



BIROn - Birkbeck Institutional Research Online

Johnson, Mark H. and Senju, Atsushi and Tomalski, Przemyslaw (2015) The two-process theory of face processing: modifications based on two decades of data from infants and adults. *Neuroscience & Biobehavioral Reviews* 50 , pp. 169-179. ISSN 0149-7634.

Downloaded from: <https://eprints.bbk.ac.uk/id/eprint/10708/>

Usage Guidelines:

Please refer to usage guidelines at <https://eprints.bbk.ac.uk/policies.html>
contact lib-eprints@bbk.ac.uk.

or alternatively



Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev



Review

The two-process theory of face processing: Modifications based on two decades of data from infants and adults

Mark H. Johnson^{a,*}, Atsushi Senju^a, Przemyslaw Tomalski^{b,*}

^a Centre for Brain & Cognitive Development, Birkbeck, University of London, Malet Street, London WC1E 7HX, UK

^b Neurocognitive Development Lab, Faculty of Psychology, University of Warsaw, Stawki 5/7, 00-183 Warsaw, Poland

ARTICLE INFO

Article history:

Received 9 February 2014
Received in revised form 24 August 2014
Accepted 12 October 2014
Available online xxx

Keywords:

Two-process theory of face processing development
Filial imprinting
Face detection
Gaze processing
Conspic
Conlern
Sub-cortical face pathway
Superior colliculus
Pulvinar
Amygdala

ABSTRACT

Johnson and Morton (1991. *Biology and Cognitive Development: The Case of Face Recognition*. Blackwell, Oxford) used Gabriel Horn's work on the filial imprinting model to inspire a two-process theory of the development of face processing in humans. In this paper we review evidence accrued over the past two decades from infants and adults, and from other primates, that informs this two-process model. While work with newborns and infants has been broadly consistent with predictions from the model, further refinements and questions have been raised. With regard to adults, we discuss more recent evidence on the extension of the model to eye contact detection, and to subcortical face processing, reviewing functional imaging and patient studies. We conclude with discussion of outstanding caveats and future directions of research in this field.

© 2014 Published by Elsevier Ltd.

Contents

1.	Introduction	00
2.	The two-process theory of filial imprinting	00
3.	The two-process theory of face processing	00
3.1.	The newborn response to faces	00
3.2.	Neonatal imitation	00
3.3.	Emerging specialization of cortical face processing areas	00
4.	Sub-cortical route in the adult brain	00
4.1.	Anatomy of the sub-cortical pathway	00
4.2.	Rapid orienting to faces in adults	00
4.3.	Rapid detection and processing of threat expressions	00
4.4.	Subcortical pathway influences cortical face processing	00
5.	Expanding the two-process theory to eye gaze	00
6.	General discussion	00
	Acknowledgements	00
	References	00

1. Introduction

Arguably, Gabriel Horn's most significant achievement was the development of a well-characterized model system for the study of memory: Filial imprinting in the domestic chick. However, while

* Corresponding author at: Centre for Brain & Cognitive Development, Birkbeck, University of London, Malet Street, London WC1E 7HX, UK. Tel.: +44 0 20 7631 6258.
E-mail addresses: mark.johnson@bbk.ac.uk (M.H. Johnson), p.tomalski@uw.edu.pl, tomalski@mac.com (P. Tomalski).

50 Q4 this model had clear relevance to memory (see Bateson, this issue),
51 it has also had a broader impact on the fields of typical and atyp-
52 ical social development in humans and the cognitive neuroscience
53 Q5 of face processing. In particular, Johnson and Morton (1991) and
54 Morton and Johnson (1991) used the chick model as inspiration for
55 their two-process theory of the development of face processing in
56 humans.

57 Filial imprinting is the process by which young precocial birds
58 such as chicks recognize and develop an attachment for the first
59 conspicuous object that they see after hatching (for reviews see
60 Bolhuis, 1991; Bateson, this issue). While filial imprinting has been
61 reported in the young of a variety of species, including spiny mice,
62 guinea pigs, chicks, and ducklings, the wider notion of sensitive
63 periods for the acquisition of social preferences and expertise is
64 readily extendable to primates including mankind.

65 In this paper we review evidence from human infants and adults
66 that relates to the two-process model of face processing originally
67 published in 1991. In particular, we discuss more recent evidence
68 on the extension of the model to eye contact detection, and the
69 modifications necessary as a result functional imaging and patient
70 studies with adults. The evidence we review is biased towards stud-
71 ies that have appeared since Johnson's (2005) paper.

72 2. The two-process theory of filial imprinting

73 Horn, Bateson and their collaborators confirmed earlier reports
74 that in the laboratory day-old domestic chicks will imprint onto a
75 variety of different objects after a few hours of exposure. Chicks
76 then develop strong and robust preferences for the training object
77 or sound over novel stimuli. Importantly, in the absence of a
78 mother hen this learning is relatively unconstrained: virtually any
79 conspicuous moving object larger than a matchbox will serve as
80 an imprinting stimulus, and will come to be preferred over any
81 other. Horn and collaborators established that a particular region
82 of the chick forebrain (corresponding to mammalian cortex) has
83 been shown to be critical for imprinting, IMM (intermediate and
84 medial part of the Mesopallium—formerly called IMHV; for reviews
85 see (Horn, 1985; Horn and Johnson, 1989; Bateson, this issue).
86 Lesions to IMM placed before or after training on an object severely
87 impaired preference for that object in subsequent choice tests, but
88 did not affect other visual and learning tasks (Johnson and Horn,
89 1986, 1987; McCabe et al., 1982). Importantly, similar size lesions
90 placed elsewhere in the chick forebrain did not result in significant
91 impairments of imprinting preference (Johnson and Horn, 1987;
92 McCabe et al., 1982).

93 The next step for Horn and collaborators in analyzing the brain
94 basis of imprinting was to study the neural circuitry of IMM. In
95 terms of its connectivity, IMM's main inputs come from visual pro-
96 jection areas, and some of its projections go to regions of the bird
97 brain thought to be involved in motor control. Thus, the area is well
98 placed to integrate visual inputs and motor outputs. In terms of its
99 intrinsic connectivity, there have been attempts to build compu-
100 tational models of the intrinsic circuitry concerned (Bateson and
101 Horn, 1994; O'Reilly and Johnson, 1994; Bateson, this issue).

102 As stated earlier, a wide range of objects, such as moving red
103 boxes and blue balls, are as effective for imprinting as are more
104 naturalistic stimuli in the laboratory. However, in the wild, pre-
105 cocial birds such as chicks invariably imprint on their mother hen, and
106 not on other moving objects. These observations raise the question
107 as to what constraints ensure that this plasticity in the chick brain
108 is normally guided to encode information about conspecifics (the
109 mother hen), rather than other objects in its environment.

110 Horn and his collaborators began to answer this question after
111 reviewing the results of a series of experiments in which stimulus-
112 dependent effects of IMM lesions were observed (Horn and McCabe,

113 1984). They noticed that while chicks trained on an artificial stimu-
114 lus such as a rotating red box were severely impaired by IMM
115 lesions placed either before or after training on an object, chicks
116 imprinted on a stuffed hen were only mildly impaired in their pref-
117 erence. Thereafter, other neurophysiological manipulations also
118 revealed differences between the hen-trained and box-trained
119 birds. In one example, administration of the neurotoxin DSP4
120 (which depletes forebrain levels of the neurotransmitter nore-
121 pinephrine) resulted in a severe impairment of preference in birds
122 trained on the red box, but only a mild impairment in birds trained
123 on the stuffed hen (Davies et al., 1985). In contrast to this, levels of
124 testosterone correlated with preference for the stuffed hen, but not
125 preference for the red box (Bolhuis et al., 1986).

126 Inspired by these findings, Johnson and Horn (1988) sought evi-
127 dence for the earlier suggestion of Hinde (1961) that naturalistic
128 objects such as hens may be more effective at eliciting attention
129 in chicks than are other objects. In a series of experiments these
130 authors presented dark-reared chicks with a choice between a
131 stuffed hen and a variety of test stimuli created from cutting up
132 and jumbling the pelt of a stuffed hen (Johnson and Horn, 1988).
133 The results indicated that chicks are predisposed to attend towards
134 features of the head and neck region of the hen. While this bias was
135 specific to the correct arrangement of features of the face/head, it
136 was not specific to the species, as the heads of other bird species
137 elicited attention equally well.

138 The results of these and other experiments led Horn (1985) and
139 Johnson et al. (1985) to the proposal that there are two indepen-
140 dent brain systems that control filial preference in the chick. First, a
141 specific predisposition for newly hatched chicks to orient towards
142 objects resembling a mother hen. While this predisposition was
143 specifically tuned to the correct spatial arrangement of elements of
144 the head and neck region, it is not species- or genus-specific, but it
145 is sufficient to pick out the mother hen from other objects the chick
146 is likely to be exposed to in the first few days after hatching. The
147 optic tectum, the homolog of the mammalian superior colliculus,
148 is likely to be critical for this bias.

149 The second brain system is associated with IMM, and acquires
150 information about the objects to which the young chick attends.
151 In the natural environment, it was argued, the first brain sys-
152 tem guides the second system to acquire information about the
153 closest mother hen. Biochemical, electrophysiological, and lesion
154 evidence all support the conclusion that these two brain systems
155 have largely independent neural substrates (for review see Horn,
156 1985). For example, while selective lesions to IMM impair prefer-
157 ences acquired through exposure to an object, they do not impair
158 the specific predisposition (Johnson and Horn, 1986).

159 There are several different ways in which the predisposition
160 could constrain the information acquired by the IMM system. For
161 example, the information in the predisposition could act as a sen-
162 sory 'filter' or template through which information had to pass
163 before reaching the IMM system. However, the currently available
164 evidence is consistent with the view that the input to the IMM sys-
165 tem is selected simply as a result of the predisposition biasing the
166 chick to orient towards any hen-like objects in the environment.
167 Given that the species-typical environment of the chick includes a
168 mother hen in close proximity, and that the predisposition includes
169 adequate information to pick the hen out from other objects in the
170 early environment, the input to the learning system will be highly
171 selected.

