer groups. One potential explanation for the lack of 'same' group benefit relates to the trend towards increased variability in the kinematics of the autistic relative to typical generators. For example, there was a trend for the four animation-specific jerk values to differ more in each individual in the autism group (between-group t-test on the standard deviations of the four jerk values; $t(29)=1.94$, $p=.062$). Increased variability in autistic actions may mean that a given autistic participant's action models are a poorer fit to those of other autistic individuals (note that autistic facial expressions have also been shown to have more

idiosyncratic qualities, which may similarly impair expression understanding; Brewer et al., 2016; Macdonald et al., 1989). Alternatively, autistic action models may be tuned to both atypical (autistic) and typical movements. Throughout their lives most individuals with autism have much experience observing and interacting with typical others, who move typically, as well as experience with their own atypical movements. In contrast, typical individuals are likely to have experience of typical movements only. These hypotheses could be elucidated by studying perception of autistic movements in individuals without autism but who have increased experience with this group.

In conclusion, the current study has replicated previous findings that individuals with autism produce actions with atypical kinematics. Moreover, typical individuals are less accurate in ascribing internal states to autistic actions relative to the actions of other typical individuals. This result suggests that kinematic differences might exacerbate social-communication difficulties between autistic and typical individuals.

Chapter 7: Action kinematics at 10 months are associated with later social abilities at 14 months in infants at high- and low-risk for developing autism

Under the current hypothesis some of the social and communication difficulties between individuals with autism and typical individuals can be explained by differences in how actions are produced. Autism is a neurodevelopmental disorder and therefore it is important to ask if differences in movement kinematics can be identified early in development. Findings of this nature would be important for designing interventions, and possibly understanding the cascade of social-cognitive difficulties that occur across autistic development. The current study therefore measured the jerk of movements of 10-month-old infants with either a high or low familial risk of developing autism during a ‘free-play’ session and related it to later social skills (measured at 14 months). It was found that infants who made movements that were less jerky had more atypical social skills later in development. Although this pattern is opposite to that predicted based on the adult literature, it is in line with recent models about how motor variability relates to motor learning. Importantly, it also suggests that early differences in movement kinematics may indeed impact the development of early social skills, and that movement kinematics may represent a good candidate biomarker for social disorder.

7.1. Introduction

Autism is a neurodevelopmental disorder, and diagnosis only reliably occurs around 3 years of age (Baird et al., 2003; Charman et al., 2005). Despite the earlier identification of some autistic traits and behaviours through standardised assessments or questionnaires (e.g., Cox et al., 1999), the most robust means of diagnosis involves several lengthy clinical assessments in a variety of environments (Charman et al., 2016). However, early and intensive interventions are thought to yield the most beneficial outcomes (Baird et al., 2003) as the trajectory of an atypically developing brain may be shaped by providing differential experiences to scaffold development (Eldevik et al., 2009; Howlin, Magiati, & Charman, 2009; Warren et al., 2011).

The hypothesis in the current thesis posits that through our intensive experience with our own actions we generate models that we use to help us perceive and understand others' actions. In the case of autism, it is hypothesised that production of actions with kinematic parameters that are different from typical individuals can impact social communication bi-directionally between these two groups. It is therefore important to examine whether action kinematics are atypical early in the lives of those who will later develop social difficulties or receive a diagnosis of autism. Developing with atypical action could have a cascade of effects for how children with autism and those with whom they interact learn about each other's internal states. Therefore, if action differences are present early it increases the potential impact of them on social development.

As well as possibly influencing the development of internal state models, early atypical action kinematics may also be an ideal candidate biomarker of the emergence of early autistic symptomology. The sensory and motor networks within the brain are the first to mature fully in infancy (Deoni et al., 2011; Gogtay et al., 2004; Paus, 2005).

Consequently, disruptions to these systems might have the most profound effects on the development of more complex mechanisms, which might be grounded in more basic skills (Johnson, 2011; Karmiloff-Smith, 2009). Moreover action kinematics are easily measurable from a very young age, and do not necessarily require development of any specific motor skills. Identifying whether there is a relationship between atypical movements and social development might therefore also inform the aetiology of autism and aid early intervention design.

Most previous studies investigating motor abnormalities in early autism are retrospective, using home videos to code motor behaviours. In these studies infants who later develop autism show greater irregularities in postural control, such that movements often show asymmetric properties, and most motor milestones, such as rolling or crawling are often delayed (Baranek, 1999; Teitelbaum, et al., 1998). More recently, studies have capitalised on the high incidence of sibling recurrence in autism to conduct prospective longitudinal studies using infant siblings of children who have autism as participants – an estimated 20% of children who have an older sibling with autism will likely also develop autism or Broader Autism Phenotype (presentation of subclinical autistic traits and characteristics, Constantino, Zhang, Frazier, Abbacchi, & Law, 2010; Ozonoff et al., 2011). These prospective studies have also shown that infants at risk of developing autism show atypical motor development (Bhat, Galloway, & Landa, 2012; Iverson & Wozniak, 2007; Landa & Garrett-Mayer, 2006; Mulligan & White, 2012). For example, Leonard, Elsabbagh, Hill, and the BASIS team (2014) measured motor skills – via two standardised motor assessments, the Mullen Scales of Early Learning (Mullen, 1995) and the Vineland Adaptive Behaviour Scales (Sparrow, Cicchetti, & Balla, 2005) – of infants with either a high or low familial risk of developing autism. As expected, the high-risk infants had worse fine and gross motor skills measured as early as 7 months, and the developmental trajectory of their motor skills was atypical up to 36

months. Motor differences measured at 3 months on standardised assessments have also been found to relate to later communication problems (Bhat et al., 2012), and there is some evidence that better motor skills protect against poor social outcomes (Sutera et al., 2007).

To date, no studies have measured the kinematic qualities of the movements of infants who are at risk of developing autism. Advancements in wearable technology, such as accelerometers, enables reliable measures of acceleration and jerk to be easily obtained in a range of settings, making this method and measurement generally more ecologically valid and time efficient than standardised assessments. Of course, as already noted, assessing the kinematic characteristics of infants' movements could also shed light on the mechanisms underpinning any motor delays in infants at risk of developing autism, and help characterise the specific impairments that link motor and social deficits.

The current study therefore measured the jerk (due to the fact it is jerk that has been consistently found to be atypical in autistic adults) of the movements of a group of 10-month-old infants with either a high or low familial risk of developing autism in a naturalistic play setting. Four months later social skills were measured using a social and communication assessment. It was hypothesised that action kinematics would be predictive of later social skills. More precisely, based on the previous adult findings, it was predicted that infants who produced movements with more jerk would have worse social skills later in development.

7.2. Methods

Please note that the data analysed in this Chapter are taken from an on-going longitudinal study. Therefore these are preliminary results as data from more infants

from the full data-set are still to be analysed and some of the assessment scores have not been double coded to research standards.

7.2.1. Participants

Participants were families recruited via a range of means (flyers and online advertisements) to take part in a longitudinal research programme: The British Autism Study of Infant Siblings (BASIS; www.basisnetwork.org). This research programme is a multi-site network within the UK that facilitates research into infant siblings of children with a clinical diagnosis of autism. Ethical approval was granted by London Central NHS Research Ethics Committee (approval number: 13/LO/0751 STAARS). Families were invited to testing sessions when the infants were 10-months-old and 14-months-old (as well as 5-months-old where no accelerometer data were collected, and later ages which were not analysed for present purposes).

At the time the data for the current experiment was analysed 77 infant siblings of children with a clinical diagnosis of autism (High-Risk infants, HR) and 24 infants without any familial risk of autism (Low-Risk infants, LR) had been recruited for the longitudinal project. Of these participants kinematic data had been obtained from 55 infants (42 HR and 13 LR) during the 10 month testing day. 25 HR and 7 LR infants data was unusable due to technical issues during testing, e.g., the accelerometer not responding or the digital output not recognised (see Section 7.2.2.1) and 10 HR and 4 LR infants did not participate in the task where the kinematic data was analysed e.g., due to fussiness or the family not attending the 10 month testing day. Of the 55 infants who had usable data from the 10 month testing day, 44 infants (36 HR, 8 LR) returned for the 14-month testing day (see Table 7.1 for demographic data of participants who contributed to the final analysis reported in this thesis). Due to the small number of LR infants all analyses conducted were performed collapsed across all participants.

Table 7.1: Demographic data for the Low-Risk and High-Risk infants

	Mean age in days at 10 month testing session (SEM)	Mean age in days at 14 month testing session (SEM)	Gender (N=male)
High-Risk Infants (N=36)	318.33 (2.31)	453.36 (3.31)	21
Low-Risk Infants (N=8)	311.00 (5.39)	442.88 (4.90)	5

Note due to small sample sizes all participants were collapsed into one group for all analyses

7.2.2. Kinematic data

7.2.2.1. Accelerometer and behavioural task

A BioNormadix® wireless Tri-axial Accelerometer (BN-ACCL3), with a measuring range of ± 16 g (1 g [gravitational force] = 9.81 m/s^2) and sampling rate of 100 Hz was used to collect acceleration data. Data were sent online during the testing session to the BioPac® software, where it was stored to be cleaned and analysed offline using Matlab® (see Section 7.2.2.2). The device (6 cm x 4 cm x 2 cm, weight 54 g) was placed in a pouch on the left thigh to capture the acceleration of the leg movements throughout the testing session without disrupting freedom of movement. The infants all participated in a larger battery of behavioural tasks across a full day, with breaks whenever the caregiver or infant required.

The behavioural ‘free-play’ session where the acceleration data was collected was also recorded using three bespoke digital video cameras, which were remote controlled and time-locked using in-house custom software. The cameras were positioned such that all angles of the testing room were recorded. The accelerometer was synced with the video recordings via a digital output signal from a light. This digital output (the light switching on) was sent from the BioPac® software and added a time-stamped signal to

a channel on the BioPac® data. The light was also visible in the video recordings, which was verified by the experimenters. Acceleration data was recorded constantly throughout the whole ‘free-play’ testing session.

The ‘free-play’ session was an unstructured task where the infants were presented with a pre-designated range of toys on a mat and were free to engage with the toys as they pleased. The infant’s caregiver was present during the session, but was requested to try to leave the infant to play unassisted. The session lasted approximately three minutes.

7.2.2.2. Acceleration data cleaning

The accelerometer recorded acceleration, measured in ‘g’ units (gravitational force), across three axes (x, y and z) on separate channels. The three raw signals were low-pass filtered using a 5 Hz Butterworth filter, and 3D acceleration was calculated as the root sum of the square of the three axes. A high-pass Butterworth filter was then applied to the 3D acceleration, at 1 Hz, to remove the fixed 1 g acceleration experienced by the accelerometer due to the earth’s natural gravitational pull regardless of movement (i.e., to centre the acceleration recordings around 0 g when there was no movement for ease of interpretation). These filters were visually verified such that they maintained the pattern of movements. The processed data was cropped to the ‘free-play’ session using a purpose written script in Matlab®. The mean duration of the ‘free-play’ session across participants was 3 minutes 20 seconds.

From the acceleration data periods where the infant did not move were removed, by setting a threshold (acceleration values less than .01 g or .098 m/s²) through visual inspection of the data to identify the acceleration values that represented times when the infants were not moving. Jerk was calculated as the first derivative of the acceleration data (see Figure 7.1A for example of a jerk trace), and averaged to obtain a measure of

absolute mean jerk across the movement data. Finally this value was multiplied by 9.81 to transform the measure of 'g' into m/s^3 . Please note, only jerk was analysed in this Chapter as this was the only kinematic measure that distinguished autistic and typical participants in Chapter 6. The number of data-points that were classed as periods of no movement and removed from this analysis was summed to find the proportion of the testing session that the infant did not move their leg.

7.2.3. Social assessment – Autism Observation Scale for Infants

The Autism Observation Scale for Infants (AOSI, Bryson, Zwaigenbaum, McDermott, Rombough, & Brian, 2008) was conducted with the infants at 14 months of age (see Table 7.1 for demographic information). This semi-structured observational measure is conducted with a trained examiner. It consists of 18 test items which are designed to identify markers for autistic or atypical social development (note this measure is not diagnostic, see Table 7.2 for list and description of test items). Each item was coded as a 0 for a typical social response or 1 for an atypical social response. All assessments are required to be double scored, once by the examiner during the assessment and again by an independent examiner who marks the assessment from a video. Any discrepancies in scores were discussed until a consensus score is decided⁸. The AOSI has previously been shown to have good inter-rater reliability, and moderate test-retest reliability (between 6 and 12 months of testing, Bryson et al., 2008).

As the current experiment is designed to measure how movement kinematics can predict social skills it was important to ensure that the social measure only included items that measured social behaviours.

⁸As the current experiment is on-going some of the AOSI scores in this data set have not been double coded, therefore they are subject to change and caution should be taken interpreting the current results.

Table 7.2: Description of the behaviours assessed in the AOSI

Item	Behaviour assessed
Visual tracking*	Ability to visually follow a moving object laterally across the midline.
Disengagement of attention*	Ability to disengage and move eyes/attention from one of two competing visual stimuli.
Orientation to name	Ability to move head and/or eyes toward and look at the examiner when name is called.
Differential response to facial emotion	Ability to respond differentially through facial, head or other motor movements to a change in the examiner's facial expression from smiling to a neutral expression.
Anticipatory social response	Ability to anticipate and enjoy social (vs. physical) cause-effect relationships.
Imitation	Ability to reproduce an action produced by the examiner.
Social babbling	Ability to engage in back-and-forth (reciprocal) vocalisations with the examiner.
Eye contact	Ability to consistently establish appropriately sustained eye contact with the examiner.
Reciprocal social smile	Ability to smile in response to the examiner's smile.
Coordination of eye gaze and action*	Ability to co-ordinate gaze with actions on objects.
Behavioural reactivity	General responsiveness, including under reactivity and over reactivity, to the activities and toys introduced, and to the examiner's actions.
Cuddliness	Physical responsiveness to being cuddled by parent.
Soothability	Ease of being soothed by parent using social means such as touch, other forms of human contact, or verbal reassurance.
Social interest and shared affect	Ease of engagement and interest in activities, and ability to share positive affect with the examiner.
Transitions*	Ease and consistency with which toys are relinquished and movement is made from one activity to another.
Motor control*	Degree to which motor behaviour is goal-directed, organised and modulated.
Atypical motor behaviour*	Presence of developmentally atypical gait, locomotion, motor mannerisms/postures or repetitive motor behaviours.
Atypical sensory behaviour*	Presence of developmentally atypical sensory behaviours in any modality (e.g. smelling of toys, staring at hands/shapes/objects, or feeling textures).

Note: Items were scored 0 for typical response and 1 for presence of atypical response. Table taken from Bryson et al., 2008. *Denotes non-social specific items where scores were not included when calculating the total marker score.

Seven of the items on the AOSI target sensory and motor behaviours (marked with an asterisk on Table 7.2) therefore scores on these items were not included. The total number of items or ‘markers’ where the infant showed atypical behaviours (i.e., scored 1) was calculated by adding the scores for each item. The total marker score was out of 11.

7.3. Results

There was large variability in how frequently the infants moved during the testing session which contributed to the measures of jerk (i.e., infants who moved more would have greater levels of jerk). Therefore, to control for variability in the kinematic measure that was related to the amount, rather than quality of the movement the proportion of static time was entered as a control measure in the analysis. Furthermore, although all infants were approximately the same age on the day of each testing session there was some variability (see Table 7.1), which could contribute to differences motor and social development, therefore age on day of testing at 10 months and 14 months were also added as control variables. There were no multivariate outliers.

To examine the hypothesis that movement kinematics measured at 10 months predict social skills measured at 14 months a partial correlation were conducted between mean jerk and total marker score, with the proportion of time the infants were static, and age in days at the 10 month and 14 month sessions as control variables. A negative relationship was found between absolute mean jerk and total marker score ($r=-.309$, $N=44$, $p=.049$, 95% CI $[-.024, -.548]$). This pattern of results suggests that infants who moved with greater jerk had better social skills (see Figure 7.1B).