172 3. The two-process theory of face processing

173 Johnson and Morton (1991) and Morton and Johnson (1991)
174 published a two-process theory of the development of face process-
175 ing in humans. In brief, the original two-process theory sought to

reconcile apparently conflicting lines of evidence about the development of face processing. It did this by following the previous work on filial imprinting in chicks in postulating the existence of two systems; a predisposition in newborns to orient towards faces (termed *Conspex*; face detection), and an acquired specialisation of cortical circuits for other aspects of face processing (termed *Conlern*; face recognition and processing). Johnson and Morton postulated that *Conspex* served to bias the input to the developing cortical circuitry over the first weeks and months of life. In this way, *Conspex* could be said to “tutor” *Conlern*. While some now consider the two-process theory to represent the “traditional” view against which more recent theories should be judged (e.g. [Bednar and Miikkulainen, 2002](#)), some aspects of the original theory remain controversial.

3.1. The newborn response to faces

One of the most long-standing debates in developmental psychology has surrounded the evidence for face detection in newborn babies. In 1991, we replicated earlier reports that human newborns preferentially orient towards simple schematic face-like patterns ([Johnson et al., 1991](#)). On the basis of this and other findings, including those from the chick, Johnson and Morton hypothesised that this bias was controlled by a sub-cortical processing route, and that it served to bias the visual input to developing cortical circuits in order to ensure the development of specialisation for faces ([Morton and Johnson, 1991](#); see also: [de Schonen and Mathivet, 1989](#)). At the time, the idea that infants were born with face-related information had been rejected by most in the field, largely on the basis of experiments with one and two month old infants that failed to show face preferences (see [Johnson and Morton, 1991](#), for review). The two-process theory, however, suggested that this failure to detect a preference was due to inappropriate testing methods that did not engage sub-cortical visuo-motor systems.

The notion that infants have information about the characteristics of others faces from birth ([Morton and Johnson, 1991](#); see also: [de Schonen and Mathivet, 1989](#)), and that this is largely supported by sub-cortical processing, has come under continuing scrutiny over the past decades (e.g. [Gauthier and Nelson, 2001](#); [Macchi Cassia et al., 2001](#); [Nelson, 2001](#)). The early experiments with newborns indicated that a stimulus with three high-contrast blobs corresponding to the approximate location of the eyes and mouth might be sufficient to elicit the newborn preference. This stimulus has characteristics of a low spatial frequency image of a face (see [Fig. 1](#)).

Several studies of face-related behaviour in human newborns have been published since 1991 (see [Johnson, 2005](#), for review). While most of these papers agreed with the conclusion that newborns are biased to attend to stimuli that possess certain characteristics of faces, two alternative views have been expressed. The first of these alternative views (the “sensory hypothesis”) is that all newborn visual preferences, including those for face-related stimuli, can be accounted for simply in terms of the relative visibility of the stimuli. The newborn visual system is restricted to the lower part of the range of spatial frequencies that is visible to adults. Thus, it has been proposed that newborns prefer to look at faces merely because the amplitude at different frequencies of these stimuli happen to best match the sensitivity of the newborn visual system ([Kleiner and Banks, 1987](#)). This “sensory hypothesis” fell out of favour because, even when amplitude is controlled, phase information (configuration) still influences the newborn preference towards faces ([Johnson and Morton, 1991](#); [Morton et al., 1990](#)). In addition, attempts to simulate newborn preferences with neural network models based on the sensory hypothesis ([Acerra et al., 2002](#)) are unlikely to account for other experiments involving realistic faces within the complex visual scenes to which newborns are

exposed ([Bednar and Miikkulainen, 2003](#)). The second alternative to the *Conspex* view is that we have complex face processing abilities already present from birth ([Quinn and Slater, 2003](#)). Findings used to support this claim include a preference for images of attractive faces ([Slater et al., 1998, 2000](#)), data indicating that newborns are sensitive to the presence of eyes in a face ([Batki et al., 2000](#)), and evidence that they prefer to look at faces that engage them in eye contact ([Farroni et al., 2002](#)). However, in addition to the immaturity of the visual cortex at birth in humans, all of these results could potentially be accounted for by the detection of low spatial frequency (LSF) face configuration (see [Johnson, 2005](#) for details). More recently, a binocular correlation model (BCM) has been put forward, which purports to explain the neonatal face bias as a result of a visual filtering mechanism related to the limited binocular integration possessed by newborns ([Wilkinson et al., 2014](#)). The correlation of salient areas in image from each eye (i.e. the eyes and the mouth) may thus serve to further amplify these areas to create a representation of the face-like stimulus in the visual system. Indeed, a robotic model implementing BCM has been able to replicate some of the results from the original study by [Johnson et al. \(1991\)](#). However, while the BCM may offer a potential explanation of some results, like other sensory accounts it fails to offer a satisfactory explanation of orientation effects as revealed in the inversion effects present at birth (see [Farroni et al., 2005, 1999](#)).

Thus, taken overall the current prevailing view on the mechanisms that underlie the preference of newborn babies for face-like stimuli is that newborns have one or more biases in visual processing that are sufficient, in their natural environment, to ensure that they fixate faces. [Johnson and Morton \(1991\)](#) proposed that a stimulus equivalent to the LSF components of the configuration of a face is optimal for eliciting the preference (see [Fig. 1](#)). However, it has been proposed that the configuration of high-contrast areas associated with the eyes and mouth are not required, but that newborns might prefer up-down asymmetrical patterns with more elements or features being contained in the upper half of a bounded object or area ([Simion et al., 2003](#)). Although such preferences are sometimes said to be due to several “domain-general” biases, such as a putative upper visual field bias ([Turati et al., 2002](#)), experiments indicate that there is a crucial interdependency between the borders of the stimulus and the elements within it ([Turati and Simion, 2002](#)), indicating some complexity to the bias. Some evidence from 2- to 6-month-old infants suggests that face preference at this age is better explained by a specific bias than general upper field bias ([Chien, 2011](#); [Chien et al., 2010](#)). Experiments that independently manipulate upper visual field elements and bounded areas, and experiments that measure eye movements sufficiently to control upper/lower visual field presentation, have not yet been done.

Other experiments indicate that the phase contrast of stimuli is also important for newborns preferences ([Farroni et al., 2005](#)). In these experiments newborn preferences for upright face configuration patterns, and photographic face images, were assessed with both black elements on white (positive contrast polarity—as in previous studies) and the same stimuli with contrast polarity reversed. If the newborns are merely seeking particular elements or features then phase contrast should either make no difference, or cause them to prefer lighter elements on a dark background (since lighter elements are typically closer to the viewer in natural scenes). In contrast, if the function of the bias is to detect faces then black elements on white should be more effective, since the eyes and mouth region are recessed into the face, and appear in shadow under natural (top-down) lighting conditions. In addition, for stimuli at close range to the infant, such a preference may also be consistent with detecting the pupils of the eyes in relation to the background white of the sclera (see later). Consistent with the face-sensitive view, [Farroni et al., \(2005\)](#) found the preference for an upright face (with both schematic and naturalistic images) only

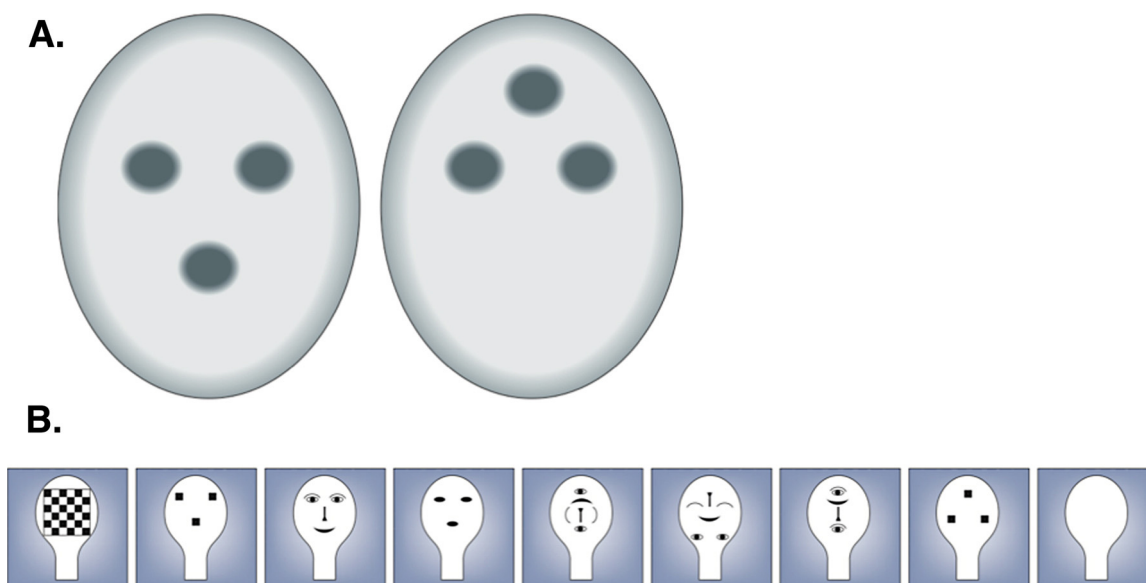


Fig. 1. Panel (A) Schematic illustration of the stimuli that might be optimal for eliciting a face-related preference in newborns. These hypothetical representations were created by putting together the results of several experiments on newborns' face-related preferences, showing the importance of the number of elements in the upper half of a bounded area or surface, the importance of a face-relevant pattern of phase contrast, and the importance of the basic face configuration as viewed at low spatial frequencies. Panel (B) Schematic stimuli used to test newborn preferences. Some of the stimuli are designed to test the importance of the spatial arrangement of a face (configuration), and others the importance of particular features. Newborns will preferentially attend to patterns that contain the basic configuration of high-contrast areas of a face (for example, the second, third and fourth stimuli from the left are preferred to those on the right). Reproduced with permission from Johnson (2005).

under positive (face-like) contrast conditions. If phase contrast is added to the previous requirements for the "top heavy bias" underlying newborn face preference, it is clear that a considerably more complex representation is required than merely an upper visual field bias.

When recent evidence is considered we are left with two candidate stimuli that could best elicit newborn face-related preferences. One of these is a raised surface or area with more indentations or dark areas in the upper half, while the other involves indentations or darker blobs corresponding to the approximate locations of eyes and mouth (see Fig. 2). At a distance, or in the periphery, a mechanism activated by these stimuli would direct attention towards faces. When closer to the infant, the same mechanism may direct attention to the eyes of a face.

Although there is an increasing literature on the neural basis of face detection in human infants of 2 months and older (Grossmann and Johnson, 2013), for several technical and ethical reasons it has not yet proved possible to use functional MRI, MEG or PET to study face perception in healthy newborns. However, a number of converging lines of evidence support the view that orienting to faces in newborns is largely controlled by a subcortical pathway. First, neuroanatomical, functional imaging, electrophysiological and behavioural evidence indicates that while visual cortical areas can be partially activated in newborns, they are relatively immature (Atkinson, 2000; Johnson, 2011). Further, the partial activation of visual cortical areas in the first months has little control over the visually-guided behaviour of the infant (Csibra et al., 2000). Compared with the cortical visual route, structures on the sub-cortical route seem to be more developed around the time of birth (see Johnson, 2005 for review). A second line of evidence supporting the view that newborn face preference is sub-cortical comes from other species, including the work on chicks discussed earlier.

As the nasal and temporal visual fields feed differentially into the cortical and sub-cortical visual routes (Conley et al., 1985; Perry and Cowey, 1985; Sylvester et al., 2007), it is possible to gain indirect evidence for sub-cortical processing by presenting stimuli in either the temporal or nasal visual fields only. Specifically, stimuli presented in the nasal field differentially feed in to the cortical

route, while those in the temporal field feed into the sub-cortical route. In one experiment newborns wore patches on one eye while face-like stimuli were presented to the other eye in either visual field. Consistent with the view that face preferences in newborns are due to the action of sub-cortical processes, the preference was observed only when stimuli were presented in the temporal visual field (Simion et al., 1995, 1998).

3.2. Neonatal imitation

Despite the evidence for sub-cortical mediation of face preference at birth it has been proposed that the phenomenon of the neonatal imitation of facial gestures indicates the existence of more complex face processing skills at birth (Meltzoff and Moore, 1989). A number of studies have demonstrated imitation of selected facial gestures at birth since the original report by Meltzoff and Moore (1977). Imitation of facial gestures involves sufficient visual processing of the imitating model's face in order to prepare a relevant and matching motor program. Thus, a newborn's ability to imitate model's actions such as tongue and lip protrusion or mouth opening would imply face processing skills beyond mere preferential orienting to face-like patterns.

The body of research on neonatal imitation has been critically reviewed identifying both methodological and interpretational caveats (Anisfeld, 2005; Jones, 2009). For example, Ray and Heyes (2011) systematically reviewed all existing studies and concluded that of the 18 imitated gestures that have been studied reliable and replicable imitation has only been obtained for tongue protrusion. These authors suggest that tongue protrusion can potentially be explained by non-specific mechanisms, such as a general response to arousing stimulation. Additionally, specific imitation of mouth opening gestures has been found in individuals with cerebral palsy, who showed little voluntary movement of extremities due to cortical brain damage. This suggests that in at least some cases imitation can be explained by sub-cortical rather than cortical mechanisms (Go and Konishi, 2008). In conclusion, the existing research on neonatal imitation does not offer strong evidence against the sub-cortical account of face preference at birth.

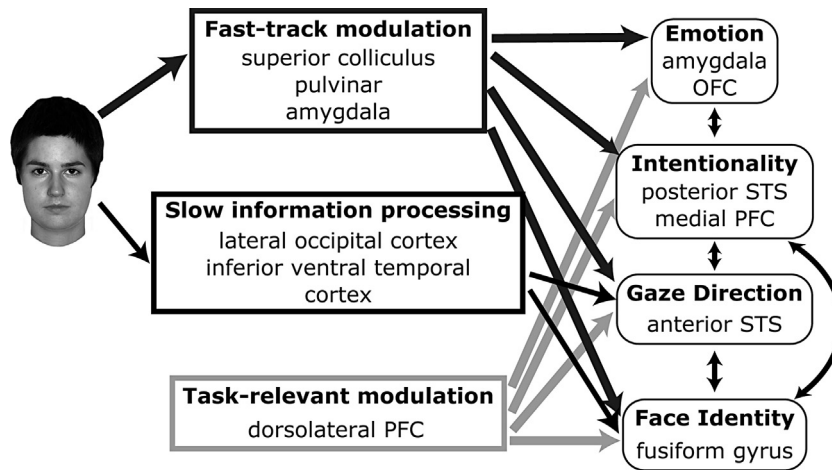


Fig. 2. An illustration of fast-track modulator model. Reproduced from: Senju and Johnson (2009b), with permission.

380 3.3. Emerging specialization of cortical face processing areas

381 Literature on the neural organization of face processing in the
 382 adult brain has generated arguments both for and against the
 383 domain-specific view of cortical face processing (for a review see:
 384 Gauthier and Nelson, 2001; Kanwisher, 2010). The former view is
 385 associated with the idea that cortical processes underlying face pro-
 386 cessing are innate, whereas the latter is usually accompanied that
 387 face expertise is acquired through experience. This debate has gen-
 388 erated data that may shed new light on the experience-dependent
 389 *Conlern* process originally proposed by Johnson and Morton (1991).
 390 While Johnson's account of this debate has been described else-
 391 where (Johnson, 2011), here we specifically seek to clarify the
 392 definition of the *Conlern* process in light of this evidence. In brief,
 393 *Conlern* can be best described as a domain-relevant system that
 394 under typical circumstances comes to specialise in faces.

395 In the absence of research on the neural basis of face pro-
 396 cessing at the time of writing their original 1991 paper, Johnson
 397 and Morton described *Conlern* in simple functional terms as "a
 398 system that acquires and retains specific information about the
 399 visual characteristics of conspecifics". As evidence has accrued
 400 over the years, Johnson (2010) has provided a more mechanistic
 401 account in which cortical specialization for face processing gradu-
 402 ally emerges as a result of accumulating experience, but it is also
 403 constrained by intrinsic biases associated with cortical architec-
 404 ture and inter-regional connectivity. This emerging specialisation
 405 account can explain evidence that has previously been taken to
 406 support either domain-specific (e.g. Kanwisher, 2010) or domain-
 407 general (Gauthier and Nelson, 2001; Slater et al., 2010) views of
 408 cortical organization of face processing. For example, a series of
 409 studies on macaque monkeys which were reared from birth with-
 410 out visual experience with faces has been interpreted as providing
 411 support for a innate domain-specific view (Sugita, 2008). Despite
 412 their selective visual deprivation the animals still showed clear face
 413 preference over objects but did not show greater preference for
 414 monkey over human faces, a pattern of preference consistent with
 415 the human sub-cortical route (see Johnson 2010 for further discus-
 416 sion). However, a group of previously deprived macaques exposed
 417 to human faces for only one month showed rapid experience-
 418 dependent perceptual narrowing in their face processing skills:
 419 they discriminated between individual human faces far better than
 420 monkey faces. A reverse effect was observed for animals exposed
 421 to monkey rather than human faces. The process of perceptual nar-
 422 rowing, i.e. the narrowing of the class of visual face-like stimuli
 423 that are processed more rapidly and/or efficiently has been demon-
 424 strated in infants under 12 months of age in several studies (see

Anzures et al., 2013), and is entirely consistent with *Conlern* involv-
 ing processes of emerging specialization.

425
 426
 427
 428
 429
 430
 431
 432
 433
 434
 435
 436
 437
 438
 439
 440
 441
 442
 443
 444
 445
 446
 447
 448
 449
 450
 451
 452
 453
 454
 455
 456
 457
 458
 459
 460
 461
 462
 463
 464
 465
 466
 467
 468

4. Sub-cortical route in the adult brain

Since Johnson and colleagues (Johnson et al., 1991) demon-
 strated neonatal orienting to face-like patterns, and later showed
 that this effect wanes by the age of 4 months (Johnson et al.,
 2000), it has been assumed that the subcortical face pathway in
 adults is either inactive, or influences face processing only indi-
 rectly. This view was consistent with work in adults at the time
 apparently showing no "special attention" for faces, or faster detec-
 tion or preferential orienting towards them (Suzuki and Cavanagh,
 1995; VanRullen, 2006). Thus, until recently the large proportion of
 evidence in support of the sub-cortical route for detection of con-
 specificity has come from animal research and studies with human
 neonates. The relative scarcity of human adult data on sub-cortical
 face processing has led some to suggest that the reported rapid
 processing of emotional faces depends primarily, if not exclusively,
 on visual information conveyed by the main thalamic visual pro-
 jections via lateral geniculate nucleus (LGN) to the primary visual
 cortex (Pessoa and Adolphs, 2010). However, over the last decade
 converging lines of work have demonstrated continuity in the activ-
 ity of sub-cortical face pathways in the adult brain supporting the
 rapid processing of social information.

It is important to note that rapid detection of, and preferential
 orienting towards, face-like stimuli may reflect partially differ-
 ent processes, which under certain conditions can be mediated
 by sub-cortical visual pathways. While in the first months of life
 the detection of conspecifics will trigger preferential orienting
 towards them, the development of attention control leads to signif-
 icant dissociations of these processes later in life. In the following
 section we review the adult literature demonstrating how the sub-
 cortical pathway may support rapid detection of faces, which in
 turn may facilitate later processing. We also note that in a number of

studies sub-cortically mediated rapid detection has been revealed by demonstrating its effects on visual orienting.

4.1. Anatomy of the sub-cortical pathway

The subcortical pathway, also called as the retino-tectal pathway or extrageniculate pathway, encompasses: the superior colliculus (SC), the pulvinar complex (PV) and the amygdala complex (AM) with projections to the dorsal visual cortex (Berman and Wurtz, 2010; Kaas and Lyon, 2007). The superior colliculus receives direct retinal input through fast-conducting magnocellular cells, which determines its sensitivity to rapid motion in the periphery and visual stimulation with predominantly low spatial frequency (LSF), achromatic and luminance-based content (Schneider and Kastner, 2005; Waleszczyk et al., 2007).

The visual pulvinar nuclei receive both direct retinal input and magnocellular projections from the SC (Stepniewska, 2004) and are interconnected with visual cortex at both early (V1, V2) and late stages (V3 and MT) of visual processing (Holliday et al., 1997; Kaas and Lyon, 2007). The activity of this route has been confirmed in adult non-human primates: visual input from the SC can drive neurons in dorsal visual areas even after the inactivation of V1 (Rodman et al., 1989; Rosa et al., 2000). In human adults who suffer from hemianopia due to primary visual cortex damage this pathway mediates orientation and direction of movement discrimination (Weiskrantz, 1996), influences responses to stimuli in the spared visual field (Leh et al., 2006; Ptito and Leh, 2007; Tamietto et al., 2010) and mediates interhemispheric transfer following callosotomy (Savazzi et al., 2007) and cross-modal stimulus localization in the blind field (Leo et al., 2008). Similar effects can be reproduced in healthy patients with TMS-induced temporary hemianopia (Boyer and Harrison, 2005; Ro et al., 2004).