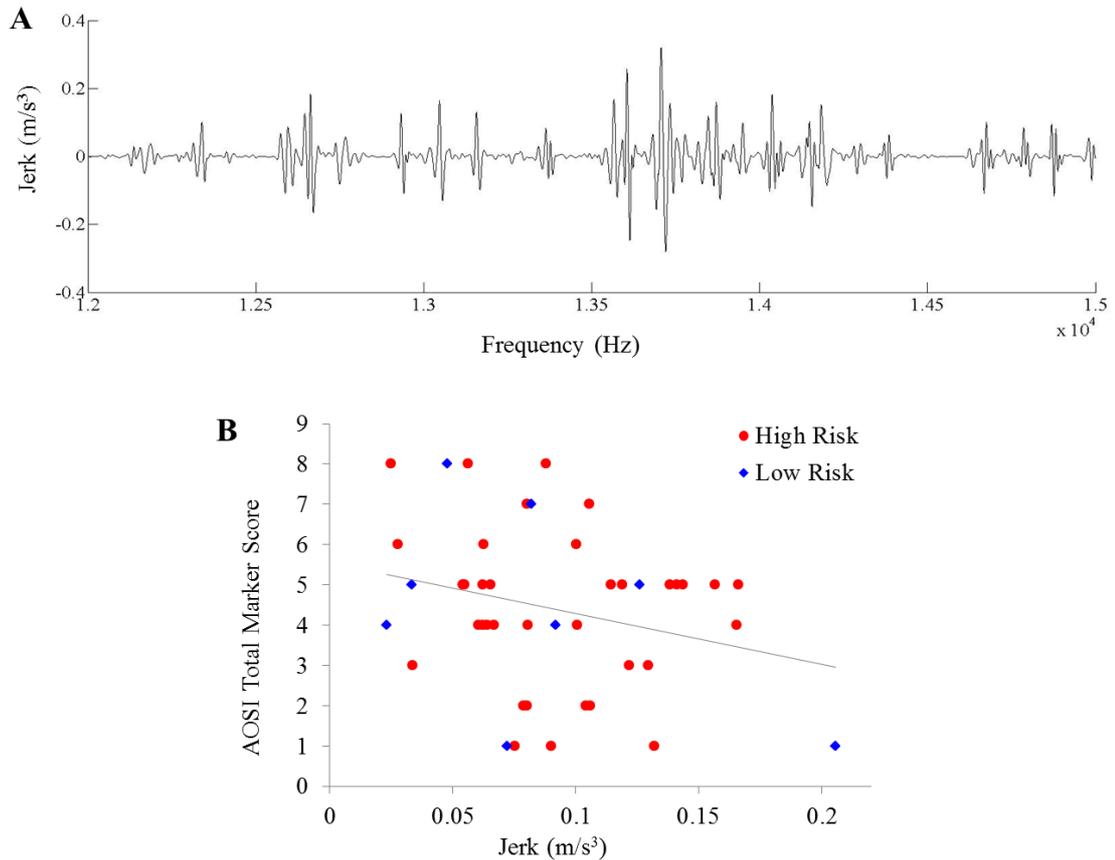


Figure 7.1: (A) Example jerk traces across a section of the free-play session. (B) Scatterplot showing negative correlation between absolute mean jerk during the free play session at 10 months and total number of atypical social markers the infants scored in the AOSI at 14 months.

7.4. Discussion

The current experiment measured the mean jerk of leg movements of a group of 10-month-old infants with either a high or low familial risk of developing autism in a naturalistic play setting. Social skills were measured in the same infants at 14 months using a standardised social and communication assessment. The preliminary results revealed there was a negative relationship between the kinematic measure and later social skills. More precisely, infants who produced more jerky movements at 10 months of age had better social skills at 14 months of age. These results tentatively suggest that the movement kinematics of infants at 10 months are related to the development of social skills.

The direction of the relationship between movement kinematics and social skills in the current experiment is opposite to that predicted based on the findings of adult studies of autism. Specifically, adults with autism have previously been found to produce movements with greater jerk compared to typically developed adults (e.g., see results of the Generation Phase of Chapter 6) and therefore it was predicted that greater jerk would predict poorer, not better social skills. It is possible that the relationship between the kinematic characteristics of movements and social skills reverses from infancy to adulthood. For example, several characteristics of autism observed in children and adults, such as reduced attention to others' eyes (Jones & Klin, 2013) or reduced social smiling (Ozonoff et al., 2010), indeed show evidence of initial increases in early infancy which then decline by toddlerhood (see Jones et al., 2014, for review).

However, most prospective and retrospective studies investigating motor differences in infants who later develop autism consistently find impairments or atypical motor development and do not find patterns that reverse in these macro-level behavioural differences (Bhat, et al., 2012; Iverson & Wozniak, 2007; Landa & Garrett-Mayer, 2006; Leonard et al., 2014; Mulligan & White, 2012). These motor atypicalities continue to be reliably observed across childhood and into adulthood in individuals with autism (Cook, 2016; Fournier, et al., 2010; Gowen & Hamilton, 2013). Considering these previous findings of similar types of atypical motor production throughout autistic development, it is possible that kinematic atypicalities are representative of an underlying motor control deficit which manifests differently in infancy and adulthood. More precisely, movements that have low jerk in infancy, but high jerk in adulthood could both be symptomatic of an atypical motor system, which, most importantly, might also affect social and communication skill development and utilisation. In support of a hypothesis of a reversal in the characteristics of action kinematics from early development to adulthood in autism, toddlers at a high-risk of developing autism

initially produce reaching movements that are less accelerated than toddlers without a familial risk (at 18 months), but by 36 months the group difference is smaller (Focaroli, Taffoni, Parsons, Keller, & Iverson, 2016).

Kinematic variants early in life might therefore signify the beginning of an atypical motor developmental trajectory, which might impede learning from and about others, leading to social difficulties and possibly an autism diagnosis later in life. One possible explanation of the present findings is that high kinematic variability – which would be signalled through high jerk – is a necessary stage of typical motor development, where the cortical visual-motor and subcortical motor control systems learn through trial and error how to produce the most efficient actions (Hadders-Algra, 2000). Motor variability is argued to be an essential feature of efficient motor learning, such that through controlled spatial and temporal exploration of novel movement trajectories one is able to transfer knowledge and learn novel actions faster (Wu, Miyamoto, Castro, Ölveczky, & Smith, 2014). Indeed, studies classifying the kinematic trajectories of typical infants' reaching movements show that movements are initially highly variable and contain multiple peaks in acceleration (i.e., increased jerk), before eventually following the most efficient trajectory by late toddlerhood (e.g., minimum jerk; Berthier & Keen, 2006; Rönnqvist & Domellöf, 2006; von Hofsten, 1991). It is conceivable that infants who miss, or are perhaps delayed in experiencing a necessary period of increased motor variability early in the development of their motor control systems fail to learn how to effectively modulate and exploit the kinematic variability of their movements, and therefore are slower to learn novel actions as well as possibly having generally poor motor control throughout life. By adulthood, it could be therefore speculated that those who have learnt good motor control through initial high variability in movements are able to produce well-controlled movements with low jerk.

Due to the large variability in the types of movements that infants are producing during the ‘free-play’ session in the current experiment it currently is not possible to examine the kinematic trajectories of individual movements in detail. Therefore, it is not possible to make any strong assumptions about the underlying cause of kinematic differences that predict later social difficulties. Future work could look to isolate specific movement types (e.g., periods of crawling or reaching) to analyse more precisely the kinematic disturbances in the infants who later develop social difficulties, and identify what qualities are making their movements less jerky. Regardless of the underlying mechanism driving the effect found in the current experiment these preliminary results are encouraging, suggesting atypical movement kinematics may be an early biomarker for the development of autism. Accelerometers are relatively inexpensive, non-intrusive and can be easily used in a range of settings. Movement kinematics can therefore be measured in a variety of ecologically valid naturalistic settings, and on a large scale. This methodology is useful as it is possible to measure a wide range of behaviours, environments and contexts, and ages to try to unpick the precise nature of the process which generates differences in movement kinematics across development, as well as how exactly kinematic characteristics relate to social difficulties throughout life. Further information about the infants in the existing dataset will help to answer some of these questions, particularly as it becomes known which infants receive a clinical diagnosis of autism.

In conclusion, developing our understanding of the relationship between early atypical kinematics and social learning might be fundamental to understanding autistic development, as well as finding a connection between the disparate symptoms that are often studied in isolation, e.g., social communication difficulties and repetitive and stereotyped behaviours. Furthermore, early action atypicalities may provide a useful marker of infants likely to develop social disorders such as autism.

Chapter 8: General Discussion

8.1. Overview

The kinematic cues embedded within our movements are important signals that can communicate our internal states to others. The current thesis examined the hypothesis that our intensive experience producing our own actions calibrates mental representations of our actions, which we use to aid perception and understanding of others' actions from kinematic cues. The presented studies supported this hypothesis by demonstrating that the recognition of others' internal states can be predicted by the kinematics of an individual's own movements.

Chapters 2 and 3 showed that perception of others' affective states is determined by one's own movement kinematics across typical development. Chapters 4, 5 and 6 tested the hypothesis that atypical movement kinematics in autism contribute to social and communication difficulties. Chapters 4 and 5 measured two basic skills required to make internal state judgments from observing others' actions: visual time perception and sensitivity to kinematic signals that describe 'natural' motion. Both studies found no deficits in the autism group compared to the typically developed group – and some enhanced abilities – suggesting that these basic skills are intact. However, Chapter 6 demonstrated that typical individuals exhibit disrupted understanding of autistic internal states expressed through their atypical movements. Atypical actions may therefore contribute to social and communicative problems in autism given that typical individuals will often misread the internal states of those with autism from action cues. Finally, in a longitudinal developmental study presented in Chapter 7, differences in movement kinematics were found to be associated with later social skills, adding

support to the notion that action kinematics are important for social understanding and may even be used as a biomarker for atypical social development.

In the following sections of the discussion I will examine several overarching theoretical factors that are relevant to the conclusions of the studies presented and main hypothesis tested in this thesis. I will also provide some suggestions for future work that can develop the findings of the current thesis in line with these theoretical factors, which will further our understanding of how one's movements can influence the quality of social communication and interactions with others who move differently.

8.2. The effect of observational learning on the generation of action models

There is vast evidence that we learn most efficiently about consistent and contingent information in our environment (Elsner & Hommel, 2004; Cook, Bird, Catmur, Press, & Heyes, 2014; de Klerk et al., 2015; Hebb, 1949; Perin, Berger, & Markram, 2011; Ray & Heyes, 2011). The most consistent and contingent action-effects come from visual-motor experiences with our own actions. Hence, the primary prediction of the current hypothesis was that our action models are tuned to experiences of our own actions. This hypothesis was supported by the findings of studies presented in the current thesis, suggesting our action models are yoked to our own movements, and our social judgments about others are calibrated to these models.

However, it is important to note that much of our visual experience of actions comes from observing others. There is ample evidence that we are able to learn vast amounts of information from observing others' actions throughout our lives, such as how to use tools, and understanding action-effect mappings (Hunnius & Bekkering, 2014; Paulus, Hunnius, & Bekkering, 2013). Some even argue that we learn to categorise our own internal states early in life through observing others' behavioural responses to our own

actions (Gergely & Watson, 1996), which may be particularly relevant when learning to self-regulate one's internal state expressions (Halberstadt, 1986; Heller & Casey, 2016; Meyer et al., 2014; Sanders et al., 2015; Zeman et al., 2013). We therefore might expect that our perceptual models of internal states include information that we have garnered through observing and interacting with others as well as our own actions. For example, our interaction partners can often verbally communicate to us how they feel, which we can associate with how they are moving.

In the case of those with autism, observational learning from others is likely to contribute to the specific pattern of results in Chapter 6 – the fact that typical individuals exhibited disrupted recognition of internal states from autistic relative to typical actions but there was no same group advantage in the autistic group. Specifically, those with autism are likely to have much observational experience with typical others because the majority of the population are typically developing. In contrast, most typical individuals will have little observational experience of those with autism. Therefore, if observational learning plays a role in our action model generation, we might expect autistic individuals to have perceptual models that are tuned to both types of kinematics. It is worth noting that the diversity of perceptual tuning (i.e., of both autistic and typical visual inputs) may also result in action models that are generally less precise, leading to less accurate interpretation when observing either movement types, and hence the generally deficient internal state attribution when interacting with most others (Brewer, et al, 2017; Happé, 2015). The ability to incorporate successfully information acquired from observation of others and one's own actions into perceptual models may also depend on other higher-level executive abilities, such as cognitive flexibility, which are also known to be impaired within the autistic populations (see Section 8.4 and 8.5 for further discussion of this point).

Importantly, if we tune our action models through observational learning of others as well as from our own movements, we would predict that individuals who have more autistic action experience, but are not autistic might be better placed to interpret the actions of those with autism. To examine this prediction the experiment conducted in Chapter 6 could be repeated using typically developed individuals who have greater experience with autistic individuals (e.g., care-workers or clinicians) and compare them to other typical individuals who have no experience with autistic individuals. If action models are also tuned to our observational experiences of others we would expect the group with more visual experience of autistic individuals to show superior performance on the autistic animations relative to the individuals without autistic experience. However, if observational learning does not contribute to our generation of action models, then both groups should show a similar pattern of performance to the typical group in Chapter 6. Results from this proposed study might be helpful in informing interventions with individuals with autism, such that social interactions between typical and autistic individuals could be improved following intensive observational training of ‘non-autistic’ key workers.

8.3. Criterion setting and perceptual narrowing – mutually exclusive accounts?

The findings of the studies presented in the current thesis provide some support for the ‘criterion setting’ version of the current hypothesis (see Section 1.4.1). Under this account, experience with our movements furnishes models with distinct criteria for identifying internal states – for instance, a fast walker’s criterion for identifying anger will be faster than a slow walker’s criterion, as suggested by the findings in Chapters 2 and 3. Such a criterion setting account could also explain the findings in Chapter 6. For example, a typical individual tends to move with lower jerk than autistic individuals. Therefore, an animation demonstrating seducing – which is conveyed through low jerk,

smooth movements – may not be identified as such when a typical individual is interpreting an autistic action because the jerk is too high to be categorised this way.

An alternative to the criterion setting account is that experience with one's own actions results in 'perceptual narrowing' of action models, such that we are most sensitive to kinematic information that aligns with one's own action kinematics. Chapter 5 found no evidence to support such a hypothesis given that autistic and typical individuals exhibited no 'own-group' perceptual enhancement, which also makes this interpretation of the results of Chapter 6 less likely.

However, as outlined in Chapter 1 (see Section 1.2.3) there are several action perception studies that do demonstrate enhanced perceptual sensitivity for actions specific to one's own motoric repertoire. One important distinction between these previous action perception studies and the studies presented in the current thesis are the type of actions and perceptual judgments measured. For example, in the previous studies participants are often asked to predict the outcomes of another's action sequence (Aglioti et al., 2008; Brault, et al., 2012; Diersch, et al., 2012; Diersch et al., 2013; Kandel, et al., 2000; Sebanz & Shiffrar, 2009) or distinguish self-action from that of others (Knoblich & Prinz, 2001; Loula et al., 2005) using movement stimuli that are highly practiced by the participants. As mentioned in Chapter 1, the sensitivity account likely requires exclusive, extensive and highly repetitive experience with a rigid action in order to finely tune action models. An expert will, by definition, have the necessary rigid motoric experiences to develop highly precise models of action sequences that enable very accurate predictions about others movements that fall within their specific motoric expertise. In contrast a novice, despite possibly having the perceptual capabilities to detect kinematic information within others' actions, might not have any model of the observed action sequence by which to assess the kinematic information which they

perceive. The perceptual sensitivity effects observed in these previous studies could be due to fine-tuning of kinematic models which only occurs following highly specific action experiences. The kinematic features of an individual's actions as measured in the studies presented in this thesis – e.g., high velocity or high jerk actions – are generalised features that are perhaps not akin to the restrained action sequences experienced by professional athletes.

Moreover, it is possible that an initial step, before fine-tuning of one's action models occurs, is a criterion setting process. For example, one might initially learn coarse mappings between kinematic cues and goals (in the case of experts, learning the predicted action sequence and outcome) or internal states, and hence furnish action models with specific kinematic criteria that represent different outcomes or internal states, before models are refined and become more precise following extensive and rigid rehearsal. 'Perceptual narrowing' or this secondary fine-tuning may be unlikely to occur with respect to the vast range of internal states we experience in our varied everyday lives. For example, when we feel sad there will be some continuity between our experiences (e.g., decrease in velocity from typical pace), but this might vary depending on the context (e.g., whether we are at home or at work) and we will also perform a range of actions depending on what we are doing (e.g., walking to catch a bus or cooking). Therefore our models of our internal states might not be as precise as specific action sequences that we perform repetitively in order to produce actions with expert precision, and thus internal state attribution may rely more on a criterion setting type mechanism.

It is possible, however, that 'perceptual narrowing' for specific internal states occurs following intensive experience conveying that given state. For example, individuals who experience clinical depression will frequently move much slower than average,

while concurrently experiencing feelings of sadness (Michalak et al., 2009). These individuals may have criteria for different internal states, which are centred around their action experiences, but also become highly sensitive to variations in sad (or slow) kinematic signals. Subsequently, these depressed individuals may be able to distinguish very accurately subtle differences in others' slow (sad) movements, but fail to recognise similar subtleties in faster movements, and therefore cannot differentiate their interaction partner's bliss from jubilation. On the other hand, an individual who frequently experiences aggression and moves very quickly may be astute at reading differing levels of anger in others, but fail to recognise varying levels of sadness (or fear). Future work could look to further address the relationship between 'perceptual narrowing' and internal state experiences by studying groups of individuals who have more extreme internal state experiences (e.g., individuals with clinical depression or antisocial personality disorder) and measuring their different internal state criteria (which are predicted to follow a similar pattern as that presented in the current thesis based on their typical action kinematics) as well as perceptual sensitivity to variations in different internal state cues (which are predicted to show greatest sensitivity for internal states they frequently experience).

8.4. The role of executive processes in using models of action to interpret others' internal states

The evidence presented in the current thesis demonstrates that when deliberating upon the internal states of those with whom we interact the low-level properties of movements (kinematics) can constrain one's ability to understand, highlighting the relevance of bottom-up processes during action perception. However, higher-level cognitive processes, or top-down mechanisms (Adolphs, 2003), are of course also critical to one's ability to generate and utilise mental representations of action. For example, executive processes, such as cognitive flexibility or one's ability to allocate

attention to relevant sensory information, are likely pivotal processes that enable us to extract relevant kinematic information from the stream of sensory inputs during social interactions.