The amygdala is involved in the majority of socio-emotional information processing, with a particular role in threat detection and aversive learning (for review see Costafreda et al., 2008). It receives visual input predominantly from the infero-temporal visual cortex, but not earlier visual areas (Iwai and Yuki, 1987; Stefanacci and Amaral, 2000; Webster et al., 1991); this pathway is capable of providing detailed object representations, but at relatively long latencies (150–200 ms) given the hierarchical nature of object processing in the ventral stream. For amygdala responses at much shorter latencies, an alternative input arrives via the retino-tectal visual pathway and medial pulvinar (Linke et al., 1999; Romanski et al., 1997).

4.2. Rapid orienting to faces in adults

An orienting bias towards faces and face-like patterns has been revealed indirectly in a number of recent studies. Adults detect target faces faster than other object categories, particularly when presented in the visual periphery (Hershler et al., 2010). In addition, faces are also difficult to ignore as distracters in visual search tasks (Langton et al., 2008; Ro et al., 2007). Masked, low-spatial frequency images of faces in the periphery facilitate judgment of other stimuli, while high-spatial frequency images of faces do not (Khalid et al., 2013). Particularly when presented in the visual periphery upright faces may affect relatively low-level attentional processes such as overcoming inter-ocular suppression (Stein et al., 2011; Stein et al., 2012b), and producing stronger inhibition of return (Theeuwes and Van der Stigchel, 2006).

Importantly, adults show faster overt orienting towards patterns with a face-like configuration of internal elements and normal contrast polarity, in comparison to upside-down or reversed polarity patterns (Tomalski et al., 2009a). This result closely resembles preference biases observed in newborns (Farroni et al., 2005). Several lines of evidence suggest that these biases depend on the

activity of the retino-tectal pathway. First, the orienting bias was found in temporal but not in the nasal visual hemifields, consistent with the collicular mediation hypothesis (Tomalski et al., 2009b). Second, when viewing naturalistic scenes adults show extremely rapid saccades towards faces at latencies of just 100–110 ms (Crouzet et al., 2010), shorter than cortical face processing mechanisms would permit (e.g. Schmolesky et al., 1998). Lastly, the facilitation of orienting towards faces is abolished when they are rendered “invisible” to the SC with S-cone pink stimuli (Nakano et al., 2013).

Crucial support for the role of the sub-cortical route in rapid face detection in adults that may facilitate orienting comes from a single-cell study of the macaque pulvinar. Nguyen et al. (2013) have found a small number of neurons that respond specifically to face-like patterns at latencies of less than 50 ms. Such short response latencies are highly unlikely to be the result of re-entrant input to the pulvinar, and instead are most likely due to ascending magnocellular input from the superior colliculus. Interestingly, other pulvinar neurons sensitive to human faces and eye-gaze responded with latencies significantly longer than 50 ms, suggesting that the pulvinar integrates both ascending and descending visual inputs, modulating their saliency (Corbetta and Shulman, 2002).

4.3. Rapid detection and processing of threat expressions

Studies of subcortical processing of facial emotion expressions, especially signals of threat—fearful faces, indicates that the subcortical pathway may also mediate rapid detection of visual threat. This issue has been studied with hemianopic patients with “blindsight”, i.e. individuals who show residual visual processing despite being completely unaware of stimuli in their blind field. When presented with fearful faces in their blind field such patients still show above chance recognition of ‘unseen’ expressions (de Gelder et al., 1999), along with enhanced activity in the superior colliculus and amygdala (Morris et al., 1999). Superior detection of fearful expressions in the blind field may facilitate emotion or gender discrimination in the intact visual field in hemianopics (Bertini et al., 2013), or in healthy adults with V1 temporarily inhibited by transcranial direct current stimulation (tDCS) (Cecere et al., 2013).

We note that some have argued that the visual extrageniculate pathway to the amygdala does not exist in primates, and that residual visual processing in blindsight relies on geniculate connections and spared visual cortical activity with (Pessoa and Adolphs, 2010). However, this view is contradicted by recent work on non-human primates, which has shed further light on the connectivity and sensitivity of single neurons in key structures of the sub-cortical route in the intact primate brain. Bilateral lesions to the SC in capuchin monkeys result in long-term impairment in recognition and responsiveness to natural threat (Maior et al., 2011), while the macaque monkey pulvinar has cells selectively responding to human faces with emotion expressions at latencies <100 ms (Maior et al., 2010). These results are consistent with studies on patients with pulvinar lesions, who show slower responses to visual threat and impaired emotion recognition, despite their main visual route through LGN being intact (Ward et al., 2005, 2007).

Neuroimaging studies of the adult brain demonstrate further functional properties of the subcortical pathway. Facial threat elicits electromagnetic activations at extremely short latencies (<30 ms) in the thalamus and the amygdala (Luo et al., 2007), and the amygdala is particularly sensitive to magnocellular, LSF filtered faces (Vuilleumier et al., 2003). When fearful faces are consciously perceived by participants the amygdala is activated in addition to face-sensitive areas, such as the fusiform face area (Costafreda et al., 2008). But when perception of the same stimuli is suppressed by masking or binocular rivalry, it is the superior colliculus, the pulvinar and the amygdala alone that are activated by the unseen fearful

expressions (Jiang and He, 2006; Liddell et al., 2005; Pasley et al., 2004).

Taken together these results not only directly support the existence of the ‘sub-cortical route, but also demonstrate its important role for the rapid processing of visual threat in the adult brain. In fact, fearful facial expressions may serve as optimal stimuli for the sub-cortical face detection network. Fearful faces, with dilated pupils, widened eyes and open mouth, which highlight the basic configuration and contrast properties are optimal face-like stimuli or “superstimuli”. Susskind et al. (2008) suggested that in evolutionary terms human facial expressions originate from internal regulatory requirements reflecting, for example, preparation of defensive responses, and only later became functionally relevant for social communication. It is possible that this process evolved fearful expressions such that they elicited the strongest activation from the sub-cortical route for the detection of conspecifics. Thus selective pressure may have lead to fearful expressions matching the properties of the sub-cortical route. One aspect of this process is how such stimuli may influence face processing at later stages, recruiting a wide network of cortical areas.

A related question is the engagement of the sub-cortical pathway in the detection of visual threat from other species, e.g. snakes or spiders. Isbell (2006) has argued that a long, shared history of snakes and primates co-existing in their habitats led to selective pressure for visual system to more rapidly detect such threats. This would mean that the Conspic mechanism (see Section 3) should be sensitive from birth not only to conspecifics but also to selected non-primate visual threat. Although there is evidence for preferential orienting (LoBue and DeLoache, 2010) or longer looking towards images of snakes or spiders (Rakison and Derringer, 2008) from the age of 5 months, no preference for fearful emotion expression was found at birth (Farroni et al., 2007). However, animal model work suggests that capacity for fear conditioning is either inhibited or diminished soon after birth (Sullivan et al., 2000), which is consistent with relatively late emergence of infant sensitivity to fearful facial expressions (Nelson and Dolgin, 1985; Peltola et al., 2009). Thus it is possible that sensitivity to threat-related stimuli emerges throughout the first year of life as a result of experience. It is also possible that sensitivity to threat (including sub-cortically mediated orienting to threat) emerges due to changes in amygdala activity related to decrease in dependence on the mother and increase in exploratory behaviour (see animal model: Moriceau and Sullivan, 2006). Further neuroimaging research with humans and non-human primates is necessary to clarify these questions.

4.4. Subcortical pathway influences cortical face processing

Human faces, and particularly those signalling threat, not only elicit orienting, but also cue spatial attention and increase salience of other stimuli in the same location (Pourtois et al., 2005). Thus the sub-cortical pathway may provide a gating mechanism for socially relevant information through amygdala projections to prefrontal and parietal attention networks (Pourtois et al., 2013).

While the subcortical pathway primarily mediates detection and orienting to face-like stimuli, its activity also modulates later stages of cortical face processing. Traditionally, the earliest component of visual evoked potentials that was considered sensitive to facial configuration and phase contrast appeared approximately 170 ms after the stimulus onset (Eimer, 2011). However, studies that employed the temporal-nasal asymmetry of retinal projections to the SC have shown that the N170 is indeed modulated by visual input to the colliculus (de Gelder and Stekelenburg, 2005), and in particular the inversion and phase contrast reversal effects on the N170 are hemifield asymmetric (Tomalski and Johnson, 2012). Electrical responses specific to fearful expressions have been observed

even earlier, at the latency of 100–140 ms, for either masked or LSF-filtered stimuli (Kiss and Eimer, 2008; Vlaming et al., 2009). Similarly amygdala damage diminishes cortical responses to fearful faces as early as 100–150 ms (Rotshtein et al., 2010)

One model of how the subcortical pathway may modulate cortical activity comes from studies on the role of pulvinar synchronization of cortical areas in attention modulation and selection (Saalmann et al., 2012). It is likely that the subcortical pathway for face detection plays a key role in allocating attentional and visual processing resources. Functional MRI studies of the early processing of fearful faces without awareness show that parts of the dorsal visual stream (e.g. inferior parietal cortex) are activated along with the SC, pulvinar and amygdala, without corresponding activation of face-sensitive areas in the ventral stream (Troiani et al., 2012; Troiani and Schultz, 2013). These results suggest that the function of the sub-cortical pathway may go far beyond mere detection of socially relevant stimuli, and into the realms of attention selection on the basis of motivational factors for the purpose of executing adequate social actions.

5. Expanding the two-process theory to eye gaze

In addition to the recent research investigating subcortical face processing reviewed above, the two-process theory has also been extended to explain eye gaze processing, and particularly the ‘eye contact effect’ (Senju and Johnson, 2009b). The eye contact effect is defined as the phenomenon that perceived eye contact modulates the concurrent and/or immediately following cognitive processing and/or behavioural response. For example, psychological studies have revealed that perceived eye contact facilitates the detection of a face (Conty et al., 2006; Doi and Shinohara, 2013; Senju et al., 2005, 2008), holds attention on the face (Senju and Hasegawa, 2005) and facilitates other face-related tasks such as gender discrimination (Macrae et al., 2002) and the encoding and decoding of identity (Hood et al., 2003). Functional neuroimaging studies have also been used to compare the patterns of brain activation in response to the perception of direct gaze as compared to that elicited during averted gaze. In reviewing these studies, those brain regions constituting the so-called ‘social brain network’ (Brothers, 1990; Grossmann and Johnson, 2007), such as fusiform gyrus, anterior and posterior parts of superior temporal sulcus (STS), medial prefrontal and orbitofrontal cortex and amygdala, have been reported to show differential activity when the individual views either direct or averted gaze. However, this activation of the social brain network interacts with task demands, as well as the social context, to influence which regions in the social brain network are activated during eye contact gaze (for a review, see Senju and Johnson, 2009b).

To explain the neural mechanism underlying the eye contact effect, Senju and Johnson (2009b) proposed the fast-track modulator model, which extends the two-systems theory (Fig. 3). This model proposes that the eye contact effect is mediated by the sub-cortical face detection pathway discussed in the previous section. We (Senju and Johnson, 2009b) hypothesized that the combination of this subcortical pathway, and contextual modulation driven by task demands and social context (implemented as top-down modulation from prefrontal cortex) modulates key structures involved in the cortical social brain network, such as the fusiform gyrus, STS, and prefrontal cortex.

Initial evidence supporting the fast-track modulator model comes from the research in human newborns. As discussed earlier, Farroni et al. (2002, 2006) demonstrated that newborns preferentially orient to faces with direct gaze, rather than faces with averted gaze. These results are consistent with the claim that sub-cortical route mediates the detection of, and orienting towards, direct gaze in newborns. Recent studies with human adults also

demonstrate the crucial role of the subcortical route in the eye contact effect. For example, Stein et al. (2011) examined the processing of direct gaze under interocular suppression, using continuous flash suppression (CFS) paradigm. In the CFS paradigm, the conscious awareness of the stimuli presented in one eye was suppressed by flashing Mondrian images presented to the other eye. A recent fMRI study (Troiani and Schultz, 2013) demonstrated that processing of suppressed images involves subcortical structures such as superior colliculus, amygdala, thalamus and hippocampus, but the activations in early visual cortex was suppressed. Stein et al. (2012a) found that direct gaze overcame CFS faster than averted gaze, suggesting that subcortical pathway contributes to the detection of direct gaze in the absence of conscious awareness. Even more recently, Burra et al. (2013) demonstrated that a cortically blind patient showed enhanced activation of amygdala when they observed direct, as compared to averted, gaze. This result is also consistent with the claim that subcortical pathway can detect direct gaze even without an intact primary visual cortex.

Other lines of evidence also support the claim that the subcortical pathway modulates the processing of direct gaze in the cortical pathway. First, George et al. (2001) reported that direct gaze increases the functional connectivity, or temporal correlation of regional activity, between the amygdala and the fusiform gyrus. This is consistent with the hypothesis in that the amygdala specifically modulates the functional connectivity of the fusiform gyrus in response to eye contact. Second, Conty et al. (2007) found that the effect of eye contact on prefrontal cortex (possibly encoding communicative intention), occurs as early as 150–170 ms after the stimulus onset, preceding in time the response in STS. This suggests that the mechanism underlying the eye contact effect is fast and occurs before the full and detailed cortical analysis of gaze direction (Calder et al., 2007) or human action subserved by STS (Pelphrey et al., 2004). These observations are consistent with the fast-track modulator model in that the subcortical pathway initially detects eye contact, and then subsequently modulates cortical processing. In a third line of evidence, Burra et al. (2013) reported that preferential activation of the amygdala in response to observed direct gaze in a cortically blind patient is functionally correlated with activity in several key cortical and subcortical areas associated with face processing, including the right lingual gyrus and the right temporal pole, the insula, the hippocampus, and the locus coeruleus. This result is consistent with the model in that input to amygdala through subcortical pathway modulates other cortical and subcortical processing. Taken together, the lines of evidence we have reviewed strongly suggest that subcortical pathway detects direct gaze, and modulates cortical processing (i.e. the eye contact effect).

Future studies will be required to clarify the relationship between the eye contact processing and face processing in the subcortical pathway. One possibility is that they are subserved by a common bias to orient to the low spatial frequency configuration of a face (see Fig. 1), and matches more closely faces with direct gaze than to those with averted gaze when viewed close-up (at the distance of face-to-face social interaction). Another possibility is that the bias to detect direct gaze is distinct from the bias to orient to faces. Direct gaze signals attention from another animals directed to oneself, which can be aggressive in many species (Emery, 2000), and communicative/affiliative in humans (Csibra and Gergely, 2009; Gliga and Csibra, 2007). Thus, it would be beneficial to detect and orient to direct gaze either to avoid predators, or to engage in affiliative communication. This latter possibility also raises an interesting question about cross-species difference in the preferential orienting to direct gaze. For example, Kobayashi and Kohshima (1997, 2001) argued that the depigmentation of sclera in humans could be an adaptation to the communicative use of eye gaze, by signalling rather than concealing gaze direction. It will be

important to clarify whether such cross-species difference in eye morphology is linked to the subcortical processing of eye contact.

6. General discussion

In over two decades years since the original two-process account of face processing was presented, a considerable body of evidence has accrued broadly supportive of the theory, albeit with some extensions and modifications. The primary extension to the account has centred on the putative additional role of the subcortical route in detecting eye contact, and in facilitating other sensory processing during the presence of eye contact. The primary modification to the theory has been that the subcortical route may continue to have an important role in the orienting towards, and processing of, faces through to the adulthood. Future work will concern obtaining a better understanding of the neural and computational interaction between the subcortical route (Conspec) and the cortical social brain network (Conlern).

The two-process hypothesis generates predictions, for both adult and infant experiments and for both typical and atypical development (see Klin, this issue). The theory entails that the subcortical route not only detects the presence of faces and eye contact, and orients the newborn towards them, but also activates relevant cortical regions such as the lateral occipital, fusiform, and orbito-frontal cortex. Indeed, it is possible that the projection pattern to the cortex from the subcortical route partly determines which cortical regions become incorporated into the social brain network during development. Although the amygdala has widespread projections to cortical areas, it is notable that the cortical areas associated with the 'social brain' network in adults receive input from this structure (Adolphs, 2003). Such early enhancement of activity in selected cortical areas, together with other architectural biases (Johnson, 2005), might facilitate the recruitment of these cortical areas into the "social brain" network. Evidence of early activation of cortical social brain areas emerging over the first few days after birth is consistent with this proposal (Farroni et al., 2013).

Another developmental change in the relationship between the sub-cortical pathway and the cortical social network may relate to the types of faces that best activate the sub-cortical route. As discussed above, fearful faces tend to elicit greater activation in the adult amygdala than do neutral faces. However, this pattern of activation is not observed in children, who show at least equal activation in response to neutral faces (Thomas et al., 2001). One explanation for such functional changes could be that amygdalo-cortical connectivity continues to mature into adolescence (Cunningham et al., 2002).

Future work will need to address several issues. First, to what extent are the stimulus conditions that elicit the bias in newborns the same as those that elicit maximal activation of the sub-cortical route in adults, and vice-versa? Only a handful of studies have examined whether the stimuli optimal for eliciting newborn preferences are also optimal for eliciting face orienting and enhanced processing in adults (Caldara et al., 2006; Shah et al., 2013; Stein et al., 2011; Tomalski et al., 2009a; Tomalski and Johnson, 2012).

A second issue is the relevance of the two-process model for our understanding of clinical conditions such as autism and developmental prosopagnosia. Klin (this issue) discusses the application of the two-process model to our understanding of autism. We (Senju and Johnson, 2009a) have previously reviewed evidence on eye contact in autism, and speculated on the mechanisms that may underlie the patterns of deficit observed. Developmental prosopagnosia has been less well investigated with reference to the two-process model, but new paradigms that reveal the activity of the sub-cortical route in adults makes this a promising area for future investigation.

851 **Acknowledgements**

852 **MJ** acknowledges core funding from the UK Medical Research
853 **Council** and Birkbeck, University of London. **AS** acknowledges
854 the UK Medical Research Council Career Development Award
855 (G1100252). **PT** acknowledges the Polish National Science Centre
856 awards (2011/03/D/HS6/05655; 2012/07/B/HS6/01464).