As outlined in Chapter 1, when attributing internal states to biological motion stimuli a network, which includes frontal (e.g., mPFC) and posterior (e.g., pSTS) regions (Blakemore, 2008; Castelli et al., 2000; Gobbini et al., 2007; Grossman et al., 2000; Herrington, Nymberg, & Schultz, 2011; Kaiser & Pelphrey, 2012; Van Overwalle & Baetens, 2009), and in some cases also motor regions (e.g., the PMC or IPL; Tidoni et al., 2013; van Kemenade et al., 2012) is often active. The activation within this network when observing biological motion stimuli appears to be partially governed by task demands (Alaerts, Swinnen, & Wenderoth, 2017; Herrington, Nymberg, Faja, Price, & Schultz, 2012; Van Overwalle & Baetens, 2009). Specifically, these studies find top-down signals from frontal regions modulate activity in the integrative sensory regions, which in turn modulates activity in lower-level visual areas (e.g., V5, Hillebrandt et al., 2015). Consequently, high-level regions might not only be important for helping us interpret the low-level information, but also for directing our neural resources and attention to the relevant sensory signals in order to obtain the most informative information.

During social interactions there are numerous signals one must interpret simultaneously (e.g., facial expression, voice, body movements, other non-animate objects involved in the interaction), and therefore attention must be divided and allocated to the signals deemed to be most relevant and informative. Attention allocation is likely an online process which involves rapid analysis and integration of incoming sensory cues and stored information. Other areas of the brain may feed into the centres that help us encode and interpret others' behaviour (e.g., other frontal regions, such as the

dorsolateral prefrontal cortex, and subcortical regions, such as the insula, Menon & Uddin, 2010). Therefore, to make accurate judgments about others' internal states from their actions one must finely tune both top-down and bottom-up processes, as well as proficiently integrating signals from both systems.

Individuals with autism have previously been found to exhibit atypicalities modulating top-down and bottom-up neural signals when observing others' actions and attributing intentions (Alaerts et al., 2017; Castelli et al., 2002; Koldewyn, Whitney, & Rivera, 2011). Moreover, they exhibit differences in attention allocation to dynamic social information (Ames & Fletcher-Watson, 2010;) and attention modulation to sensory distractors (even if task relevant, Keehn, Westerfield, Müller, & Townsend, 2017) relative to typical individuals, which has also been identified as an early marker of autistic symptomology in high-risk infants (Elsabbagh et al., 2013; Jones et al., 2014). Therefore, individuals with autism might have similar levels of exposure to the relevant kinematic information required to generate models and learn from others, yet poor ability to flexibly move their attention to learn about socially relevant kinematic information. To test this hypothesis further one could study detailed eye-movement trajectories during observation of dynamic social events, to distinguish not only *what* information is salient to autistic individuals, but also *when* they decide to attend.

8.5. Generalisations and implications for other clinical populations

8.5.1. Is there a core motor deficit specific to autism?

Atypical motor production appears to be a relatively consistent finding throughout the autism literature (Cook 2016; Fournier, et al., 2010; Gowen & Hamilton, 2013).

Following the findings of the current thesis (e.g., Chapter 6), future work characterising more specifically the 'autistic movement signature' will likely be fundamental for

helping typical individuals to understand individuals with autism, as well as possibly improving social development in individuals who develop autism. More longitudinal studies, such as the study presented in Chapter 7, will markedly enhance our understanding of how early motor production differences translate into social difficulties. Studies of this nature will be essential to disentangling the precise role motor dysfunctions play in autistic development, and critically identifying whether motor differences of the type studied in this thesis represent a core deficit that results in a highly complex cascade of social difficulties, or – perhaps more likely – they exacerbate social problems that also have a variety of additional causes e.g., reduced attention towards others, deficient executive functioning.

Autism is also a highly heterogeneous disorder, and recently work has been conducted to operationalise some of the specific characteristics that define possible subgroups of the autistic phenotype (Lombardo et al., 2016) in an attempt to identify whether there are separable categories of traits or risk factors that can intensify symptomology. It is important to note that all studies testing perceptual abilities in autism in this thesis were conducted with high-functioning adults with autism and matched typically developed adults. A range of studies suggest that intellectual ability in autism may improve ‘social outcomes’ (see Howlin & Magiati, 2017 for review). More specifically for the current thesis some previous studies suggest that individuals with autism who have greater intellectual difficulties also have more impaired biological motion processing difficulties (e.g., Jones et al., 2011; Koldewyn et al., 2010; Rutherford & Troje, 2011). However, it is unclear whether the effect of increased cognitive or intellectual abilities play a protective role in alleviating some features of autism, or those with autism and higher IQs are able to develop more efficient compensatory mechanisms, which improve their social abilities at a surface level but the underlying deficit still persists (Livingston & Happé, 2017). As demonstrated in Chapter 7, action kinematics can be

measured easily in a range of settings, without complex instructions or task demands. Collecting kinematic measures from individuals with autism but who have lower intellectual abilities could be an interesting avenue to further specify the relationship between motor and social skills and whether it generalises to lower functioning individuals.

8.5.2. Implications for other clinical populations who move differently

The findings in the current thesis linking motor production differences to social development (Chapter 7), as well as demonstrating social understanding difficulties in non-autistic individuals when interpreting movements that are dissimilar to their own (Chapter 3 and 6) are essential for furthering our understanding of the connection between motor production and social and communication skills. These findings have important implications for a range of clinical disorders that present with motor abnormalities. For example, other clinical populations characterised by developmental (e.g., Tourette Syndrome or cerebral palsy) or neurodegenerative (e.g., Huntington's Disease or cerebellar ataxia) motor atypicalities have also been found to exhibit poor social skills such as disrupted internal state attribution (Caillies, Hody, & Calmus, 2012; Eddy & Cavanna, 2015; Eddy & Rickards, 2015; Garrard, Martin, Giunti, & Cipolotti, 2008). Furthermore, the studies presented may help to explain why children with Attention Deficit Hyperactivity Disorder (ADHD) and motor dysfunctions are rated as having more social interaction difficulties than children with ADHD only (Tervo, Azuma, Fogas, & Fiechtner, 2007). Internal states expressed by these children with ADHD may be misunderstood by their typical peers, possibly resulting in increased frustration and inadequate social interactions (Nijmeijer et al., 2008). Even children and adults with motor dysfunction, without any clinical diagnosis, are more likely to experience less favourable social interactions (Bejerot & Humble, 2013).

The findings presented in the current thesis are therefore likely to apply to a number of conditions characterised by atypical movements, and suggest that interaction difficulties between typical and atypical individuals may not be attributable solely to the individual who has received a clinical diagnosis. Future work could take the paradigms presented in this thesis to ask similar questions within these different populations. This work might not only inform the current hypothesis, as to how movement differences between different groups affects social communication, but also identify additional mechanisms that support the association between action and perception that might vary across individuals with different behavioural profiles. For instance, it would inform whether the motor atypicalities are similar in nature, e.g., reflected in similar kinematic profiles between individuals with autism and ADHD, and which other processes are necessary to produce different types of social deficits.

8.6. Conclusion

In conclusion, the present thesis has demonstrated that the kinematic information embedded within our movements is a critical signal to communicate our internal states to others, and we interpret this information via models tuned to our own actions. We show enhanced understanding of those who move most like ourselves, and fail to identify accurately the internal states of others who move dissimilarly. These findings can have important implications for how groups of individuals who move in markedly different ways interact, and highlights the importance of action for understanding social cognition across typical and atypical development.

9. Reference List

- Abell, F., Happé, F., & Frith, U. (2000). Do triangles play tricks? Attribution of mental states to animated shapes in normal and abnormal development. *Cognitive Development*, 15(1), 1–16. [https://doi.org/10.1016/S0885-2014\(00\)00014-9](https://doi.org/10.1016/S0885-2014(00)00014-9)
- Abernethy, B., Zawi, K., & Jackson, R. C. (2008). Expertise and attunement to kinematic constraints. *Perception*, 37(6), 931–48. <https://doi.org/10.1068/p5340>
- Ada, M. S., Suda, K., & Ishii, M. (2003). Expression of emotions in dance: relation between arm movement characteristics and emotion. *Perceptual and Motor Skills*, 97(3), 697–708. <https://doi.org/10.2466/pms.2003.97.3.697>
- Adolphs, R. (2003). Cognitive neuroscience: cognitive neuroscience of human social behaviour. *Nature Reviews Neuroscience*, 4(3), 165–78. <https://doi.org/10.1038/nrn1056>
- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11(9), 1109–1116. <https://doi.org/10.1038/nn.2182>
- Alaerts, K., Swinnen, S. P., & Wenderoth, N. (2017). Neural processing of biological motion in autism: An investigation of brain activity and effective connectivity. *Scientific Reports*, 7, 5612. <https://doi.org/10.1038/s41598-017-05786-z>
- Allman, M. J., DeLeon, I. G., & Wearden, J. H. (2011). Psychophysical assessment of timing in individuals with autism. *American Journal on Intellectual and Developmental Disabilities*, 116(2), 165–78. <https://doi.org/10.1352/1944-7558-116.2.165>

American Psychiatric Association (1994). *Diagnostic and statistical manual of mental disorders: DSM-IV* (4th ed). Washington, D.C: American Psychiatric Association.

American Psychiatric Association (2013). *Diagnostic and statistical manual of mental disorders: DSM-5* (5th ed). Washington, D.C: American Psychiatric Association. <http://dx.doi.org/10.1176/appi.books.9780890425596>

Ames, C., & Fletcher-Watson, S. (2010). A review of methods in the study of attention in autism. *Developmental Review*, 30(1), 52–73.

<https://doi.org/10.1016/j.dr.2009.12.003>

Amsterdam, B. (1972). Mirror self-image reactions before age two. *Developmental Psychobiology*, 5(4), 297–305. <https://doi.org/10.1002/dev.420050403>

Annaz, D., Campbell, R., Coleman, M., Milne, E., & Swettenham, J. (2011). Young children with autism spectrum disorder do not preferentially attend to biological motion. *Journal of Autism and Developmental Disorders*, 42(3), 401–08.

<https://doi.org/10.1007/s10803-011-1256-3>

Anzulewicz, A., Sobota, K., & Delafield-Butt, J. T. (2016). Toward the autism motor signature: gesture patterns during smart tablet gameplay identify children with autism. *Scientific Reports*, 6, 31107. <https://doi.org/10.1038/srep31107>

App, B., McIntosh, D. N., Reed, C. L., & Hertenstein, M. J. (2011). Nonverbal channel use in communication of emotion: how may depend on why. *Emotion*, 11(3), 603–17. <https://doi.org/10.1037/a0023164>

Asendorpf, J. B., Conner, M., De Fruyt, F., De Houwer, J., Denissen, J. J. A., Fiedler, K., ... & Wicherts, J. M. (2013). Recommendations for increasing replicability

in psychology: recommendations for increasing replicability. *European Journal of Personality*, 27(2), 108–19. <https://doi.org/10.1002/per.1919>

Atkeson, C. G., & Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *The Journal of Neuroscience*, 5(9), 2318–30.

Atkinson, A. P. (2009). Impaired recognition of emotions from body movements is associated with elevated motion coherence thresholds in autism spectrum disorders. *Neuropsychologia*, 47(13), 3023–9. <https://doi.org/10.1016/j.neuropsychologia.2009.05.019>

Atkinson, A. P., Dittrich, W. H., Gemmell, A. J., & Young, A. W. (2004). Emotion perception from dynamic and static body expressions in point-light and full-light displays. *Perception*, 33(6), 717–46. <https://doi.org/10.1068/p5096>

Atkinson, A. P., Tunstall, M. L., & Dittrich, W. H. (2007). Evidence for distinct contributions of form and motion information to the recognition of emotions from body gestures. *Cognition*, 104(1), 59–72. <https://doi.org/10.1016/j.cognition.2006.05.005>

Auvray, M., Hoellinger, T., Hanne-ton, S., & Roby-Brami, A. (2011). Perceptual weight judgments when viewing one's own and others' movements under minimalist conditions of visual presentation. *Perception*, 40(9), 1081–103. <https://doi.org/10.1068/p6879>

Baird, G., Cass, H., & Slonims, V. (2003). Diagnosis of autism. *British Medical Journal*, 327(7413), 488–93. <https://doi.org/10.1136/bmj.327.7413.488>

Baranek, G. T. (1999). Autism during infancy: a retrospective video analysis of sensory-motor and social behaviours at 9-12 months of age. *Journal of Autism*

and Developmental Disorders, 29(3), 213–24.

<https://doi.org/10.1023/A:1023080005650>

Bardi, L., Regolin, L., & Simion, F. (2011). Biological motion preference in humans at birth: role of dynamic and configural properties: biological motion preference. *Developmental Science*, 14(2), 353–9. <https://doi.org/10.1111/j.1467-7687.2010.00985.x>

Barliya, A., Omlor, L., Giese, M. A., Berthoz, A., & Flash, T. (2013). Expression of emotion in the kinematics of locomotion. *Experimental Brain Research*, 225(2), 159–76. <https://doi.org/10.1007/s00221-012-3357-4>

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a ‘theory of mind’ ? *Cognition*, 21(1), 37–46. [https://doi.org/10.1016/0010-0277\(85\)90022-8](https://doi.org/10.1016/0010-0277(85)90022-8)

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): evidence from Asperger Syndrome /high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, 31(1), 5–17. <https://doi.org/10.1023/A:1005653411471>

<https://doi.org/10.1023/A:1005653411471> Barrett, H. C., Todd, P. M., Miller, G. F., & Blythe, P. W. (2005). Accurate judgments of intention from motion cues alone: A cross-cultural study. *Evolution and Human Behaviour*, 26(4), 313–31. <https://doi.org/10.1016/j.evolhumbehav.2004.08.015>

- Bartlett, N. R., & Bartlett, S. C. (1959). Synchronization of a motor response with an anticipated sensory event. *Psychological Review*, 66(4), 203–18.
<https://doi.org/10.1037/h0046490>
- Bassili, J. N. (1976). Temporal and spatial contingencies in the perception of social events. *Journal of Personality and Social Psychology*, 33(6), 680–85.
<https://doi.org/10.1037/0022-3514.33.6.680>
- Batty, M., & Taylor, M. J. (2006). The development of emotional face processing during childhood. *Developmental Science*, 9(2), 207–20.
<https://doi.org/10.1111/j.1467-7687.2006.00480.x>
- Bedford, R., Gliga, T., Pickles, A., Senju, A., Charman, T., Johnson, M. H., & the BASIS team. (2012). Precursors to social and communication difficulties in infants at-risk for autism: gaze following and attentional engagement. *Journal of Autism and Developmental Disorders*, 42(10), 2208–18.
<https://doi.org/10.1007/s10803-012-1450-y>
- Behrends, A., Müller, S., & Dziobek, I. (2012). Moving in and out of synchrony: A concept for a new intervention fostering empathy through interactional movement and dance. *The Arts in Psychotherapy*, 39(2), 107–16.
<https://doi.org/10.1016/j.aip.2012.02.003>
- Bejerot, S., & Humble, M. B. (2013). Childhood clumsiness and peer victimization: a case–control study of psychiatric patients. *BMC Psychiatry*, 13, 68.
<https://doi.org/10.1186/1471-244X-13-68>
- Benasich, A. A., Choudhury, N. A., Realpe-Bonilla, T., & Roesler, C. P. (2014). Plasticity in developing brain: active auditory exposure impacts prelinguistic

acoustic mapping. *Journal of Neuroscience*, 34(40), 13349–63.

<https://doi.org/10.1523/JNEUROSCI.0972-14.2014>

Bertenthal, B. I., & Pinto, J. (1994). Global processing of biological motions.

Psychological Science, 5(4), 221–4. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-9280.1994.tb00504.x)

[9280.1994.tb00504.x](https://doi.org/10.1111/j.1467-9280.1994.tb00504.x)

Berthier, N. E., & Keen, R. (2006). Development of reaching in infancy. *Experimental*

Brain Research, 169(4), 507–18. <https://doi.org/10.1007/s00221-005-0169-9>

Bhat, A.N., Galloway, J. C., & Landa, R. J. (2012). Relation between early motor delay

and later communication delay in infants at risk for autism. *Infant Behaviour*

and Development, 35(4), 838–46. <https://doi.org/10.1016/j.infbeh.2012.07.019>

Bhat, A. N., Landa, R. J., & Galloway, J. C. (2011). Current perspectives on motor

functioning in infants, children, and adults with autism spectrum disorders.

Physical Therapy, 91(7), 1116–29. <https://doi.org/10.2522/ptj.20100294>

Bhatara, A., Babikian, T., Laugeson, E., Tachdjian, R., & Sininger, Y. S. (2013).