857 **References**

- 858 Acerra, F., Burnod, Y., de Schonen, S., 2002. Modelling aspects of face processing in
859 early infancy. *Dev. Sci.* 5, 98–117.
- 860 Adolphs, R., 2003. Is the human amygdala specialized for processing social informa-
861 tion? *Ann. N.Y. Acad. Sci.* 985, 326–340.
- 862 Anisfeld, M., 2005. No compelling evidence to dispute Piaget's timetable of the devel-
863 opment of representational imitation in infancy. In: Hurley, S., Chater, N. (Eds.),
864 *Perspectives on Imitation: From Cognitive Neuroscience to Social Science*. MIT
865 Press, Cambridge, MA, pp. 107–131.
- 866 Anzures, G., Quinn, P.C., Pascalis, O., Slater, A.M., Tanaka, J.W., Lee, K., 2013. Devel-
867 opmental origins of the other-race effect. *Curr. Dir. Psychol. Sci.* 22, 173–178.
- 868 Atkinson, J., 2000. *The Developing Visual Brain*. Oxford University Press, Oxford.
- 869 Bateson, P., Horn, G., 1994. Imprinting and recognition memory: a neural net model.
870 *Anim. Behav.* 48, 695–715.
- 871 Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., Ahluwalia, J., 2000. Is there
872 an innate gaze module? Evidence from human neonates. *Inf. Behav. Dev.* 23, 223.
- 873 Bednar, J., Miikkulainen, R., 2002. Neonatal learning of faces: interactions between
874 genetic and environmental inputs. In: *Proceedings of the 24th Annual Confer-
875 ence of the Cognitive Science Society*, pp. 107–112.
- 876 Bednar, J.A., Miikkulainen, R., 2003. Learning innate face preferences. *Neural Com-
877 put.* 15, 1525–1557.
- 878 Berman, R.A., Wurtz, R.H., 2010. Functional identification of a pulvinar path from
879 superior colliculus to cortical area MT. *J. Neurosci.* 30, 6342–6354.
- 880 Bertini, C., Cecere, R., Ladavas, E., 2013. I am blind, but I “see” fear. *Cortex* 49, 985–993.
- 881 Bolhuis, J.J., 1991. Mechanisms of avian imprinting: a review. *Biol. Rev. Camb. Philos.
882 Soc.* 66, 303–345.
- 883 Bolhuis, J.J., McCabe, B.J., Horn, G., 1986. Androgens and imprinting: differential
884 effects of testosterone on filial preference in the domestic chick. *Behav. Neurosci.*
885 100, 51–56.
- 886 Boyer, J.L., Harrison, S.T.R., 2005. Unconscious processing of orienting and color
887 without primary visual cortex. *PNAS* 102, 16875–16879.
- 888 Brothers, L., 1990. The neural basis of primate social communication. *Motiv. Emot.*
889 14, 81–91.
- 890 Burra, N., Hervais-Adelman, A., Kerzel, D., Tamietto, M., de Gelder, B., Pegna, A.J.,
891 2013. Amygdala activation for eye contact despite complete cortical blindness.
892 *J. Neurosci.* 33, 10483–10489.
- 893 Caldara, R., Seghier, M.L., Rossion, B., Lazeyras, F., Michel, C., Hauert, C.A., 2006. The
894 fusiform face area is tuned for curvilinear patterns with more high-contrast
895 elements in the upper part. *NeuroImage* 31, 313–319.
- 896 Calder, A.J., Beaver, J.D., Winston, J.S., Dolan, R.J., Jenkins, R., Eger, E., Henson, R.N.,
897 2007. Separate coding of different gaze directions in the superior temporal sul-
898 cus and inferior parietal lobule. *Curr. Biol.* 17, 20–25.
- 899 Cecere, R., Bertini, C., Ladavas, E., 2013. Differential contribution of cortical and sub-
900 cortical visual pathways to the implicit processing of emotional faces: a tDCS
901 study. *J. Neurosci.* 33, 6469–6475.
- 902 **Q10** Chien, S.H., 2011. No more top-heavy bias: infants and adults prefer upright faces
903 but not top-heavy geometric or face-like patterns. *J. Vis.* 11.
- 904 Chien, S.H.-L., Hsu, H.-Y., Su, B.-H., 2010. Discriminating “top-heavy” versus
905 “bottom-heavy” geometric patterns in 2- to 4.5-month-old infants. *Vis. Res.* 50,
906 2029–2036.
- 907 Cohen Kadosh, K., Cohen Kadosh, R., Dick, F., Johnson, M.H., 2011. Developmen-
908 tal changes in effective connectivity in the emerging core face network. *Cereb.
909 Cortex* 21, 1389–1394.
- 910 Cohen Kadosh, K., Johnson, M.H., Henson, R.N., Dick, F., Blakemore, S.J., 2013. Differ-
911 ential face-network adaptation in children, adolescents and adults. *NeuroImage*
912 69, 11–20.
- 913 Conley, M., Lachica, E.A., Casagrande, V.A., 1985. Demonstration of ipsilateral
914 retinocollicular projections in tree shrew. *Brain Res.* 346, 181–185.
- 915 Conty, L., N'Diaye, K., Tijus, C., George, N., 2007. When eye creates the contact!
916 ERP evidence for early dissociation between direct and averted gaze motion
917 processing. *Neuropsychologia* 45, 3024–3037.
- 918 Conty, L., Tijus, C., Hugueville, L., Coelho, E., George, N., 2006. Searching for asymme-
919 tries in the detection of gaze contact versus averted gaze under different head
920 views: a behavioural study. *Spat. Vis.* 19, 529–545.
- 921 Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven
922 attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
- 923 Costafreda, S.G., Brammer, M.J., David, A.S., Fu, C.H.Y., 2008. Predictors of amygdala
924 activation during the processing of emotional stimuli: a meta-analysis of 385
925 PET and fMRI studies. *Brain Res. Rev.* 58, 57–70.
- 926 Crouzet, S.M., Kirchner, H., Thorpe, S.J., 2010. Fast saccades toward faces: face detec-
927 tion in just 100 ms. *J. Vis.* 10, 16.11–17.
- 928 Csibra, G., Gergely, G., 2009. Natural pedagogy. *Trends Cogn. Sci.* 13, 148–153.
- Csibra, G., Tucker, L.A., Volein, A., Johnson, M.H., 2000. Cortical development and sac-
cade planning: the ontogeny of the spike potential. *NeuroReport* 11, 1069–1073.
- Cunningham, M.G., Bhattacharyya, S., Benes, F.M., 2002. Amygdalo-cortical sprout-
ing continues into early adulthood: implications for the development of
normal and abnormal function during adolescence. *J. Comp. Neurol.* 453,
116–130.
- Davies, D.C., Horn, G., McCabe, B.J., 1985. Noradrenaline and learning: the effects of
the noradrenergic neurotoxin DSP4 on imprinting in the domestic chick. *Behav.
Neurosci.* 99, 652–660.
- de Gelder, B., Stekelenburg, J.J., 2005. Naso-temporal asymmetry of the N170 for
processing faces in normal viewers but not in developmental prosopagnosia.
Neurosci. Lett. 376, 40–45.
- de Gelder, B., Vroomen, J., Pourtois, G., Weiskrantz, L., 1999. Non-conscious recog-
nition of affect in the absence of striate cortex. *NeuroReport* 10, 3759–3763.
- de Schonen, S., Mathivet, H., 1989. First come, first served: a scenario about the devel-
opment of hemispheric specialization in face recognition during early infancy.
Eur. Bull. Cogn. Psychol. 9, 3–44.
- Doi, H., Shinohara, K., 2013. Unconscious presentation of fearful face modulates
electrophysiological responses to emotional prosody. *Cereb. Cortex.* **Q11** 946
- Eimer, M., 2011. The face-sensitive N170 component of the event-related brain
potential. In: Calder, A.J., Rhodes, G., Johnson, M.H., Haxby, J. (Eds.), *The Oxford
947 Handbook of Face Perception*. Oxford University Press, Oxford, pp. 329–344.
- Emery, N.J., 2000. The eyes have it: the neuroethology, function and evolution of
social gaze. *Neurosci. Biobehav. Rev.* 24, 581–604.
- Farroni, T., Chiarelli, A.M., Lloyd-Fox, S., Massaccesi, S., Merla, A., Di Gangi, V.,
Mattarello, T., Faraguna, D., Johnson, M.H., 2013. Infant cortex responds to other
humans from shortly after birth. *Sci. Rep.* 3, 2851.
- Farroni, T., Csibra, G., Simion, G., Johnson, M.H., 2002. Eye contact detection in
humans from birth. *PNAS* 99, 9602–9605.
- Farroni, T., Johnson, M.H., Menon, E., Zulian, L., Faraguna, D., Csibra, G., 2005. New-
borns' preference for face-relevant stimuli: effects of contrast polarity. *PNAS*
102, 17245–17250.
- Farroni, T., Menon, E., Johnson, M.H., 2006. Factors influencing newborns' preference
for faces with eye contact. *J. Exp. Child Psychol.* 95, 298–308.
- Farroni, T., Menon, E., Rigato, S., Johnson, M.H., 2007. The perception of facial expres-
sions in newborns. *Eur. J. Dev. Psychol.* 4, 2–13.
- Gauthier, I., Nelson, C.A., 2001. The development of face expertise. *Curr. Opin. Neu-
robiol.* 11, 219–224.
- George, N., Driver, J., Dolan, R., 2001. Seeing gaze-direction modulates fusiform activ-
ity and its coupling with other brain areas during face processing. *NeuroImage*
13, 1102–1112.
- Gliga, T., Csibra, G., 2007. Seeing the face through the eyes: a developmental per-
spective on face expertise. *Prog. Brain Res.* 164, 323–339.
- Go, T., Konishi, Y., 2008. Neonatal oral imitation in patients with severe brain dam-
age. *PLoS One* 3, e3668.
- Grossmann, T., Johnson, M.H., 2007. The development of the social brain in human
infancy. *Eur. J. Neurosci.* 25, 909–919.
- Grossmann, T., Johnson, M.H., 2013. The early development of the brain bases for
social cognition. In: Ochsner, K., Kosslyn, S.M. (Eds.), *The Oxford Handbook of
976 Cognitive Neuroscience*. Oxford University Press, Oxford, pp. 257–274.
- Hershler, O., Golan, T., Bentin, S., Hochstein, S., 2010. The wide window of face
977 detection. *J. Vis.* 10, 21.
- Hinde, R.A., 1961. Factors governing changes in strength of a partially inborn
978 response, as shown by mobbing behaviour of chaffinch (*Fringilla coelebs*). 3.
Interaction of short-term and long-term incremental and decremental effects.
Proc. R. Soc., Ser. B—Biol. Sci. 153, 398.
- Holliday, I.E., Anderson, S.J., Harding, G.F.A., 1997. Magnetoencephalographic
985 evidence for non-geniculostriate visual input to human cortical area V5. *Neu-
986 ropsychologia* 35, 1139–1146.
- Hood, B.M., Macrae, C.N., Cole-Davies, V., Dias, M., 2003. Eye remember you: the
987 effects of gaze direction on face recognition in children and adults. *Dev. Sci.* 6,
988 69–73.
- Horn, G., 1985. Imprinting and the neural basis of memory. In: Will, B., Schmitt,
991 P., Dalrymple-Alford, J.C. (Eds.), *Brain Plasticity, Learning and Memory*. Plenum,
992 New York, NY, pp. 13–19.
- Horn, G., Johnson, M.H., 1989. Memory systems in the chick: dissociations and neu-
993 ronal analysis. *Neuropsychologia* 27, 1–22.
- Horn, G., McCabe, B.J., 1984. Predispositions and preferences: effects on imprinting
994 of lesions to the chick brain. *Anim. Behav.* 32, 288–292.
- Huang, L., Song, Y., Li, J., Zhen, Z., Yang, Z., Liu, J., 2014. Individual differences in cor-
995 tical face selectivity predict behavioral performance in face recognition. *Front.
996 Hum. Neurosci.* 8, 483.
- Isbell, L.A., 2006. Snakes as agents of evolutionary change in primate brains. *J. Hum.
1000 Evol.* 51, 1–35.
- Iwai, E., Yukie, M., 1987. Amygdalofugal and amygdalopetal connections with
modality-specific visual cortical areas in macaques (*Macaca fuscata*, *M. mulatta*,
1004 *M. fascicularis*). *J. Comp. Neurol.* 261, 362–387.
- Jiang, Y., He, S., 2006. Cortical responses to invisible faces: dissociating subsystems
1005 for facial-information processing. *Curr. Biol.* 16, 2023–2029.
- Johnson, M.H., 2005. Subcortical face processing. *Nat. Rev. Neurosci.* 6, 766–774.
- Johnson, M.H., 2011. Face processing as a brain adaptation at multiple timescales.
1007 *Q. J. Exp. Psychol. (Hove)* 64, 1873–1888.
- Johnson, M.H., Bolhuis, J.J., Horn, G., 1985. Interaction between acquired preferences
1008 and developing predispositions during imprinting. *Anim. Behav.* 33, 1000–1006.
- Johnson, M.H., Dziurawiec, S., Ellis, H., Morton, J., 1991. Newborns' preferential
1009 tracking of face-like stimuli and its subsequent decline. *Cognition* 40, 1–19.