Impaired timing and frequency discrimination in high-functioning autism

spectrum disorders. *Journal of Autism and Developmental Disorders*, 43(10),

2312–28. <https://doi.org/10.1007/s10803-013-1778-y>

Binetti, N., Harrison, C., Coutrot, A., Johnston, A., & Mareschal, I. (2016). Pupil

dilation as an index of preferred mutual gaze duration. *Royal Society Open*

Science, 3(7), 160086. <https://doi.org/10.1098/rsos.160086>

Blair, R. J. R. (2003). Facial expressions, their communicatory functions and neuro-

cognitive substrates. *Philosophical Transactions of the Royal Society B:*

Biological Sciences, 358(1431), 561–72. <https://doi.org/10.1098/rstb.2002.1220>

- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, 58(1), 47–73.
<https://doi.org/10.1146/annurev.psych.57.102904.190152>
- Blake, R., Turner, L. M., Smoski, M. J., Pozdol, S. L., & Stone, W. L. (2003). Visual recognition of biological motion is impaired in children with autism. *Psychological Science*, 14(2), 151–7. <https://doi.org/10.1111/1467-9280.01434>
- Blakemore, S.-J. (2008). The social brain in adolescence. *Nature Reviews Neuroscience*, 9(4), 267–77. <https://doi.org/10.1038/nrn2353>
- Blakemore, S.-J., & Choudhury, S. (2006). Development of the adolescent brain: implications for executive function and social cognition. *Journal of Child Psychology and Psychiatry*, 47(3–4), 296–312. <https://doi.org/10.1111/j.1469-7610.2006.01611.x>
- Bowler, D. M., & Thommen, E. (2000). Attribution of mechanical and social causality to animated displays by children with autism. *Autism*, 4(2), 147–171.
<https://doi.org/10.1177/1362361300004002004>
- Brault, S., Bideau, B., Kulpa, R., & Craig, C. M. (2012). Detecting deception in movement: the case of the side-step in rugby. *PLoS ONE*, 7(6), e37494.
<https://doi.org/10.1371/journal.pone.0037494>
- Brenner, L. A., Shih, V. H., Colich, N. L., Sugar, C. A., Bearden, C. E., & Dapretto, M. (2015). Time reproduction performance is associated with age and working memory in high-functioning youth with autism spectrum disorder: autism and time reproduction. *Autism Research*, 8(1), 29–37.
<https://doi.org/10.1002/aur.1401>

- Brewer, N., Young, R. L., & Barnett, E. (2017). Measuring theory of mind in adults with autism spectrum disorder. *Journal of Autism and Developmental Disorders*, 47(7), 1927–41. <https://doi.org/10.1007/s10803-017-3080-x>
- Brewer, R., Biotti, F., Catmur, C., Press, C., Happé, F., Cook, R., & Bird, G. (2016). Can neurotypical individuals read autistic facial expressions? Atypical production of emotional facial expressions in autism spectrum disorders: expression production in autism. *Autism Research*, 9(2), 262–71. <https://doi.org/10.1002/aur.1508>
- Brown, B. B. (2013). Adolescents' relationships with peers. In R. M. Lerner & L. Steinberg (Eds.), *Handbook of Adolescent Psychology* (pp. 363–94). Hoboken, NJ, USA: John Wiley & Sons, Inc. <https://doi.org/10.1002/9780471726746.ch12>
- Brown, E. C., & Brüne, M. (2012). The role of prediction in social neuroscience. *Frontiers in Human Neuroscience*, 6, 147. <https://doi.org/10.3389/fnhum.2012.00147>
- Bryson, S. E., Zwaigenbaum, L., McDermott, C., Rombough, V., & Brian, J. (2008). The autism observation scale for infants: scale development and reliability data. *Journal of Autism and Developmental Disorders*, 38(4), 731–8. <https://doi.org/10.1007/s10803-007-0440-y>
- Burnett, S., & Blakemore, S.-J. (2009). Functional connectivity during a social emotion task in adolescents and in adults. *European Journal of Neuroscience*, 29(6), 1294–1301. <https://doi.org/10.1111/j.1460-9568.2009.06674.x>

- Caillies, S., Hody, A., & Calmus, A. (2012). Theory of mind and irony comprehension in children with cerebral palsy. *Research in Developmental Disabilities, 33*(5), 1380–8. <https://doi.org/10.1016/j.ridd.2012.03.012>
- Calvo-Merino, B., Glaser, D. E., Grezes, J., Passingham, R. E., & Haggard, P. (2004). Action observation and acquired motor skills: an fMRI study with expert dancers. *Cerebral Cortex, 15*(8), 1243–9. <https://doi.org/10.1093/cercor/bhi007>
- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology, 16*(19), 1905–10. <https://doi.org/10.1016/j.cub.2006.07.065>
- Campione, G. C., Piazza, C., Villa, L., & Molteni, M. (2016). Three-dimensional kinematic analysis of prehension movements in young children with autism spectrum disorder: new insights on motor impairment. *Journal of Autism and Developmental Disorders, 46*(6), 1985–99. <https://doi.org/10.1007/s10803-016-2732-6>
- Candidi, M., Urgesi, C., Ionta, S., & Aglioti, S. M. (2008). Virtual lesion of ventral premotor cortex impairs visual perception of biomechanically possible but not impossible actions. *Social Neuroscience, 3*(3–4), 388–400. <https://doi.org/10.1080/17470910701676269>
- Cannon, E. N., Woodward, A. L., Gredebäck, G., von Hofsten, C., & Turek, C. (2012). Action production influences 12-month-old infants' attention to others' actions: Action production and anticipation. *Developmental Science, 15*(1), 35–42. <https://doi.org/10.1111/j.1467-7687.2011.01095.x>

- Casile, A., Dayan, E., Caggiano, V., Hendler, T., Flash, T., & Giese, M. A. (2009). Neuronal encoding of human kinematic invariants during action observation. *Cerebral Cortex*, 20(7), 1647–55. <https://doi.org/10.1093/cercor/bhp229>
- Castelli, F., Frith, H., Happé, F., & Frith, U. (2002). Autism, Asperger Syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain*, 125(8), 1839–49. <https://doi.org/10.1093/brain/awf189>
- Castelli, F., Happé, F., Frith, U., & Frith, C. (2000). Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. *NeuroImage*, 12(3), 314–25. <https://doi.org/10.1006/nimg.2000.0612>
- Cattaneo, L., Fabbri-Destro, M., Boria, S., Pieraccini, C., Monti, A., Cossu, G., & Rizzolatti, G. (2007). Impairment of actions chains in autism and its possible role in intention understanding. *Proceedings of the National Academy of Sciences*, 104(45), 17825–30. <https://doi.org/10.1073/pnas.0706273104>
- Chang, D. H. F., & Troje, N. F. (2009). Acceleration carries the local inversion effect in biological motion perception. *Journal of Vision*, 9(1), 19. <https://doi.org/10.1167/9.1.19>
- Charman, T. (2003). Why is joint attention a pivotal skill in autism? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 358(1430), 315–24. <https://doi.org/10.1098/rstb.2002.1199>
- Charman, T., Baird, G., Simonoff, E., Chandler, S., Davison-Jenkins, A., Sharma, A., ... & Pickles, A. (2016). Testing two screening instruments for autism spectrum disorder in UK community child health services. *Developmental Medicine & Child Neurology*, 58(4), 369–75. <https://doi.org/10.1111/dmcn.12874>

Charman, T., Taylor, E., Drew, A., Cockerill, H., Brown, J.-A., & Baird, G. (2005).

Outcome at 7 years of children diagnosed with autism at age 2: predictive validity of assessments conducted at 2 and 3 years of age and pattern of symptom change over time. *Journal of Child Psychology and Psychiatry*, *46*(5), 500–13. <https://doi.org/10.1111/j.1469-7610.2004.00377.x>

Clarke, T. J., Bradshaw, M. F., Field, D. T., Hampson, S. E., & Rose, D. (2005). The perception of emotion from body movement in point-light displays of interpersonal dialogue. *Perception*, *34*(10), 1171–80.

<https://doi.org/10.1068/p5203>

Constantino, J. N., Zhang, Y., Frazier, T., Abbacchi, A. M., & Law, P. (2010). Sibling recurrence and the genetic epidemiology of autism. *American Journal of Psychiatry*, *167*(11), 1349–56. <https://doi.org/10.1176/appi.ajp.2010.09101470>

Cook, J. L. (2016). From movement kinematics to social cognition: the case of autism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1693), 20150372. <https://doi.org/10.1098/rstb.2015.0372>

Cook, J. L., Blakemore, S.-J., & Press, C. (2013). Atypical basic movement kinematics in autism spectrum conditions. *Brain*, *136*(9), 2816–24.

<https://doi.org/10.1093/brain/awt208>

Cook, J. L., Saygin, A. P., Swain, R., & Blakemore, S.-J. (2009). Reduced sensitivity to minimum-jerk biological motion in autism spectrum conditions.

Neuropsychologia, *47*(14), 3275–8.

<https://doi.org/10.1016/j.neuropsychologia.2009.07.010>

- Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. (2014). Mirror neurons: from origin to function. *Behavioural and Brain Sciences*, *37*(2), 177–92.
<https://doi.org/10.1017/S0140525X13000903>
- Cox, A., Klein, K., Charman, T., Baird, G., Baron-Cohen, S., Swettenham, J., ... & Wheelwright, S. (1999). Autism spectrum disorders at 20 and 42 months of age: stability of clinical and ADI-R diagnosis. *Journal of Child Psychology and Psychiatry, and Allied Disciplines*, *40*(5), 719–32.
<http://dx.doi.org/10.1111/1469-7610.00488>
- Crone, E. A., & Steinbeis, N. (2017). Neural perspectives on cognitive control development during childhood and adolescence. *Trends in Cognitive Sciences*, *21*(3), 205–15. <https://doi.org/10.1016/j.tics.2017.01.003>
- Dael, N., Mortillaro, M., & Scherer, K. R. (2012). Emotion expression in body action and posture. *Emotion*, *12*(5), 1085–101. <https://doi.org/10.1037/a0025737>
- Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron*, *48*(3), 497–507. <https://doi.org/10.1016/j.neuron.2005.10.018>
- Davies, P. L., & Rose, J. D. (2000). Motor skills of typically developing adolescents: awkwardness or improvement? *Physical and Occupational Therapy In Paediatrics*, *20*(1), 19–42. https://doi.org/10.1080/J006v20n01_03
- Dayan, E., Casile, A., Levit-Binnun, N., Giese, M., Hendler, T., & Flash, T. (2007). Neural representations of kinematic laws of motion: Evidence for action-perception coupling. *PNAS*, *104*(51), 20582–20587.
<http://dx.doi.org/10.1073/pnas.0710033104>

- Dayan, E., Sella, I., Mukovskiy, A., Douek, Y., Giese, M. A., Malach, R., & Flash, T. (2016). The default mode network differentiates biological from non-biological motion. *Cerebral Cortex*, 26(1), 234–45. <https://doi.org/10.1093/cercor/bhu199>
- de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nature Reviews Neuroscience*, 7(3), 242–9. <https://doi.org/10.1038/nrn1872>
- de Klerk, C. C. J. M., Johnson, M. H., Heyes, C. M., & Southgate, V. (2015). Baby steps: investigating the development of perceptual-motor couplings in infancy. *Developmental Science*, 18(2), 270–80. <https://doi.org/10.1111/desc.12226>
- de Lange, F. P., Spronk, M., Willems, R. M., Toni, I., & Bekkering, H. (2008). Complementary systems for understanding action intentions. *Current Biology*, 18(6), 454–7. <https://doi.org/10.1016/j.cub.2008.02.057>
- de'Sperati, C., & Viviani, P. (1997). The relationship between curvature and velocity in two-dimensional smooth pursuit eye movements. *The Journal of Neuroscience*, 17(10), 3932–45.
- Deoni, S. C. L., Mercure, E., Blasi, A., Gasston, D., Thomson, A., Johnson, M., ... & Murphy, D. G. M. (2011). Mapping infant brain myelination with magnetic resonance imaging. *Journal of Neuroscience*, 31(2), 784–91. <https://doi.org/10.1523/JNEUROSCI.2106-10.2011>
- Di Cesare, G., Sparaci, L., Pelosi, A., Mazzone, L., Giovagnoli, G., Menghini, D., ... & Vicari, S. (2017). Differences in action style recognition in children with autism spectrum disorders. *Frontiers in Psychology*, 8, 1456. <https://doi.org/10.3389/fpsyg.2017.01456>

Diersch, N., Cross, E. S., Stadler, W., Schütz-Bosbach, S., & Rieger, M. (2012).

Representing others' actions: the role of expertise in the aging mind.

Psychological Research, 76(4), 525–41. <https://doi.org/10.1007/s00426-011-0404-x>

Diersch, N., Mueller, K., Cross, E. S., Stadler, W., Rieger, M., & Schütz-Bosbach, S.

(2013). Action prediction in younger versus older adults: neural correlates of motor familiarity. *PLoS ONE*, 8(5), e64195.

<https://doi.org/10.1371/journal.pone.0064195>

Dittrich, W. H. (1993). Action categories and the perception of biological motion.

Perception, 22(1), 15–22. <https://doi.org/10.1068/p220015>

Dumontheil, I. (2016). Adolescent brain development. *Current Opinion in Behavioural*

Sciences, 10, 39–44. <https://doi.org/10.1016/j.cobeha.2016.04.012>

Dumontheil, I., Apperly, I. A., & Blakemore, S.-J. (2010). Online usage of theory of

mind continues to develop in late adolescence. *Developmental Science*, 13(2),

331–8. <https://doi.org/10.1111/j.1467-7687.2009.00888.x>

Eddy, C. M., & Cavanna, A. E. (2015). Triangles, tricks and tics: Hyper-mentalizing in

response to animated shapes in Tourette syndrome. *Cortex*, 71, 68–75.

<https://doi.org/10.1016/j.cortex.2015.06.003>

Eddy, C. M., & Rickards, H. E. (2015). Interaction without intent: the shape of the

social world in Huntington's disease. *Social Cognitive and Affective*

Neuroscience, 10(9), 1228–35. <https://doi.org/10.1093/scan/nsv012>

Ekberg, T. L., Falck-Ytter, T., Bölte, S., Gredebäck, G., & the EASE Team. (2016).

Reduced prospective motor control in 10-month-olds at risk for autism spectrum

disorder. *Clinical Psychological Science*, 4(1), 129–35.

<https://doi.org/10.1177/2167702615576697>

Ekman, P., & Friesen, W. V. (1975). *Unmasking the face; a guide to recognizing emotions from facial clues*. Englewood Cliffs, N.J: Prentice-Hall.

Eldevik, S., Hastings, R. P., Hughes, J. C., Jahr, E., Eikeseth, S., & Cross, S. (2009). Meta-analysis of early intensive behavioural intervention for children with autism. *Journal of Clinical Child and Adolescent Psychology*, 38(3), 439–50.

<https://doi.org/10.1080/15374410902851739>

Elsabbagh, M., Fernandes, J., Jane Webb, S., Dawson, G., Charman, T., & Johnson, M. H. (2013). Disengagement of visual attention in infancy is associated with emerging autism in toddlerhood. *Biological Psychiatry*, 74(3), 189–94.

<https://doi.org/10.1016/j.biopsych.2012.11.030>

Elsner, B., & Hommel, B. (2004). Contiguity and contingency in action-effect learning. *Psychological Research*, 68(2–3), 138–54. [https://doi.org/10.1007/s00426-003-](https://doi.org/10.1007/s00426-003-0151-8)

[0151-8](https://doi.org/10.1007/s00426-003-0151-8)

Endedijk, H. M., Meyer, M., Bekkering, H., Cillessen, A. H. N., & Hunnius, S. (2017). Neural mirroring and social interaction: Motor system involvement during action observation relates to early peer cooperation. *Developmental Cognitive Neuroscience*, 24, 33–41. <https://doi.org/10.1016/j.dcn.2017.01.001>

Fabbri-Destro, M., Cattaneo, L., Boria, S., & Rizzolatti, G. (2009). Planning actions in autism. *Experimental Brain Research*, 192(3), 521–5.

<https://doi.org/10.1007/s00221-008-1578-3>

- Falck-Ytter, T., Rehnberg, E., & Bölte, S. (2013). Lack of visual orienting to biological motion and audiovisual synchrony in 3-year-olds with autism. *PLoS ONE*, 8(7), e68816. <https://doi.org/10.1371/journal.pone.0068816>
- Falter, C. M., Elliott, M. A., & Bailey, A. J. (2012b). Enhanced visual temporal resolution in autism spectrum disorders. *PLoS ONE*, 7(3), e32774. <https://doi.org/10.1371/journal.pone.0032774>
- Falter, C. M., & Noreika, V. (2011). Interval timing deficits and abnormal cognitive development. *Frontiers in Integrative Neuroscience*, 5, 26. <https://doi.org/10.3389/fnint.2011.00026>
- Falter, C. M., Noreika, V., Wearden, J. H., & Bailey, A. J. (2012a). More consistent, yet less sensitive: interval timing in autism spectrum disorders. *The Quarterly Journal of Experimental Psychology*, 65(11), 2093–107. <https://doi.org/10.1080/17470218.2012.690770>
- Fausey, C. M., Jayaraman, S., & Smith, L. B. (2016). From faces to hands: Changing visual input in the first two years. *Cognition*, 152, 101–7. <https://doi.org/10.1016/j.cognition.2016.03.005>
- Fawcett, C., & Tuncgenç, B. (2017). Infants' use of movement synchrony to infer social affiliation in others. *Journal of Experimental Child Psychology*, 160, 127-36. <http://dx.doi.org/10.1016/j.jecp.2017.03.014>
- Fiedler, K., Nickel, S., Muehlfriedel, T., & Unkelbach, C. (2001). Is mood congruency an effect of genuine memory or response bias? *Journal of Experimental Social Psychology*, 37(3), 201–14. <https://doi.org/10.1006/jesp.2000.1442>

- Fitzpatrick, P., Frazier, J. A., Cochran, D. M., Mitchell, T., Coleman, C., & Schmidt, R. C. (2016). Impairments of social motor synchrony evident in autism spectrum disorder. *Frontiers in Psychology, 7*, 1323.
<https://doi.org/10.3389/fpsyg.2016.01323>
- Flannery, D., Montemayor, R., Eberly, M., & Torquati, J. (1993). Unravelling the ties that bind: affective expression and perceived conflict in parent-adolescent interactions. *Journal of Social and Interpersonal Relationships, 10*, 495–509.
<https://doi.org/10.1177/0265407593104002>
- Fleming, J., Klatzky, R. L., & Behrmann, M. (2002). Time course of planning for object and action parameters in visually guided manipulation. *Visual Cognition, 9*(4–5), 502–27. <https://doi.org/10.1080/13506280143000557>
- Focaroli, V., Taffoni, F., Parsons, S. M., Keller, F., & Iverson, J. M. (2016). Performance of motor sequences in children at heightened vs. low risk for ASD: a longitudinal study from 18 to 36 months of age. *Frontiers in Psychology, 7*, 724. <https://doi.org/10.3389/fpsyg.2016.00724>
- Fogassi, L. (2005). Parietal lobe: from action organization to intention understanding. *Science, 308*(5722), 662–7. <https://doi.org/10.1126/science.1106138>
- Forgas, J. P. (1995). Mood and judgment: the affect infusion model (AIM). *Psychological Bulletin, 117*(1), 39–66. <https://doi.org/10.1037/0033-2909.117.1.39>
- Forti, S., Valli, A., Perego, P., Nobile, M., Crippa, A., & Molteni, M. (2011). Motor planning and control in autism. A kinematic analysis of preschool children.

Research in Autism Spectrum Disorders, 5(2), 834–42.

<https://doi.org/10.1016/j.rasd.2010.09.013>

Fournier, K. A., Hass, C. J., Naik, S. K., Lodha, N., & Cauraugh, J. H. (2010). Motor coordination in autism spectrum disorders: a synthesis and meta-analysis.

Journal of Autism and Developmental Disorders, 40(10), 1227–40.

<https://doi.org/10.1007/s10803-010-0981-3>

Fox, R., & McDaniel, C. (1982). The perception of biological motion by human infants.

Science, 218(4571), 486–7. <https://doi.org/10.1126/science.7123249>

Freire, A., Lewis, T. L., Maurer, D., & Blake, R. (2006). The development of sensitivity to biological motion in noise. *Perception*, 35(5), 647–57.

<https://doi.org/10.1068/p5403>

Freitag, C. M., Konrad, C., Häberlen, M., Kleser, C., von Gontard, A., Reith, W., ... & Krick, C. (2008). Perception of biological motion in autism spectrum disorders.

Neuropsychologia, 46(5), 1480–94.

<https://doi.org/10.1016/j.neuropsychologia.2007.12.025>

Frijda, N. H. (2010). Impulsive action and motivation. *Biological Psychology*, 84(3),

570–9. <https://doi.org/10.1016/j.biopsycho.2010.01.005>

Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50(4), 531–4.

<https://doi.org/10.1016/j.neuron.2006.05.001>

Froehle, A. W., Nahhas, R. W., Sherwood, R. J., & Duren, D. L. (2013). Age-related changes in spatiotemporal characteristics of gait accompany ongoing lower limb linear growth in late childhood and early adolescence. *Gait & Posture*, 38(1),

14–9. <https://doi.org/10.1016/j.gaitpost.2012.10.005>

- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*(2), 593–609.
<https://doi.org/10.1093/brain/119.2.593>
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, *4*(7), 252-4.
[https://doi.org/10.1016/S1364-6613\(98\)01262-5](https://doi.org/10.1016/S1364-6613(98)01262-5)
- Garrard, P., Martin, N. H., Giunti, P., & Cipolotti, L. (2008). Cognitive and social cognitive functioning in spinocerebellar ataxia: A preliminary characterization. *Journal of Neurology*, *255*(3), 398–405. <https://doi.org/10.1007/s00415-008-0680-6>
- Georgiou, I., Becchio, C., Glover, S., & Castiello, U. (2007). Different action patterns for cooperative and competitive behaviour. *Cognition*, *102*(3), 415–33.
<https://doi.org/10.1016/j.cognition.2006.01.008>
- Gergely, G., & Watson, J. S. (1999). Early socio-emotional development: contingency perception and the social-biofeedback model. In *Early Social Cognition: Understanding others in the first months of life* (101–136). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.
- Gerson, S. A., Bekkering, H., & Hunnius, S. (2015). Short-term motor training, but not observational training, alters neurocognitive mechanisms of action processing in infancy. *Journal of Cognitive Neuroscience*, *27*(6), 1207-14.
https://doi.org/10.1162/jocn_a_00774

- Gerson, S. A., & Woodward, A. L. (2014). The joint role of trained, untrained, and observed actions at the origins of goal recognition. *Infant Behaviour and Development*, 37(1), 94–104. <https://doi.org/10.1016/j.infbeh.2013.12.013>
- Giese, M. A., & Poggio, T. (2003). Cognitive neuroscience: Neural mechanisms for the recognition of biological movements. *Nature Reviews Neuroscience*, 4(3), 179–92. <https://doi.org/10.1038/nrn1057>
- Gil, S., Chambres, P., Hyvert, C., Fanget, M., & Droit-Volet, S. (2012). Children with autism spectrum disorders have ‘the working raw material’ for time perception. *PLoS ONE*, 7(11), e49116. <https://doi.org/10.1371/journal.pone.0049116>
- Glazebrook, C. M., Elliott, D., & Lyons, J. (2006). A kinematic analysis of how young adults with and without autism plan and control goal-directed movements. *Motor Control*, 10(3), 244–64. <https://doi.org/10.1123/mcj.10.3.244>
- Gobbini, M. I., Koralek, A. C., Bryan, R. E., Montgomery, K. J., & Haxby, J. V. (2007). Two takes on the social brain: a comparison of theory of mind tasks. *Journal of Cognitive Neuroscience*, 19(11), 1803–14. <https://doi.org/10.1162/jocn.2007.19.11.1803>
- Goddings, A.-L., Burnett Heyes, S., Bird, G., Viner, R. M., & Blakemore, S.-J. (2012). The relationship between puberty and social emotion processing: puberty and social brain development. *Developmental Science*, 15(6), 801–11. <https://doi.org/10.1111/j.1467-7687.2012.01174.x>
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., ... & Thompson, P. M. (2004). Dynamic mapping of human cortical development

during childhood through early adulthood. *Proceedings of the National Academy of Sciences*, 101(21), 8174–9. <https://doi.org/10.1073/pnas.0402680101>

Gowen, E., & Hamilton, A. (2013). Motor abilities in autism: a review using a computational context. *Journal of Autism and Developmental Disorders*, 43(2), 323–44. <https://doi.org/10.1007/s10803-012-1574-0>

Gowen, E., & Miall, R. C. (2005). Behavioural aspects of cerebellar function in adults with Asperger syndrome. *The Cerebellum*, 4(4), 279–89. <https://doi.org/10.1080/14734220500355332>

Gowen, E., & Miall, R. C. (2007). The cerebellum and motor dysfunction in neuropsychiatric disorders. *The Cerebellum*, 6(3), 268–79. <https://doi.org/10.1080/14734220601184821>

Green, D., Charman, T., Pickles, A., Chandler, S., Loucas, T., Simonoff, E., & Baird, G. (2009). Impairment in movement skills of children with autistic spectrum disorders. *Developmental Medicine & Child Neurology*, 51(4), 311–6. <https://doi.org/10.1111/j.1469-8749.2008.03242.x>

Greenleaf, E. A. (1992). Improving rating scale measures by detecting and correcting bias components in some response styles. *Journal of Marketing Research*, 29(2), 176–88. <https://doi.org/10.2307/3172568>

Grondin, S. (1993). Duration discrimination of empty and filled intervals marked by auditory and visual signals. *Perception and Psychophysics*, 54(3), 383–94. <https://doi.org/10.3758/BF03205274>

- Grondin, S. (2010). Timing and time perception: A review of recent behavioural and neuroscience findings and theoretical directions. *Attention, Perception, and Psychophysics*, 72(3), 561–82. <https://doi.org/10.3758/APP.72.3.561>
- Grondin, S., Meilleur-Wells, G., Ouellette, C., & Macar, F. (1998). Sensory effects on judgments of short time-intervals. *Psychological Research*, 61(4), 261–8. <https://doi.org/10.1007/s004260050030>
- Grossberg, S., & Myers, C. W. (2000). The resonant dynamics of speech perception: interword integration and duration-dependent backward effects. *Psychological Review*, 107(4), 735–67. <https://doi.org/10.1037/0033-295X.107.4.735>
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, 12(5), 711–20. <https://doi.org/10.1162/089892900562417>
- Hadad, B., Schwartz, S., Maurer, D., & Lewis, T. L. (2015). Motion perception: a review of developmental changes and the role of early visual experience. *Frontiers in Integrative Neuroscience*, 9, 49. <https://doi.org/10.3389/fnint.2015.00049>
- Hadders-Algra, M. (2000). The neuronal group selection theory: a framework to explain variation in normal motor development. *Developmental Medicine and Child Neurology*, 42(8), 566–72. <http://dx.doi.org/10.1017/S0012162200001067>

- Halberstadt, A. G. (1986). Family socialization of emotional expression and nonverbal communication styles and skills. *Journal of Personality and Social Psychology*, 51(4), 827–36. <https://doi.org/10.1037/0022-3514.51.4.827>
- Hamilton, A. F., Joyce, D. W., Flanagan, J. R., Frith, C. D., & Wolpert, D. M. (2007). Kinematic cues in perceptual weight judgment and their origins in box lifting. *Psychological Research*, 71(1), 13–21. <https://doi.org/10.1007/s00426-005-0032-4>
- Happé, F. (2015). Autism as a neurodevelopmental disorder of mind-reading. *Journal of the British Academy*, 3, 197-209. <https://doi.org/10.5871/jba/003.197>
- Happé, F., & Frith, U. (2006). The weak coherence account: detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 36(1), 5–25. <https://doi.org/10.1007/s10803-005-0039-0>
- Hareli, S., Kafetsios, K., & Hess, U. (2015). A cross-cultural study on emotion expression and the learning of social norms. *Frontiers in Psychology*, 6, 1501. <https://doi.org/10.3389/fpsyg.2015.01501>
- Hebb, D. (1949). *The organisation of behaviour: A neuropsychological theory*. New York: Wiley.
- Heider, F., & Simmel, M. (1944). An Experimental Study of Apparent Behaviour. *The American Journal of Psychology*, 57(2), 243-59. <https://doi.org/10.2307/1416950>
- Heller, A. S., & Casey, B. J. (2016). The neurodynamics of emotion: delineating typical and atypical emotional processes during adolescence. *Developmental Science*, 19(1), 3–18. <https://doi.org/10.1111/desc.12373>

- Herba, C. M., Landau, S., Russell, T., Ecker, C., & Phillips, M. L. (2006). The development of emotion-processing in children: effects of age, emotion, and intensity. *Journal of Child Psychology and Psychiatry*, 47(11), 1098–106.
<https://doi.org/10.1111/j.1469-7610.2006.01652.x>
- Herrington, J. D., Baron-Cohen, S., Wheelwright, S. J., Singh, K. D., Bullmore, E. T., Brammer, M., & Williams, S. C. R. (2007). The role of MT+/V5 during biological motion perception in Asperger Syndrome: An fMRI study. *Research in Autism Spectrum Disorders*, 1(1), 14–27.
<https://doi.org/10.1016/j.rasd.2006.07.002>
- Herrington, J. D., Nymberg, C., & Schultz, R. T. (2011). Biological motion task performance predicts superior temporal sulcus activity. *Brain and Cognition*, 77(3), 372–81. <https://doi.org/10.1016/j.bandc.2011.09.001>
- Herrington, J., Nymberg, C., Faja, S., Price, E., & Schultz, R. (2012). The responsiveness of biological motion processing areas to selective attention towards goals. *NeuroImage*, 63(1), 581–90.
<https://doi.org/10.1016/j.neuroimage.2012.06.077>
- Hertenstein, M. J., Holmes, R., McCullough, M., & Keltner, D. (2009). The communication of emotion via touch. *Emotion*, 9(4), 566–73.
<https://doi.org/10.1037/a0016108>
- Hietanen, J. K., Leppänen, J. M., & Lehtonen, U. (2004). Perception of emotions in the hand movement quality of Finnish Sign Language. *Journal of Nonverbal Behaviour*, 28(1), 53–64.
<https://doi.org/10.1023/B:JONB.0000017867.70191.68>

- Hill, H., & Pollick, F. E. (2000). Exaggerating temporal differences enhances recognition of individuals from point light displays. *Psychological Science*, *11*(3), 223–8. <https://doi.org/10.1111/1467-9280.00245>
- Hillebrandt, H., Friston, K. J., & Blakemore, S.-J. (2015). Effective connectivity during animacy perception – dynamic causal modelling of Human Connectome Project data. *Scientific Reports*, *4*, 6240. <https://doi.org/10.1038/srep06240>
- Hirai, M., Watanabe, S., Honda, Y., & Kakigi, R. (2009). Developmental changes in point-light walker processing during childhood and adolescence: An event-related potential study. *Neuroscience*, *161*(1), 311–25. <https://doi.org/10.1016/j.neuroscience.2009.03.026>
- Hirsch, H. V., & Spinelli, D. N. (1970). Visual experience modifies distribution of horizontally and vertically oriented receptive fields in cats. *Science*, *168*(3933), 869–71. <http://dx.doi.org/10.1126/science.168.3933.869>
- Howlin, P., & Magiati, I. (2017). Autism spectrum disorder: outcomes in adulthood. *Current Opinion in Psychiatry*, *30*(2), 69–76. <https://doi.org/10.1097/YCO.0000000000000308>
- Howlin, P., Magiati, I., & Charman, T. (2009). Systematic review of early intensive behavioural interventions for children with autism. *American Journal on Intellectual and Developmental Disabilities*, *114*(1), 23–41. <https://doi.org/10.1352/2009.114:23-41>
- Hubert, B., Wicker, B., Moore, D. G., Monfardini, E., Duverger, H., Fonséca, D. D., & Deruelle, C. (2006). Brief report: recognition of emotional and non-emotional biological motion in individuals with autistic spectrum disorders. *Journal of*

Autism and Developmental Disorders, 37(7), 1386–92.

<https://doi.org/10.1007/s10803-006-0275-y>

Hunnius, S., & Bekkering, H. (2014). What are you doing? How active and observational experience shape infants' action understanding. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1644), 20130490. <https://doi.org/10.1098/rstb.2013.0490>

Ikeda, H., & Watanabe, K. (2009). Anger and happiness are linked differently to the explicit detection of biological motion. *Perception*, 38(7), 1002–11. <https://doi.org/10.1068/p6250>

Iverson, J. M., & Wozniak, R. H. (2007). Variation in vocal-motor development in infant siblings of children with autism. *Journal of Autism and Developmental Disorders*, 37(1), 158–70. <https://doi.org/10.1007/s10803-006-0339-z>

Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Sciences*, 12(7), 273–80. <https://doi.org/10.1016/j.tics.2008.04.002>

Ivry, R., & Spencer, R. (2004). The neural representation of time. *Current Opinion in Neurobiology*, 14(2), 225–32. <https://doi.org/10.1016/j.conb.2004.03.013>

Jackson, R. C., Warren, S., & Abernethy, B. (2006). Anticipation skill and susceptibility to deceptive movement. *Acta Psychologica*, 123(3), 355–71. <https://doi.org/10.1016/j.actpsy.2006.02.002>

Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and

grasp kinematics. *Experimental Brain Research*, 102(3), 519-30.

<https://doi.org/10.1007/BF00230656>

Jansiewicz, E. M., Goldberg, M. C., Newschaffer, C. J., Denckla, M. B., Landa, R., & Mostofsky, S. H. (2006). Motor signs distinguish children with high-functioning autism and Asperger's Syndrome from controls. *Journal of Autism and Developmental Disorders*, 36(5), 613–21. <https://doi.org/10.1007/s10803-006-0109-y>

Jastorff, J., & Orban, G. A. (2009). Human functional magnetic resonance imaging reveals separation and integration of shape and motion cues in biological motion processing. *Journal of Neuroscience*, 29(22), 7315–29. <https://doi.org/10.1523/JNEUROSCI.4870-08.2009>

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics*, 14(2), 201–11. <https://doi.org/10.3758/BF03212378>

Johnson, M. H. (2011). Interactive specialization: a domain-general framework for human functional brain development? *Developmental Cognitive Neuroscience*, 1(1), 7–21. <https://doi.org/10.1016/j.dcn.2010.07.003>

Johnston, P. J., Kaufman, J., Bajic, J., Sercombe, A., Michie, P. T., & Karayanidis, F. (2011). Facial emotion and identity processing development in 5- to 15-year-old children. *Frontiers in Psychology*, 2, 26. <https://doi.org/10.3389/fpsyg.2011.00026>

Jones, C. R. G., Happé, F., Baird, G., Simonoff, E., Marsden, A. J. S., Tregay, J., ... & Charman, T. (2009). Auditory discrimination and auditory sensory behaviours in

autism spectrum disorders. *Neuropsychologia*, 47(13), 2850–8.