- Johnson, M.H., Farroni, T., Brockbank, M., Simion, F., 2000. Preferential orienting to faces in 4 month olds: analysis of temporal–nasal visual field differences. *Dev. Sci.* 3, 41–45.
- Johnson, M.H., Grossmann, T., Cohen Kadosh, K., 2009. Mapping functional brain development: building a social brain through interactive specialization. *Dev. Psychol.* 45, 151–159.
- Johnson, M.H., Horn, G., 1986. Dissociation of recognition memory and associative learning by a restricted lesion of the chick forebrain. *Neuropsychologia* 24, 329–340.
- Johnson, M.H., Horn, G., 1987. The role of a restricted region of the chick forebrain in the recognition of individual conspecifics. *Behav. Brain Res.* 23, 269–275.
- Johnson, M.H., Horn, G., 1988. Development of filial preferences in dark-reared chicks. *Anim. Behav.* 36, 675–683.
- Johnson, M.H., Morton, J., 1991. *Biology and Cognitive Development: The Case of Face Recognition*. Blackwell, Oxford.
- Jones, S.S., 2009. The development of imitation in infancy. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 364, 2325–2335.
- Kaas, J.H., Lyon, D.C., 2007. Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. *Brain Res. Rev.* 55, 285–296.
- Kanwisher, N., 2010. Functional specificity in the human brain a window into the functional architecture of the mind. *PNAS* 107, 11163–11170.
- Khalid, S., Finkbeiner, M., Konig, P., Ansorge, U., 2013. Subcortical human face processing? Evidence from masked priming. *J. Exp. Psychol. Hum. Percept. Perform.* 39, 989–1002.
- Kiss, M., Eimer, M., 2008. ERPs reveal subliminal processing of fearful faces. *Psychophysiology* 45, 318–326.
- Kleiner, K.A., Banks, M.S., 1987. Stimulus energy does not account for 2-month-olds face preferences. *J. Exp. Psychol.—Hum. Percept. Perform.* 13, 594–600.
- Kobayashi, H., Kohshima, S., 1997. Unique morphology of the human eye. *Nature* 387, 767–768.
- Kobayashi, H., Kohshima, S., 2001. Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *J. Hum. Evol.* 40, 419–435.
- Langton, S.R., Law, A.S., Burton, A.M., Schweinberger, S.R., 2008. Attention capture by faces. *Cognition* 107, 330–342.
- Leh, S.E., Mullen, K.T., Ptitto, A., 2006. Absence of S-cone input in human blindsight following hemispherectomy. *Eur. J. Neurosci.* 24, 2954–2960.
- Leo, F., Bolognini, N., Passamonti, C., Stein, B.E., Ladavas, E., 2008. Cross-modal localization in hemianopia: new insights on multisensory integration. *Brain* 131, 855–865.
- Liddell, B.J., Brown, K.J., Kemp, A.H., Barton, M.J., Das, P., Peduto, A., Gordon, E., Williams, L.M., 2005. A direct brainstem–amygdala–cortical ‘alarm’ system for subliminal signals of fear. *NeuroImage* 24, 235–243.
- Linke, R., De Lima, A.D., Schwegler, H., Pape, H.C., 1999. Direct synaptic connections of axons from superior colliculus with identified thalamo–amygdaloid projection neurons in the rat: possible substrates of a subcortical visual pathway to the amygdala. *J. Comp. Neurol.* 403, 158–170.
- LoBue, V., DeLoache, J.S., 2010. Superior detection of threat-relevant stimuli in infancy. *Dev. Sci.* 13, 221–228.
- Luo, Q., Holroyd, T., Jones, M., Hendler, T., Blair, J., 2007. Neural dynamics for facial threat processing as revealed by gamma band synchronization using MEG. *NeuroImage* 34, 839–847.
- Macchi Cassia, V., Simion, F., Umiltà, C., 2001. Face preference at birth: the role of an orienting mechanism. *Dev. Sci.* 4, 101–108.
- Macrae, C.N., Hood, B.M., Milne, A.B., Rowe, A.C., Mason, M.F., 2002. Are you looking at me? Eye gaze and person perception. *Psychol. Sci.* 13, 460–464.
- Maior, R.S., Hori, E., Barros, M., Teixeira, D.S., Tavares, M.C.H., Ono, T., Nishijo, H., Tomaz, C., 2011. Superior colliculus lesions impair threat responsiveness in infant capuchin monkeys. *Neurosci. Lett.* 504, 257–260.
- Maior, R.S., Hori, E., Tomaz, C., Ono, T., Nishijo, H., 2010. The monkey pulvinar neurons differentially respond to emotional expressions of human faces. *Behav. Brain Res.* 215, 129–135.
- McCabe, B.J., Cipolla-Neto, J., Horn, G., Bateson, P., 1982. Amnesic effects of bilateral lesions placed in the hyperstriatum ventrale of the chick after imprinting. *Exp. Brain Res.* 48, 13–21.
- Meltzoff, A.N., Moore, M.K., 1977. Imitation of facial and manual gestures by neonates. *Science* 198, 75–78.
- Meltzoff, A.N., Moore, M.K., 1989. Imitation in newborn infants: exploring the range of gestures imitated and the underlying mechanisms. *Dev. Psychol.* 25, 954–962.
- Moriceau, S., Sullivan, R.M., 2006. Maternal presence serves as a switch between learning fear and attraction in infancy. *Nat. Neurosci.* 9, 1004–1006.
- Morris, J.S., Ohman, A., Dolan, R.J., 1999. A subcortical pathway to the right amygdala mediating “unseen” fear. *PNAS* 96, 1680–1685.
- Morton, J., Johnson, M.H., 1991. CONSPEC and CONLERN: a two-process theory of infant face recognition. *Psychol. Rev.* 98, 164–181.
- Morton, J., Johnson, M.H., Maurer, D., 1990. On the reasons for newborns’ responses to faces. *Inf. Behav. Dev.* 13, 99–103.
- Nakano, T., Higashida, N., Kitazawa, S., 2013. Facilitation of face recognition through the retino–tectal pathway. *Neuropsychologia* 51, 2043–2049.
- Nelson, C.A., 2001. The development and neural bases of face recognition. *Inf. Child Dev.* 10, 3–18.
- Nelson, C.A., Dolgin, K., 1985. The generalized discrimination of facial expressions by 7-month-old infants. *Child Dev.* 56, 58.
- Nguyen, M.N., Hori, E., Matsumoto, J., Tran, A.H., Ono, T., Nishijo, H., 2013. Neuronal responses to face-like stimuli in the monkey pulvinar. *Eur. J. Neurosci.* 37, 35–51.
- O’Reilly, R.C., Johnson, M.H., 1994. Object recognition and sensitive periods: a computational analysis of visual imprinting. *Neural Comput.* 6, 357–389.
- Pasley, B.N., Mayes, L.C., Schultz, R.T., 2004. Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42, 163–172.
- Pelphrey, K.A., Viola, R.J., McCarthy, G., 2004. When strangers pass: processing of mutual and averted social gaze in the superior temporal sulcus. *Psychol. Sci.* 15, 598–603.
- Peltola, M.J., Leppanen, J.M., Maki, S., Hietanen, J.K., 2009. Emergence of enhanced attention to fearful faces between 5 and 7 months of age. *Soc. Cogn. Affect. Neurosci.* 4, 134–142.
- Perry, V.H., Cowey, A., 1985. The ganglion cell and cone distribution in the monkey’s retina: implications for central magnification factors. *Vis. Res.* 25, 1795–1810.
- Pessoa, L., Adolphs, R., 2010. Emotion processing and the amygdala: from a ‘low road’ to ‘many roads’ of evaluating biological significance. *Nat. Rev. Neurosci.* 11, 773–783.
- Pourtois, G., Schettino, A., Vuilleumier, P., 2013. Brain mechanisms for emotional influences on perception and attention: what is magic and what is not. *Biol. Psychol.* 92, 492–512.
- Pourtois, G., Thut, G., Grave de Peralta, R., Michel, C., Vuilleumier, P., 2005. Two electrophysiological stages of spatial orienting towards fearful faces: early temporo–parietal activation preceding gain control in extrastriate visual cortex. *NeuroImage* 26, 149–163.
- Ptitto, A., Leh, S.E., 2007. Neural substrates of blindsight after hemispherectomy. *Neuroscientist* 13, 506–518.
- Quinn, P.C., Slater, A., 2003. *Face Perception in Infancy and Early Childhood: Current Perspectives*.
- Rakison, D.H., Derringer, J., 2008. Do infants possess an evolved spider-detection mechanism? *Cognition* 107, 381–393.
- Ray, E., Heyes, C., 2011. Imitation in infancy: the wealth of the stimulus. *Dev. Sci.* 14, 92–105.
- Ro, T., Friggel, A., Lavie, N., 2007. Attentional biases for faces and body parts. *Vis. Cogn.* 15, 322–348.
- Ro, T., Shelton, D., Lee, O.L., Chang, E., 2004. Extrageniculate mediation of unconscious vision in transcranial magnetic stimulation-induced blindsight. *PNAS* 101, 9933–9935.
- Rodman, H.R., Gross, C.G., Albright, T.D., 1989. Afferent basis of visual response properties in area MT of the macaque. I. Effects of striate cortex removal. *J. Neurosci.* 9, 2033–2050.
- Romanski, L.M., Giguere, M., Bates, J.F., Goldman-Rakic, P.S., 1997. Topographic organization of medial pulvinar connections with the prefrontal cortex in the rhesus monkey. *J. Comp. Neurol.* 379, 313–332.
- Rosa, M.G., Tweeddale, R., Elston, G.N., 2000. Visual responses of neurons in the middle temporal area of New World monkeys after lesions of striate cortex. *J. Neurosci.* 20, 5552–5563.
- Rotshtein, P., Richardson, M.P., Winston, J.S., Kiebel, S.J., Vuilleumier, P., Eimer, M., Driver, J., Dolan, R.J., 2010. Amygdala damage affects event-related potentials for fearful faces at specific time windows. *Hum. Brain Mapp.* 31, 1089–1105.
- Saalmann, Y.B., Pinsk, M.A., Wang, L., Li, X., Kastner, S., 2012. The pulvinar regulates information transmission between cortical areas based on attention demands. *Science (New York, NY)* 337, 753–756.
- Savazzi, S., Fabri, M., Rubboli, G., Paggi, A., Tassinari, C.A., Marzi, C.A., 2007. Interhemispheric transfer following callosotomy in humans: role of the superior colliculus. *Neuropsychologia* 45, 2417–2427.
- Schmoleky, M.T., Wang, Y., Hanes, D.P., Thompson, K.G., Leutgeb, S., Schall, J.D., Leventhal, A.G., 1998. Signal timing across the macaque visual system. *J. Neurophysiol.* 79, 3272–3278.
- Schneider, K.A., Kastner, S., 2005. Visual responses of the human superior colliculus: a high-resolution functional magnetic resonance imaging study. *J. Neurophysiol.* 94, 2491–2503.
- Senju, A., Hasegawa, H., 2005. Direct gaze captures visuospatial attention. *Vis. Cogn.* 12, 127–144.
- Senju, A., Johnson, M.H., 2009a. Atypical eye contact in autism: models, mechanisms and development. *Neurosci. Biobehav. Rev.* 33, 1204–1214.
- Senju, A., Johnson, M.H., 2009b. The eye contact effect: mechanisms and development. *Trends Cogn. Sci.* 13, 127–134.
- Senju, A., Kikuchi, Y., Hasegawa, T., Tojo, Y., Osanai, H., 2008. Is anyone looking at me? Direct gaze detection in children with and without autism. *Brain Cogn.* 67, 127–139.
- Senju, A., Tojo, Y., Yaguchi, K., Hasegawa, T., 2005. Deviant gaze processing in children with autism: an ERP study. *Neuropsychologia* 43, 1297–1306.
- Shah, P., Gaule, A., Bird, G., Cook, R., 2013. Robust orienting to protofacial stimuli in autism. *Curr. Biol.* 23, R1087–R1088.
- Simion, F., Macchi Cassia, V., Turati, C., Valenza, E., 2003. Non-specific perceptual biases at the origins of face processing. In: Pascalis, O., Slater, A. (Eds.), *The Development of Face Processing in Infancy and Early Childhood: Current Perspectives*. Nova Science Publisher, New York, NY, pp. 13–26.
- Simion, F., Valenza, E., Umiltà, C., Dalla Barba, B., 1995. In Newborns Preferential Orienting to Faces is Subcortically Mediated.
- Simion, F., Valenza, E., Umiltà, C., Dalla Barba, B., 1998. Preferential orienting to faces in newborns: a temporal–nasal asymmetry. *J. Exp. Psychol.—Hum. Percept. Perform.* 24, 1399–1405.
- Slater, A., Quinn, P.C., Hayes, R., Brown, E., 2000. The role of facial orientation in newborn infants’ preference for attractive faces. *Dev. Sci.* 3, 181–185.
- Slater, A., Quinn, P.C., Kelly, D.J., Lee, K., Longmore, C.A., McDonald, P.R., Pascalis, O., 2010. The shaping of the face space in early infancy: becoming a native face processor. *Child Dev. Perspect.* 4, 205–211.