<https://doi.org/10.1016/j.neuropsychologia.2009.06.015>

Jones, C. R. G., Swettenham, J., Charman, T., Marsden, A. J. S., Tregay, J., Baird, G., ... & Happé, F. (2011). No evidence for a fundamental visual motion processing deficit in adolescents with autism spectrum disorders. *Autism Research*, 4(5), 347–57. <https://doi.org/10.1002/aur.209>

Jones, E. J. H., Gliga, T., Bedford, R., Charman, T., & Johnson, M. H. (2014). Developmental pathways to autism: A review of prospective studies of infants at risk. *Neuroscience and Biobehavioural Reviews*, 39, 1–33.

<https://doi.org/10.1016/j.neubiorev.2013.12.001>

Jones, W., & Klin, A. (2013). Attention to eyes is present but in decline in 2–6-month-old infants later diagnosed with autism. *Nature*, 504(7480), 427–31.

<https://doi.org/10.1038/nature12715>

Kaiser, M. D., Delmolino, L., Tanaka, J. W., & Shiffrar, M. (2010). Comparison of visual sensitivity to human and object motion in autism spectrum disorder.

Autism Research, 3(4), 191–5. <https://doi.org/10.1002/aur.137>

Kaiser, M. D., & Pelphrey, K. A. (2012). Disrupted action perception in autism: Behavioural evidence, neuroendophenotypes, and diagnostic utility.

Developmental Cognitive Neuroscience, 2(1), 25–35.

<https://doi.org/10.1016/j.dcn.2011.05.005>

Kandel, S., Orliaguet, J.-P., & Viviani, P. (2000). Perceptual anticipation in handwriting: The role of implicit motor competence. *Perception and Psychophysics*, 62(4), 706–16.

<https://doi.org/10.3758/BF03206917>

- Karaminis, T., Cicchini, G. M., Neil, L., Cappagli, G., Aagten-Murphy, D., Burr, D., & Pellicano, E. (2016). Central tendency effects in time interval reproduction in autism. *Scientific Reports*, 6, 28570. <https://doi.org/10.1038/srep28570>
- Karmiloff-Smith, A. (2009). Nativism versus neuroconstructivism: Rethinking the study of developmental disorders. *Developmental Psychology*, 45(1), 56–63. <https://doi.org/10.1037/a0014506>
- Keehn, B., Westerfield, M., Müller, R.-A., & Townsend, J. (2017). Autism, attention, and alpha oscillations: an electrophysiological study of attentional capture. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, 2(6), 528–36. <https://doi.org/10.1016/j.bpsc.2017.06.006>
- Kelly, D. J., Liu, S., Lee, K., Quinn, P. C., Pascalis, O., Slater, A. M., & Ge, L. (2009). Development of the other-race effect during infancy: Evidence toward universality? *Journal of Experimental Child Psychology*, 104(1), 105–14. <https://doi.org/10.1016/j.jecp.2009.01.006>
- Kemner, C., van der Geest, J. N., Verbaten, M. N., & van Engeland, H. (2007). Effects of object complexity and type on the gaze behaviour of children with pervasive developmental disorder. *Brain and Cognition*, 65(1), 107–11. <https://doi.org/10.1016/j.bandc.2006.05.006>
- Kingdom, F., & Prins, N. (2010). *Psychophysics: A Practical Introduction* (1st ed.). London: Elsevier.
- Kirkham, N. Z., Slemmer, J. A., & Johnson, S. P. (2002). Visual statistical learning in infancy: evidence for a domain general learning mechanism. *Cognition*, 83(2), B35-42. [http://dx.doi.org/10.1016/S0010-0277\(02\)00004-5](http://dx.doi.org/10.1016/S0010-0277(02)00004-5)

- Klein, A. M., Zwickel, J., Prinz, W., & Frith, U. (2009). Animated triangles: an eye tracking investigation. *The Quarterly Journal of Experimental Psychology*, 62(6), 1189–97. <https://doi.org/10.1080/17470210802384214>
- Kleinsmith, A., De Silva, P. R., & Bianchi-Berthouze, N. (2006). Cross-cultural differences in recognizing affect from body posture. *Interacting with Computers*, 18(6), 1371–89. <https://doi.org/10.1016/j.intcom.2006.04.003>
- Klin, A., Jones, W., Schultz, R., & Volkmar, F. (2003). The enactive mind, or from actions to cognition: lessons from autism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 358(1430), 345–60. <https://doi.org/10.1098/rstb.2002.1202>
- Klin, A. (2000). Attributing social meaning to ambiguous visual stimuli in higher-functioning autism and Asperger Syndrome: the social attribution task. *Journal of Child Psychology and Psychiatry*, 41(7), 831–46. <https://doi.org/10.1111/1469-7610.00671>
- Klin, A, Lin, D. J., Gorrindo, P., Ramsay, G., & Jones, W. (2009). Two-year-olds with autism orient to non-social contingencies rather than biological motion. *Nature*, 459(7244), 257–61. <https://doi.org/10.1038/nature07868>
- Knoblich, G., & Prinz, W. (2001). Recognition of self-generated actions from kinematic displays of drawing. *Journal of Experimental Psychology: Human Perception and Performance*, 27(2), 456–65. <https://doi.org/10.1037//0096-1523.27.2.456>
- Kolb, B., Wilson, B., & Taylor, L. (1992). Developmental changes in the recognition and comprehension of facial expression: Implications for frontal lobe function.

Brain and Cognition, 20(1), 74–84. [https://doi.org/10.1016/0278-2626\(92\)90062-Q](https://doi.org/10.1016/0278-2626(92)90062-Q)

Koldewyn, K., Whitney, D., & Rivera, S. M. (2010). The psychophysics of visual motion and global form processing in autism. *Brain*, 133(2), 599–610. <https://doi.org/10.1093/brain/awp272>

Koldewyn, K., Whitney, D., & Rivera, S. M. (2011). Neural correlates of coherent and biological motion perception in autism. *Developmental Science*, 14(5), 1075–1088. <https://doi.org/10.1111/j.1467-7687.2011.01058.x>

Kozlowski, L. T., & Cutting, J. E. (1977). Recognizing the sex of a walker from a dynamic point-light display. *Perception & Psychophysics*, 21(6), 575–80. <https://doi.org/10.3758/BF03198740>

Krishnan-Barman, S., Forbes, P. A. G., & Hamilton, A. F. de C. (2017). How can the study of action kinematics inform our understanding of human social interaction? *Neuropsychologia*, S0028-3932(17), 30024-6. <https://doi.org/10.1016/j.neuropsychologia.2017.01.018>

Krumhuber, E., & Kappas, A. (2005). Moving smiles: the role of dynamic components for the perception of the genuineness of smiles. *Journal of Nonverbal Behaviour*, 29(1), 3–24. <https://doi.org/10.1007/s10919-004-0887-x>

Krumhuber, E., Manstead, A. S. R., Cosker, D., Marshall, D., Rosin, P. L., & Kappas, A. (2007). Facial dynamics as indicators of trustworthiness and cooperative behaviour. *Emotion*, 7(4), 730–5. <https://doi.org/10.1037/1528-3542.7.4.730>

- Landa, R., & Garrett-Mayer, E. (2006). Development in infants with autism spectrum disorders: a prospective study. *Journal of Child Psychology and Psychiatry*, 47(6), 629–38. <https://doi.org/10.1111/j.1469-7610.2006.01531.x>
- Largo, R. H., Caffisch, J. A., Hug, F., Muggli, K., Molnar, A. A., Molinari, L., ... & Gasser, T. (2001). Neuromotor development from 5 to 18 years. Part 1: timed performance. *Developmental Medicine & Child Neurology*, 43(7), 436–43. <https://doi.org/10.1111/j.1469-8749.2001.tb00739.x>
- Laursen, B., Coy, K. C., & Collins, W. A. (1998). Reconsidering changes in parent-child conflict across adolescence: a meta-analysis. *Child Development*, 69(3), 817–32. <https://doi.org/10.1111/j.1467-8624.1998.tb06245.x>
- Lawson, R. P., Rees, G., & Friston, K. J. (2014). An aberrant precision account of autism. *Frontiers in Human Neuroscience*, 8, 302. <https://doi.org/10.3389/fnhum.2014.00302>
- Leonard, H. C., Elsabbagh, M., Hill, E. L., & the BASIS team. (2014). Early and persistent motor difficulties in infants at-risk of developing autism spectrum disorder: a prospective study. *European Journal of Developmental Psychology*, 11(1), 18–35. <https://doi.org/10.1080/17405629.2013.801626>
- Lewkowicz, D., Quesque, F., Coello, Y., & Delevoye-Turrell, Y. N. (2015). Individual differences in reading social intentions from motor deviants. *Frontiers in Psychology*, 6, 1175. <https://doi.org/10.3389/fpsyg.2015.01175>
- Liew, S.-L., Han, S., & Aziz-Zadeh, L. (2011). Familiarity modulates mirror neuron and mentalizing regions during intention understanding. *Human Brain Mapping*, 32(11), 1986–97. <https://doi.org/10.1002/hbm.21164>

- Livingston, L. A., & Happé, F. (2017). Conceptualising compensation in neurodevelopmental disorders: reflections from autism spectrum disorder. *Neuroscience and Biobehavioural Reviews*, *80*, 729-42.
<https://doi.org/10.1016/j.neubiorev.2017.06.005>
- Lloyd-Fox, S., Wu, R., Richards, J. E., Elwell, C. E., & Johnson, M. H. (2015). Cortical activation to action perception is associated with action production abilities in young infants. *Cerebral Cortex*, *25*(2), 289–97.
<https://doi.org/10.1093/cercor/bht207>
- Lombardo, M. V., Lai, M.-C., Auyeung, B., Holt, R. J., Allison, C., Smith, P., ... & Baron-Cohen, S. (2016). Unsupervised data-driven stratification of mentalizing heterogeneity in autism. *Scientific Reports*, *6*, 35333.
<https://doi.org/10.1038/srep35333>
- Lord, C., Rutter, M., DiLavore, P., Risi, S., Gotham, K., & Bishop, S. (2012). *Autism Diagnostic Observation Schedule: ADOS-2* (2nd ed.). Torrance, CA: Western Psychological Services.
- Loula, F., Prasad, S., Harber, K., & Shiffrar, M. (2005). Recognizing people from their movement. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(1), 210–20. <https://doi.org/10.1037/0096-1523.31.1.210>
- Macdonald, H., Rutter, M., Howlin, P., Rios, P., Conteur, A. L., Evered, C., & Folstein, S. (1989). Recognition and expression of emotional cues by autistic and normal adults. *Journal of Child Psychology and Psychiatry*, *30*(6), 865-77.
<https://doi.org/10.1111/j.1469-7610.1989.tb00288.x>

- Macerollo, A., Bose, S., Ricciardi, L., Edwards, M. J., & Kilner, J. M. (2015). Linking differences in action perception with differences in action execution. *Social Cognitive and Affective Neuroscience*, *10*(8), 1121-27.
<https://doi.org/10.1093/scan/nsu161>
- Maister, L., & Plaisted-Grant, K. C. (2011). Time perception and its relationship to memory in autism spectrum conditions: time perception in ASC. *Developmental Science*, *14*(6), 1311–22. <https://doi.org/10.1111/j.1467-7687.2011.01077.x>
- Manera, V., Schouten, B., Verfaillie, K., & Becchio, C. (2013). Time will show: real time predictions during interpersonal action perception. *PLoS ONE*, *8*(1), e54949. <https://doi.org/10.1371/journal.pone.0054949>
- Mangels, J. A., Ivry, R. B., & Shimizu, N. (1998). Dissociable contributions of the prefrontal and neocerebellar cortex to time perception. *Cognitive Brain Research*, *7*(1), 15–39. [https://doi.org/10.1016/S0926-6410\(98\)00005-6](https://doi.org/10.1016/S0926-6410(98)00005-6)
- Manjiviona, J., & Prior, M. (1995). Comparison of Asperger Syndrome and high-functioning autistic children on a test of motor impairment. *Journal of Autism and Developmental Disorders*, *25*(1), 23–39.
<https://doi.org/10.1007/BF02178165>
- Mari, M., Castiello, U., Marks, D., Marraffa, C., & Prior, M. (2003). The reach-to-grasp movement in children with autism spectrum disorder. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *358*(1430), 393–403.
<https://doi.org/10.1098/rstb.2002.1205>
- Martin, J. S., Poirier, M., & Bowler, D. M. (2010). Brief report: impaired temporal reproduction performance in adults with autism spectrum disorder. *Journal of*

Autism and Developmental Disorders, 40(5), 640–6.

<https://doi.org/10.1007/s10803-009-0904-3>

Martineau, J., Schmitz, C., Assaiante, C., Blanc, R., & Barthélémy, C. (2004).

Impairment of a cortical event-related desynchronisation during a bimanual load-lifting task in children with autistic disorder. *Neuroscience Letters*, 367(3), 298–303. <https://doi.org/10.1016/j.neulet.2004.06.018>

Matsumoto, D., Hee Yoo, S., & Fontaine, J. (2008). Mapping expressive differences

around the world: the relationship between emotional display rules and individualism versus collectivism. *Journal of Cross-Cultural Psychology*, 39(1), 55–74. <https://doi.org/10.1177/0022022107311854>

Maurer, R. G., & Damasio, A. R. (1982). Childhood autism from the point of view of

behavioural neurology. *Journal of Autism and Developmental Disorders*, 12(2), 195–205. <https://doi.org/10.1007/BF01531309>

Maxwell, S. E., Kelley, K., & Rausch, J. R. (2008). Sample size planning for statistical

power and accuracy in parameter estimation. *Annual Review of Psychology*, 59(1), 537–63. <https://doi.org/10.1146/annurev.psych.59.103006.093735>

Mayer, J. D., Gaschke, Y. N., Braverman, D. L., & Evans, T. W. (1992). Mood-

congruent judgment is a general effect. *Journal of Personality and Social Psychology*, 63(1), 119–32. <https://doi.org/10.1037/0022-3514.63.1.119>

McAuley, J. D., Jones, M. R., Holub, S., Johnston, H. M., & Miller, N. S. (2006). The

time of our lives: life span development of timing and event tracking. *Journal of Experimental Psychology: General*, 135(3), 348–67.

<https://doi.org/10.1037/0096-3445.135.3.348>

- McGivern, R. F., Andersen, J., Byrd, D., Mutter, K. L., & Reilly, J. (2002). Cognitive efficiency on a match to sample task decreases at the onset of puberty in children. *Brain and Cognition*, 50(1), 73–89. [https://doi.org/10.1016/S0278-2626\(02\)00012-X](https://doi.org/10.1016/S0278-2626(02)00012-X)
- McKay, L. S., Simmons, D. R., McAleer, P., Marjoram, D., Piggot, J., & Pollick, F. E. (2012). Do distinct atypical cortical networks process biological motion information in adults with autism spectrum disorders? *NeuroImage*, 59(2), 1524–33. <https://doi.org/10.1016/j.neuroimage.2011.08.033>
- Meck, W. H. (2005). Neuropsychology of timing and time perception. *Brain and Cognition*, 58(1), 1–8. <https://doi.org/10.1016/j.bandc.2004.09.004>
- Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Structure and Function*, 214(5–6), 655–67. <https://doi.org/10.1007/s00429-010-0262-0>
- Merikangas, K. R., He, J., Burstein, M., Swanson, S. A., Avenevoli, S., Cui, L., ... & Swendsen, J. (2010). Lifetime prevalence of mental disorders in U.S. adolescents: results from the national comorbidity survey replication -adolescent supplement (NCS-A). *Journal of the American Academy of Child & Adolescent Psychiatry*, 49(10), 980–9. <https://doi.org/10.1016/j.jaac.2010.05.017>
- Meyer, S., Raikes, H. A., Virmani, E. A., Waters, S., & Thompson, R. A. (2014). Parent emotion representations and the socialization of emotion regulation in the family. *International Journal of Behavioural Development*, 38(2), 164–73. <https://doi.org/10.1177/0165025413519014>

- Michalak, J., Troje, N. F., Fischer, J., Vollmar, P., Heidenreich, T., & Schulte, D. (2009). Embodiment of sadness and depression—gait patterns associated with Dysphoric Mood: *Psychosomatic Medicine*, *71*(5), 580–7. <https://doi.org/10.1097/PSY.0b013e3181a2515c>
- Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. *Journal of Experimental Psychology: General*, *122*(1), 23–38. <https://doi.org/10.1037/0096-3445.122.1.23>
- Moessnang, C., Otto, K., Bilek, E., Schäfer, A., Baumeister, S., Hohmann, S., ... & Meyer-Lindenberg, A. (2017). Differential responses of the dorsomedial prefrontal cortex and right posterior superior temporal sulcus to spontaneous mentalizing: dmPFC and pSTS responses during mentalizing. *Human Brain Mapping*, *38*(8), 3791–803. <https://doi.org/10.1002/hbm.23626>
- Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neuroscience and Biobehavioural Reviews*, *36*(1), 341–9. <https://doi.org/10.1016/j.neubiorev.2011.07.004>
- Montepare, J. M., Goldstein, S. B., & Clausen, A. (1987). The identification of emotions from gait information. *Journal of Nonverbal Behaviour*, *11*(1), 33–42. <https://doi.org/10.1007/BF00999605>
- Moore, D. G., Hobson, R. P., & Lee, A. (1997). Components of person perception: an investigation with autistic, non-autistic retarded and typically developing children and adolescents. *British Journal of Developmental Psychology*, *15*(4), 401–23. <https://doi.org/10.1111/j.2044-835X.1997.tb00738.x>

- Moore, W. E., Pfeifer, J. H., Masten, C. L., Mazziotta, J. C., Iacoboni, M., & Dapretto, M. (2012). Facing puberty: associations between pubertal development and neural responses to affective facial displays. *Social Cognitive and Affective Neuroscience*, 7(1), 35–43. <https://doi.org/10.1093/scan/nsr066>
- Mostofsky, S. H., Powell, S. K., Simmonds, D. J., Goldberg, M. C., Caffo, B., & Pekar, J. J. (2009). Decreased connectivity and cerebellar activity in autism during motor task performance. *Brain*, 132(9), 2413–25. <https://doi.org/10.1093/brain/awp088>
- Mostofsky, Stewart H., Goldberg, M. C., Landa, R. J., & Denckla, M. B. (2000). Evidence for a deficit in procedural learning in children and adolescents with autism: implications for cerebellar contribution. *Journal of the International Neuropsychological Society*, 6(7), 752–759. <https://doi.org/10.1017/S1355617700677020>
- Mullen, E. M. (1995). Mullen Scales of Early Learning. Oxford: NCS Pearson
- Mulligan, S., & White, B. P. (2012). Sensory and motor Behaviours of infant siblings of children with and without autism. *American Journal of Occupational Therapy*, 66(5), 556–66. <https://doi.org/10.5014/ajot.2012.004077>
- Murphy, P., Brady, N., Fitzgerald, M., & Troje, N. F. (2009). No evidence for impaired perception of biological motion in adults with autistic spectrum disorders. *Neuropsychologia*, 47(14), 3225–35. <https://doi.org/10.1016/j.neuropsychologia.2009.07.026>
- Nackaerts, E., Wagemans, J., Helsen, W., Swinnen, S. P., Wenderoth, N., & Alaerts, K. (2012). Recognizing biological motion and emotions from point-light displays in

autism spectrum disorders. *PLoS ONE*, 7(9), e44473.

<https://doi.org/10.1371/journal.pone.0044473>

Nebel, M. B., Eloyan, A., Nettles, C. A., Sweeney, K. L., Ament, K., Ward, R. E., ... & Mostofsky, S. H. (2016). Intrinsic visual-motor synchrony correlates with social deficits in autism. *Biological Psychiatry*, 79(8), 633–41.

<https://doi.org/10.1016/j.biopsych.2015.08.029>

Neri, P., Luu, J. Y., & Levi, D. M. (2006). Meaningful interactions can enhance visual discrimination of human agents. *Nature Neuroscience*, 9(9), 1186–92.

<https://doi.org/10.1038/nn1759>

Nijmeijer, J. S., Minderaa, R. B., Buitelaar, J. K., Mulligan, A., Hartman, C. A., & Hoekstra, P. J. (2008). Attention-deficit /hyperactivity disorder and social dysfunctioning. *Clinical Psychology Review*, 28(4), 692–708.

<https://doi.org/10.1016/j.cpr.2007.10.003>

Oberg, T., Karsznia, A., & Oberg, K. (1993). Basic gait parameters: reference data for normal subjects, 10-79 years of age. *Journal of Rehabilitation Research and Development*, 30(2), 210–23.

Olsson, A., & Phelps, E. A. (2007). Social learning of fear. *Nature Neuroscience*, 10(9), 1095–102. <https://doi.org/10.1038/nn1968>

Ormel, J., Raven, D., van Oort, F., Hartman, C. A., Reijneveld, S. A., Veenstra, R., ... & Oldehinkel, A. J. (2015). Mental health in Dutch adolescents: a TRAILS report on prevalence, severity, age of onset, continuity and co-morbidity of DSM disorders. *Psychological Medicine*, 45(02), 345–60.

<https://doi.org/10.1017/S0033291714001469>

- Ostry, D. J., Cooke, J. D., & Munhall, K. G. (1987). Velocity curves of human arm and speech movements. *Experimental Brain Research*, 68(1), 37-46.
<https://doi.org/10.1007/BF00255232>
- Ozonoff, S., Young, G. S., Carter, A., Messinger, D., Yirmiya, N., Zwaigenbaum, L., ... & Stone, W. L. (2011). Recurrence Risk for Autism Spectrum Disorders: A Baby Siblings Research Consortium Study. *Paediatrics*, 128(3), e1-e8.
<https://doi.org/10.1542/peds.2010-2825>
- Ozonoff, S., Iosif, A.-M., Baguio, F., Cook, I. C., Hill, M. M., Hutman, T., ... & Young, G. S. (2010). A prospective study of the emergence of early behavioural signs of autism. *Journal of the American Academy of Child and Adolescent Psychiatry*, 49(3), 256–66. <https://doi.org/10.1016/j.jaac.2009.11.009>
- Parron, C., Da Fonseca, D., Santos, A., Moore, D., Monfardini, E., & Deruelle, C. (2008). Recognition of biological motion in children with autistic spectrum disorders. *Autism*, 12(3), 261–74. <https://doi.org/10.1177/1362361307089520>
- Patel, D., Fleming, S. M., & Kilner, J. M. (2012). Inferring subjective states through the observation of actions. *Proceedings of the Royal Society B: Biological Sciences*, 279(1748), 4853–60. <https://doi.org/10.1098/rspb.2012.1847>
- Paterson, H. M., Pollick, F. E., & Sanford, A. J. (2001). The role of velocity in affect discrimination. *Proceedings of the Annual Meeting of the Cognitive Science Society*, 23.
- Paulus, M., Hunnius, S., & Bekkering, H. (2013). Neurocognitive mechanisms underlying social learning in infancy: infants' neural processing of the effects of

others' actions. *Social Cognitive and Affective Neuroscience*, 8(7), 774–9.

<https://doi.org/10.1093/scan/nss065>

Paulus, M., Hunnius, S., van Elk, M., & Bekkering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: electrophysiological evidence for action-effect binding in infancy.

Developmental Cognitive Neuroscience, 2(1), 90–6.

<https://doi.org/10.1016/j.dcn.2011.05.006>

Paus, T. (2005). Mapping brain maturation and cognitive development during adolescence. *Trends in Cognitive Sciences*, 9(2), 60–8.

<https://doi.org/10.1016/j.tics.2004.12.008>

Pavlova, M. A. (2012). Biological motion processing as a hallmark of social cognition.

Cerebral Cortex, 22(5), 981–95. <https://doi.org/10.1093/cercor/bhr156>

Pellicano, E., & Burr, D. (2012). When the world becomes 'too real': a Bayesian explanation of autistic perception. *Trends in Cognitive Sciences*, 16(10), 504–

10. <https://doi.org/10.1016/j.tics.2012.08.009>

Perin, R., Berger, T. K., & Markram, H. (2011). A synaptic organizing principle for cortical neuronal groups. *Proceedings of the National Academy of Sciences*,

108(13), 5419–24. <https://doi.org/10.1073/pnas.1016051108>

Peters, J. C., Vlamings, P., & Kemner, C. (2013). Neural processing of high and low spatial frequency information in faces changes across development: qualitative changes in face processing during adolescence. *European Journal of*

Neuroscience, 37(9), 1448–57. <https://doi.org/10.1111/ejn.12172>

- Pfeifer, J. H., Masten, C. L., Moore, W. E., Oswald, T. M., Mazziotta, J. C., Iacoboni, M., & Dapretto, M. (2011). Entering adolescence: resistance to peer influence, risky behaviour, and neural changes in emotion reactivity. *Neuron*, *69*(5), 1029–36. <https://doi.org/10.1016/j.neuron.2011.02.019>
- Pollak, S. D., & Kistler, D. J. (2002). Early experience is associated with the development of categorical representations for facial expressions of emotion. *Proceedings of the National Academy of Sciences*, *99*(13), 9072–6. <https://doi.org/10.1073/pnas.142165999>
- Pollak, S. D., Messner, M., Kistler, D. J., & Cohn, J. F. (2009). Development of perceptual expertise in emotion recognition. *Cognition*, *110*(2), 242–7. <https://doi.org/10.1016/j.cognition.2008.10.010>
- Pollick, F. E., Paterson, H. M., Bruderlin, A., & Sanford, A. J. (2001). Perceiving affect from arm movement. *Cognition*, *82*(2), B51–61. [https://doi.org/10.1016/S0010-0277\(01\)00147-0](https://doi.org/10.1016/S0010-0277(01)00147-0)
- Press, C. M., & Kilner, J. M. (2013). The time course of eye movements during action observation reflects sequence learning: *NeuroReport*, *24*(14), 822–6. <https://doi.org/10.1097/WNR.0b013e328364d5fd>
- Quatman-Yates, C. C., Quatman, C. E., Meszaros, A. J., Paterno, M. V., & Hewett, T. E. (2012). A systematic review of sensorimotor function during adolescence: a developmental stage of increased motor awkwardness? *British Journal of Sports Medicine*, *46*(9), 649–55. <https://doi.org/10.1136/bjism.2010.079616>

- Quesque, F., Lewkowicz, D., Delevoeye-Turrell, Y. N., & Coello, Y. (2013). Effects of social intention on movement kinematics in cooperative actions. *Frontiers in Neurobotics*, 7, 14. <https://doi.org/10.3389/fnbot.2013.00014>
- Quiros-Ramirez, M. A., & Onisawa, T. (2015). Considering cross-cultural context in the automatic recognition of emotions. *International Journal of Machine Learning and Cybernetics*, 6(1), 119–27. <https://doi.org/10.1007/s13042-013-0192-2>
- Ray, E., & Heyes, C. (2011). Imitation in infancy: the wealth of the stimulus: Imitation in infancy. *Developmental Science*, 14(1), 92–105. <https://doi.org/10.1111/j.1467-7687.2010.00961.x>
- Redcay, E. (2008). The superior temporal sulcus performs a common function for social and speech perception: Implications for the emergence of autism. *Neuroscience & Biobehavioural Reviews*, 32(1), 123–42. <https://doi.org/10.1016/j.neubiorev.2007.06.004>
- Repp, B., Liberman, A., Eccardt, T., & Pesetsky, D. (1978). Perceptual integration of acoustic cues for stop, fricative, and affricate manner. *Journal of Experimental Psychology: Human Perception and Performance*, 4(4), 621–37. <http://dx.doi.org/10.1037/0096-1523.4.4.621>
- Rhodes, M. G., & Anastasi, J. S. (2012). The own-age bias in face recognition: a meta-analytic and theoretical review. *Psychological Bulletin*, 138(1), 146–74. <https://doi.org/10.1037/a0025750>
- Rinehart, N. J., Bradshaw, J. L., Brereton, A. V., & Tonge, B. J. (2001). Movement preparation in high-functioning autism and Asperger Disorder: a serial choice

reaction time task involving motor reprogramming. *Journal of Autism and Developmental Disorders*, 31(1), 79–88.

Rinehart, N. J., Tonge, B. J., Iannsek, R., McGinley, J., Brereton, A. V., Enticott, P. G., & Bradshaw, J. L. (2006). Gait function in newly diagnosed children with autism: cerebellar and basal ganglia related motor disorder. *Developmental Medicine and Child Neurology*, 48(10), 819-24.

<https://doi.org/10.1017/S0012162206001769>

Rizzolatti, G., & Craighero, L. (2004). The mirror neuron system. *Annual Review of Neuroscience*, 27(1), 169–92.

<https://doi.org/10.1146/annurev.neuro.27.070203.144230>

Rochat, P. (1998). Self-perception and action in infancy. *Experimental Brain Research*, 123(1–2), 102–9. <https://doi.org/10.1007/s002210050550>

Roether, C. L., Omlor, L., Christensen, A., & Giese, M. A. (2009a). Critical features for the perception of emotion from gait. *Journal of Vision*, 9(6), 15.

<https://doi.org/10.1167/9.6.15>

Roether, C. L., Omlor, L., & Giese, M. A. (2009b). Features in the recognition of emotions from dynamic bodily expression. In U. J. Ilg & G. S. Masson (Eds.), *Dynamics of Visual Motion Processing* (313–40). Boston, MA: Springer US.

http://link.springer.com/10.1007/978-1-4419-0781-3_14

Rogers, T. D., McKimm, E., Dickson, P. E., Goldowitz, D., Blaha, C. D., & Mittleman, G. (2013). Is autism a disease of the cerebellum? An integration of clinical and pre-clinical research. *Frontiers in Systems Neuroscience*, 7, 15.

<https://doi.org/10.3389/fnsys.2013.00015>

- Rogol, A. D., Clark, P. A., & Roemmich, J. N. (2000). Growth and pubertal development in children and adolescents: effects of diet and physical activity. *The American Journal of Clinical Nutrition*, 72(2 Suppl), 521S–8S.
- Rönnqvist, L., & Domellöf, E. (2006). Quantitative assessment of right and left reaching movements in infants: A longitudinal study from 6 to 36 months. *Developmental Psychobiology*, 48(6), 444–59.
<https://doi.org/10.1002/dev.20160>
- Rosenbaum, D. A. (1975). Perception and extrapolation of velocity and acceleration. *Journal of Experimental Psychology: Human Perception and Performance*, 1(4), 395–403. <https://doi.org/10.1037//0096-1523.1.4.395>
- Ross, P. D. (2014). Body form and body motion processing are dissociable in the visual pathways. *Frontiers in Psychology*, 5, 767.
<https://doi.org/10.3389/fpsyg.2014.00767>
- Ross, P. D., Polson, L., & Grosbras, M.-H. (2012). Developmental changes in emotion recognition from full-light and point-light displays of body movement. *PLoS ONE*, 7(9), e44815. <https://doi.org/10.1371/journal.pone.0044815>
- Rotman, G., Troje, N. F., Johansson, R. S., & Flannagan, R. (2006). Eye movements when observing predictable and unpredictable Actions. *Journal of Neurophysiology*, 96(3), 1358–69. <https://doi.org/10.1152/jn.00227.2006>
- Rueckriegel, S. M., Blankenburg, F., Burghardt, R., Ehrlich, S., Henze, G., Mergl, R., & Hernáiz Driever, P. (2008). Influence of age and movement complexity on kinematic hand movement parameters in childhood and adolescence.

International Journal of Developmental Neuroscience, 26(7), 655–63.

<https://doi.org/10.1016/j.ijdevneu.2008.07.015>

Runeson, S., & Frykholm, G. (1981). Visual perception of lifted weight. *Journal of Experimental Psychology. Human Perception and Performance*, 7(4), 733–40.

<http://dx.doi.org/10.1037/0096-1523.7.4.733>

Rutherford, M. D., & Troje, N. F. (2011). IQ predicts biological motion perception in autism spectrum disorders. *Journal of Autism and Developmental Disorders*,

42(4), 557–65. <https://doi.org/10.1007/s10803-011-1267-0>

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, 274(5294), 1926–28.

<http://dx.doi.org/10.1126/science.274.5294.1926>

Sanders, W., Zeman, J., Poon, J., & Miller, R. (2015). Child regulation of negative emotions and depressive symptoms: the moderating role of parental emotion socialization. *Journal of Child and Family Studies*, 24(2), 402–15.

<https://doi.org/10.1007/s10826-013-9850-y>

Sangrigoli, S., Pallier, C., Argenti, A. M., Ventureyra, V. A. G., & De Schonen, S.