Q12

- 1187 Slater, A., Von der Schulenburg, C., Brown, E., Badenoche, M., Butterworth, G., Parsons,
1188 S., Samuels, C., 1998. Newborn infants prefer attractive faces. *Inf. Behav. Dev.* 21,
1189 345–354. 1222
- 1190 Stefanacci, L., Amaral, D.G., 2000. Topographic organization of cortical inputs to the
1191 lateral nucleus of the macaque monkey amygdala: a retrograde tracing study. *J.*
1192 *Comp. Neurol.* 421, 52–79. 1223
- 1193 Stein, T., Peelen, M.V., Sterzer, P., 2011. Adults' awareness of faces follows newborns'
1194 looking preferences. *PLoS One* 6, e29361. 1225
- 1195 Stein, T., Peelen, M.V., Sterzer, P., 2012a. Eye gaze adaptation under interocular
1196 suppression. *J. Vis.* 12, 1. 1226
- 1197 Stein, T., Sterzer, P., Peelen, M.V., 2012b. Privileged detection of conspecifics: evi-
1198 dence from inversion effects during continuous flash suppression. *Cognition*
1199 125, 64–79. 1227
- 1200 Stepniewska, I., 2004. The pulvinar complex. In: Kaas, J.H., Collins, C.E. (Eds.), *The*
1201 *Primate Visual System*. CRC Press, Boca Raton, FL, pp. 53–80. 1228
- 1202 Sugita, Y., 2008. Face perception in monkeys reared with no exposure to faces. *PNAS*
1203 105, 394–398. 1229
- 1204 Sullivan, R.M., Landers, M., Yeaman, B., Wilson, D.A., 2000. Good memories of bad
1205 events in infancy. *Nature* 407, 38–39. 1230
- 1206 Susskind, J.M., Lee, D.H., Cusi, A., Feiman, R., Grabski, W., Anderson, A.K., 2008.
1207 Expressing fear enhances sensory acquisition. *Nat. Neurosci.* 11, 843–850. 1231
- 1208 Suzuki, S., Cavanagh, P., 1995. Facial organization blocks access to low-level features:
1209 an object inferiority effect. *J. Exp. Psychol.: Hum. Percept. Perform.* 21, 901–913. 1232
- 1210 Sylvester, R., Josephs, O., Driver, J., Rees, G., 2007. Visual fMRI responses in human
1211 superior colliculus show a temporal–nasal asymmetry that is absent in lateral
1212 geniculate and visual cortex. *J. Neurophysiol.* 97, 1495–1502. 1233
- 1213 Tamietto, M., Cauda, F., Corazzini, L.L., Savazzi, S., Marzi, C.A., Goebel, R., Weiskrantz,
1214 L., de Gelder, B., 2010. Collicular vision guides nonconscious behavior. *J. Cogn.*
1215 *Neurosci.* 22, 888–902. 1234
- 1216 Theeuwes, J., Van der Stigchel, S., 2006. Faces capture attention: evidence from
1217 inhibition of return. *Vis. Cogn.* 13, 657–665. 1235
- 1218 Thomas, K.M., Drevets, W.C., Whalen, P.J., Eccard, C.H., Dahl, R.E., Ryan, N.D., Casey,
1219 B.J., 2001. Amygdala response to facial expressions in children and adults. *Biol.*
1220 *Psychiatry* 49, 309–316. 1236
- 1221 Tomalski, P., Csibra, G., Johnson, M.H., 2009a. Rapid orienting toward face-like stim-
1222 uli with gaze-relevant contrast information. *Perception* 38, 569–578. 1237
- 1223 Tomalski, P., Johnson, M.H., 2012. Cortical sensitivity to contrast polarity and ori-
1224 entation of faces is modulated by temporal–nasal hemifield asymmetry. *Brain*
1225 *Imaging Behav.* 6, 88–101. 1238
- 1226 Tomalski, P., Johnson, M.H., Csibra, G., 2009b. Temporal–nasal asymmetry of rapid
1227 orienting to face-like stimuli. *NeuroReport* 20, 1309–1312. 1239
- 1228 Troiani, V., Price, E.T., Schultz, R.T., 2012. Unseen fearful faces promote amygdala
1229 guidance of attention. *Soc. Cogn. Affect. Neurosci.* 1240
- 1229 Troiani, V., Schultz, R.T., 2013. Amygdala, pulvinar, and inferior parietal cortex con-
1230 tribute to early processing of faces without awareness. *Front. Hum. Neurosci.* 7,
1231 241. 1241
- 1232 Turati, C., Simion, F., 2002. Newborns' recognition of changing and unchanging
1233 aspects of schematic faces. *J. Exp. Child Psychol.* 83, 239–261. 1242
- 1234 Turati, C., Simion, F., Milani, I., Umiltà, C., 2002. Newborns preference for faces: what
1235 is crucial? *Dev. Psychol.* 38, 875–882. 1243
- 1236 VanRullen, R., 2006. On second glance: still no high-level pop-out effect for faces.
1237 *Vis. Res.* 46, 3017–3027. 1244
- 1238 Vlamings, P.H., Goffaux, V., Kemner, C., 2009. Is the early modulation of brain activity
1239 by fearful facial expressions primarily mediated by coarse low spatial frequency
1240 information? *J. Vis.* 9 (12), 11–13. 1245
- 1241 Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2003. Distinct spatial frequency
1242 sensitivities for processing faces and emotional expressions. *Nat. Neurosci.* 6,
1243 624–631. 1246
- 1244 Waleszczyk, W.J., Nagy, A., Wypych, M., Berenyi, A., Paroczy, Z., Eordeghe, G., Ghaz-
1245 aryan, A., Benedek, G., 2007. Spectral receptive field properties of neurons in the
1246 feline superior colliculus. *Exp. Brain Res.* 181, 87–98. 1247
- 1247 Ward, R., Calder, A.J., Parker, M., Arend, I., 2007. Emotion recognition following
1248 human pulvinar damage. *Neuropsychologia* 45, 1973–1978. 1248
- 1249 Ward, R., Danziger, S., Bamford, S., 2005. Response to visual threat following damage
1250 to the pulvinar. *Curr. Biol.* 15, 571–573. 1249
- 1251 Webster, M.J., Ungerleider, L.G., Bachevalier, J., 1991. Connections of inferior tem-
1252 poral areas TE and TEO with medial temporal lobe structures in infant and adult
1253 monkeys. *J. Neurosci.* 11, 1095–1116. 1254
- 1254 Weiskrantz, L., 1996. Blindsight revisited. *Curr. Opin. Neurobiol.* 6, 215–220. 1255
- 1255 Wilkinson, N., Paikan, A., Gredeback, G., Rea, F., Metta, G., 2014. Staring us in the
1256 face? An embodied theory of innate face preference. *Dev. Sci.* 1256