(2005). Reversibility of the other-race effect in face recognition during

childhood. *Psychological Science*, 16(6), 440–4. [https://doi.org/10.1111/j.0956-](https://doi.org/10.1111/j.0956-7976.2005.01554.x)

[7976.2005.01554.x](https://doi.org/10.1111/j.0956-7976.2005.01554.x)

Sartori, L., Becchio, C., Bara, B. G., & Castiello, U. (2009). Does the intention to

communicate affect action kinematics? *Consciousness and Cognition*, 18(3),

766–72. <https://doi.org/10.1016/j.concog.2009.06.004>

- Sartori, L., Cavallo, A., Bucchioni, G., & Castiello, U. (2012). From simulation to reciprocity: The case of complementary actions. *Social Neuroscience*, 7(2), 146–58. <https://doi.org/10.1080/17470919.2011.586579>
- Sauter, D. A., Eisner, F., Ekman, P., & Scott, S. K. (2010). Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. *Proceedings of the National Academy of Sciences*, 107(6), 2408–12. <https://doi.org/10.1073/pnas.0908239106>
- Saygin, A. P., Cook, J. L., & Blakemore, S.-J. (2010). Unaffected perceptual thresholds for biological and non-biological form-from-motion perception in autism spectrum conditions. *PLoS ONE*, 5(10), e13491. <https://doi.org/10.1371/journal.pone.0013491>
- Scherer, K. R. (1995). Expression of emotion in voice and music. *Journal of Voice*, 9(3), 235–48. [https://doi.org/10.1016/S0892-1997\(05\)80231-0](https://doi.org/10.1016/S0892-1997(05)80231-0)
- Schmitt, L. M., Cook, E. H., Sweeney, J. A., & Mosconi, M. W. (2014). Saccadic eye movement abnormalities in autism spectrum disorder indicate dysfunctions in cerebellum and brainstem. *Molecular Autism*, 5(1), 47. <https://doi.org/10.1186/2040-2392-5-47>
- Schneiberg, S., Sveistrup, H., McFadyen, B., McKinley, P., & Levin, M. F. (2002). The development of coordination for reach-to-grasp movements in children. *Experimental Brain Research*, 146(2), 142–54. <https://doi.org/10.1007/s00221-002-1156-z>

- Schubotz, R. I., Friederici, A. D., & Yves von Cramon, D. (2000). Time Perception and motor timing: a common cortical and subcortical basis revealed by fMRI. *NeuroImage*, *11*(1), 1–12. <https://doi.org/10.1006/nimg.1999.0514>
- Scott, L. S., Pascalis, O., & Nelson, C. A. (2007). A domain-general theory of the development of perceptual discrimination. *Current Directions in Psychological Science*, *16*(4), 197–201. <https://doi.org/10.1111/j.1467-8721.2007.00503.x>
- Sebanz, N., & Shiffrar, M. (2009). Detecting deception in a bluffing body: the role of expertise. *Psychonomic Bulletin & Review*, *16*(1), 170–5. <https://doi.org/10.3758/PBR.16.1.170>
- Sepulcre, J. (2014). Integration of visual and motor functional streams in the human brain. *Neuroscience Letters*, *567*, 68–73. <https://doi.org/10.1016/j.neulet.2014.03.050>
- Shepherd, S. V. (2010). Following gaze: gaze-following behaviour as a window into social cognition. *Frontiers in Integrative Neuroscience*, *4*, 5. <https://doi.org/10.3389/fnint.2010.00005>
- Sheppard, E., Pillai, D., Wong, G. T.-L., Ropar, D., & Mitchell, P. (2016). How easy is it to read the minds of people with autism spectrum disorder? *Journal of Autism and Developmental Disorders*, *46*(4), 1247–54. <https://doi.org/10.1007/s10803-015-2662-8>
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences*, *105*(2), 809–13. <https://doi.org/10.1073/pnas.0707021105>

- Simonoff, E., Jones, C. R. G., Pickles, A., Happé, F., Baird, G., & Charman, T. (2012). Severe mood problems in adolescents with autism spectrum disorder: Mood problems in autism. *Journal of Child Psychology and Psychiatry*, 53(11), 1157–66. <https://doi.org/10.1111/j.1469-7610.2012.02600.x>
- Sinclair, J. (2013). Why I dislike ‘person first’ language. *Critical Journal of Interdisciplinary Autism Studies*, 1.2, 1–2.
- Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants’ perception of others’ actions. *Cognition*, 96(1), B1–11. <https://doi.org/10.1016/j.cognition.2004.07.004>
- Spear, L. P. (2000). The adolescent brain and age-related behavioural manifestations. *Neuroscience & Biobehavioural Reviews*, 24(4), 417–63. [https://doi.org/10.1016/S0149-7634\(00\)00014-2](https://doi.org/10.1016/S0149-7634(00)00014-2)
- Sparrow, S. S., Cicchetti, D. V., & Balla, D. A. (2005). *Vineland Adaptive Behaviour Scales* (2nd ed). Oxford: NCS Pearson.
- Stadler, W., Springer, A., Parkinson, J., & Prinz, W. (2012). Movement kinematics affect action prediction: comparing human to non-human point-light actions. *Psychological Research*, 76(4), 395–406. <https://doi.org/10.1007/s00426-012-0431-2>
- Stapel, J. C., Hunnius, S., Meyer, M., & Bekkering, H. (2016). Motor system contribution to action prediction: Temporal accuracy depends on motor experience. *Cognition*, 148, 71–8. <https://doi.org/10.1016/j.cognition.2015.12.007>

- Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences*, 9(2), 69–74. <https://doi.org/10.1016/j.tics.2004.12.005>
- Susskind, J. M., Lee, D. H., Cusi, A., Feiman, R., Grabski, W., & Anderson, A. K. (2008). Expressing fear enhances sensory acquisition. *Nature Neuroscience*, 11(7), 843–50. <https://doi.org/10.1038/nn.2138>
- Sutera, S., Pandey, J., Esser, E. L., Rosenthal, M. A., Wilson, L. B., Barton, M., ... & Fein, D. (2007). Predictors of optimal outcome in toddlers diagnosed with autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 37(1), 98–107. <https://doi.org/10.1007/s10803-006-0340-6>
- Sutherland, D. (1997). The development of mature gait. *Gait & Posture*, 6(2), 163–70. [https://doi.org/10.1016/S0966-6362\(97\)00029-5](https://doi.org/10.1016/S0966-6362(97)00029-5)
- Szelag, E., Kowalska, J., Galkowski, T., & Pöppel, E. (2004). Temporal processing deficits in high-functioning children with autism. *British Journal of Psychology*, 95(3), 269–82. <https://doi.org/10.1348/0007126041528167>
- Takarae, Y. (2004). Pursuit eye movement deficits in autism. *Brain*, 127(12), 2584–94. <https://doi.org/10.1093/brain/awh307>
- Tanner, J. M., Whitehouse, R. H., & Takaishi, M. (1966). Standards from birth to maturity for height, weight, height velocity, and weight velocity: British children, 1965. II. *Archives of Disease in Childhood*, 41(220), 613–5. <https://doi.org/10.1136/adc.41.220.613>
- Tasko, S. M., & Westbury, J. R. (2004). Speed–curvature relations for speech-related articulatory movement. *Journal of Phonetics*, 32(1), 65–80. [https://doi.org/10.1016/S0095-4470\(03\)00006-8](https://doi.org/10.1016/S0095-4470(03)00006-8)

- Taylor, S. J., Barker, L. A., Heavey, L., & McHale, S. (2013). The typical developmental trajectory of social and executive functions in late adolescence and early adulthood. *Developmental Psychology*, *49*(7), 1253–65. <https://doi.org/10.1037/a0029871>
- Teitelbaum, P., Teitelbaum, O., Nye, J., Fryman, J., & Maurer, R. G. (1998). Movement analysis in infancy may be useful for early diagnosis of autism. *Proceedings of the National Academy of Sciences*, *95*(23), 13982–7. <https://doi.org/10.1073/pnas.95.23.13982>
- Tervo, R. C., Azuma, S., Fogas, B., & Fiechtner, H. (2007). Children with ADHD and motor dysfunction compared with children with ADHD only. *Developmental Medicine and Child Neurology*, *44*(6), 383–90. <https://doi.org/10.1111/j.1469-8749.2002.tb00832.x>
- Thomas, L. A., De Bellis, M. D., Graham, R., & LaBar, K. S. (2007). Development of emotional facial recognition in late childhood and adolescence. *Developmental Science*, *10*(5), 547–58. <https://doi.org/10.1111/j.1467-7687.2007.00614.x>
- Thornton, I. M., Rensink, R. A., & Shiffrar, M. (2002). Active versus passive processing of biological motion. *Perception*, *31*(7), 837–53. <https://doi.org/10.1068/p3072>
- Tidoni, E., Borgomaneri, S., di Pellegrino, G., & Avenanti, A. (2013). Action simulation plays a critical role in deceptive action recognition. *Journal of Neuroscience*, *33*(2), 611–23. <https://doi.org/10.1523/JNEUROSCI.2228-11.2013>

- Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, 7(9), 907–15. <https://doi.org/10.1038/nn1309>
- Todorov, E., & Jordan, M. (1998). Smoothness maximization along a predefined path accurately predicts the speed profiles of complex arm movements. *Journal of Neurophysiology*, 80(2), 696–714.
- Tonks, J., Williams, W. H., Frampton, I., Yates, P., & Slater, A. (2007). Assessing emotion recognition in 9–15-years olds: preliminary analysis of abilities in reading emotion from faces, voices and eyes. *Brain Injury*, 21(6), 623–29. <https://doi.org/10.1080/02699050701426865>
- Torres, E. B., Brincker, M., Isenhower, R. W., Yanovich, P., Stigler, K. A., Nurnberger, J. I., ... & José, J. V. (2013). Autism: the micro-movement perspective. *Frontiers in Integrative Neuroscience*, 7, 32. <https://doi.org/10.3389/fnint.2013.00032>
- Tremoulet, P. D., & Feldman, J. (2000). Perception of animacy from the motion of a single object. *Perception*, 29(8), 943–51. <https://doi.org/10.1068/p3101>
- Trevarthen, C., & Delafield-Butt, J. T. (2013). Autism as a developmental disorder in intentional movement and affective engagement. *Frontiers in Integrative Neuroscience*, 7, 49. <https://doi.org/10.3389/fnint.2013.00049>
- Troje, N. F., Westhoff, C., & Lavrov, M. (2005). Person identification from biological motion: effects of structural and kinematic cues. *Perception & Psychophysics*, 67(4), 667–75. <https://doi.org/10.3758/BF03193523>
- Turner, R., & Felisberti, F. M. (2017). Measuring mindreading: a review of behavioural approaches to testing cognitive and affective mental state attribution in

neurologically typical adults. *Frontiers in Psychology*, 8, 47.

<https://doi.org/10.3389/fpsyg.2017.00047>

Urgesi, C., Calvo-Merino, B., Haggard, P., & Aglioti, S. M. (2007). Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *Journal of Neuroscience*, 27(30), 8023–30.

<https://doi.org/10.1523/JNEUROSCI.0789-07.2007>

Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences*, 98(20), 11656–61.

<https://doi.org/10.1073/pnas.191374198>

van Boxtel, J. J. A., & Lu, H. (2013). Impaired global, and compensatory local, biological motion processing in people with high levels of autistic traits. *Frontiers in Psychology*, 4, 209. <https://doi.org/10.3389/fpsyg.2013.00209>

Van den Stock, J., Righart, R., & de Gelder, B. (2007). Body expressions influence recognition of emotions in the face and voice. *Emotion*, 7(3), 487–94.

<https://doi.org/10.1037/1528-3542.7.3.487>

Van der Hallen, R., Evers, K., Brewaeys, K., Van den Noortgate, W., & Wagemans, J. (2015). Global processing takes time: a meta-analysis on local–global visual processing in ASD. *Psychological Bulletin*, 141(3), 549–73.

<https://doi.org/10.1037/bul0000004>

van Gog, T., Kester, L., Nieuwstein, F., Giesbers, B., & Paas, F. (2009). Uncovering cognitive processes: different techniques that can contribute to cognitive load

research and instruction. *Computers in Human Behaviour*, 25(2), 325–31.

<https://doi.org/10.1016/j.chb.2008.12.021>

van Kemenade, B. M., Muggleton, N., Walsh, V., & Saygin, A. P. (2012). Effects of TMS over premotor and superior temporal cortices on biological motion perception. *Journal of Cognitive Neuroscience*, 24(4), 896–904.

https://doi.org/10.1162/jocn_a_00194

Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *NeuroImage*, 48(3), 564–84.

<https://doi.org/10.1016/j.neuroimage.2009.06.009>

Villalobos, M. E., Mizuno, A., Dahl, B. C., Kemmotsu, N., & Miller, R.-A. (2005).

Reduced functional connectivity between V1 and inferior frontal cortex associated with visuomotor performance in autism. *NeuroImage*, 25(3), 916–25.

<https://doi.org/10.1016/j.neuroimage.2004.12.022>

Vink, M., Derks, J. M., Hoogendam, J. M., Hillegers, M., & Kahn, R. S. (2014).

Functional differences in emotion processing during adolescence and early adulthood. *NeuroImage*, 91, 70–6.

<https://doi.org/10.1016/j.neuroimage.2014.01.035>

Visser, J., Geuze, R. H., & Kalverboer, A. F. (1998). The relationship between physical growth, the level of activity and the development of motor skills in adolescence:

differences between children with DCD and controls. *Human Movement*

Science, 17(4–5), 573–608. [https://doi.org/10.1016/S0167-9457\(98\)00014-1](https://doi.org/10.1016/S0167-9457(98)00014-1)

Viviani, P., & Flash, T. (1995). Minimum-jerk, two-thirds power law, and isochrony:

converging approaches to movement planning. *Journal of Experimental*

Psychology. Human Perception and Performance, 21(1), 32–53.

<http://dx.doi.org/10.1037/0096-1523.21.1.32>

Viviani, P., & Schneider, R. (1991). A developmental study of the relationship between geometry and kinematics in drawing movements. *Journal of Experimental Psychology. Human Perception and Performance*, 17(1), 198–218.

<http://dx.doi.org/10.1037/0096-1523.17.1.198>

Viviani, Paolo, & Stucchi, N. (1992). Biological movements look uniform: evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*, 18(3), 603–23. [https://doi.org/10.1037/0096-](https://doi.org/10.1037/0096-1523.18.3.603)

[1523.18.3.603](https://doi.org/10.1037/0096-1523.18.3.603)

von der Lühne, T., Manera, V., Barisic, I., Becchio, C., Vogeley, K., & Schilbach, L. (2016). Interpersonal predictive coding, not action perception, is impaired in autism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(20150373), 1–8. <http://dx.doi.org/10.1098/rstb.2015.0373>

von Hofsten, C. (1991). Structuring of early reaching movements: a longitudinal study. *Journal of Motor Behaviour*, 23(4), 280–92.

<https://doi.org/10.1080/00222895.1991.9942039>

Wallace, G. L., & Happé, F. (2008). Time perception in autism spectrum disorders. *Research in Autism Spectrum Disorders*, 2(3), 447–55.

<https://doi.org/10.1016/j.rasd.2007.09.005>

Warren, Z., McPheeters, M. L., Sathe, N., Foss-Feig, J. H., Glasser, A., & Veenstra-VanderWeele, J. (2011). A systematic review of early intensive intervention for

autism spectrum disorders. *Paediatrics*, 127(5), e1303-11.

<http://dx.doi.org/10.1542/peds.2011-0426>

Watson, D., & Clark, L. A. (1994). *The PANAS-X: Manual for the positive and negative affect schedule-expanded form*. Ames: The University of Iowa.

Wechsler, D. (1999). *Wechsler abbreviated scale of intelligence*. The Psychological Corporation, Harcourt Brace and Company: New York, NY.

Werker, J. F., & Tees, R. C. (1984). Cross-language speech perception: evidence for perceptual reorganization during the first year of life. *Infant Behaviour and Development*, 7(1), 49–63. [https://doi.org/10.1016/S0163-6383\(84\)80022-3](https://doi.org/10.1016/S0163-6383(84)80022-3)

White, C. T., & Schlosberg, H. (1952). Degree of conditioning of the GSR as a function of the period of delay. *Journal of Experimental Psychology*, 43(5), 357–62.

<https://doi.org/10.1037/h0061520>

White, S. J., Coniston, D., Rogers, R., & Frith, U. (2011). Developing the Frith-Happé animations: a quick and objective test of theory of mind for adults with autism.

Autism Research, 4(2), 149–54. <https://doi.org/10.1002/aur.174>

Wilson, P. H., & Hyde, C. (2013). The development of rapid online control in children aged 6-12years: reaching performance. *Human Movement Science*, 32(5), 1138–

50. <https://doi.org/10.1016/j.humov.2013.02.008>

Wimpory, D., Nicholas, B., & Nash, S. (2002). Social timing, clock genes and autism: a new hypothesis. *Journal of Intellectual Disability Research*, 46(4), 352–8.

<https://doi.org/10.1046/j.1365-2788.2002.00423.x>

- Wolpert, D. M., Doya, K., & Kawato, M. (2003). A unifying computational framework for motor control and social interaction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 358(1431), 593–602.
<https://doi.org/10.1098/rstb.2002.1238>
- Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P., & Smith, M. A. (2014). Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nature Neuroscience*, 17(2), 312–21.
<https://doi.org/10.1038/nn.3616>
- Yoon, J. M. D., & Johnson, S. C. (2009). Biological motion displays elicit social behaviour in 12-Month-Olds. *Child Development*, 80(4), 1069–75.
<https://doi.org/10.1111/j.1467-8624.2009.01317.x>
- Zeman, J., Cassano, M., & Adrian, M. (2013). Socialization influences on children's and adolescent's emotional self-regulation processes: a developmental psychopathology perspective. In K. C. Barrett, N. A. Fox, G. A. Morgan, D. J. Fidler, & L. Daunhauer (Eds.), *Handbook of self-regulatory processes in development: New directions and international perspectives*. Psychology Press: New York.
- Zwicker, J., White, S. J., Coniston, D., Senju, A., & Frith, U. (2011). Exploring the building blocks of social cognition: spontaneous agency perception and visual perspective taking in autism. *Social Cognitive and Affective Neuroscience*, 6(5), 564–71. <https://doi.org/10.1093/scan/nsq088>