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Highlights:

- We outline the Johnson & Morton (1991) two-process model of face processing development
- We present modifications based on two decades of research with humans and other primates
- We propose an extension of the model to eye contact detection
- We outline an extension of the model to subcortical face processing
- We conclude with discussion of outstanding caveats and future directions of research

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

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Abstract

Johnson and Morton (1991) 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.

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

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 this model had clear relevance to memory (see Bateson, this issue), it has also had a broader impact on the fields of typical and atypical social development in humans and the cognitive neuroscience of face processing. In particular, Johnson and Morton (1991; Morton and Johnson, 1991) used the chick model as inspiration for their two-process theory of the development of face processing in humans.

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

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

2. The two-process theory of filial imprinting

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

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

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

Horn and his collaborators began to answer this question after reviewing the results of a series of experiments in which stimulus-dependent effects of IMM lesions were observed (Horn and McCabe, 1984). They noticed that while chicks trained on an artificial stimulus such as a rotating red box were severely impaired by IMM lesions placed either before or after training on an object, chicks imprinted on a stuffed hen were only mildly impaired in their preference. Thereafter, other neurophysiological manipulations also revealed differences between the hen-trained and box-trained birds. In one example, administration of the neurotoxin DSP4 (which depletes forebrain levels of the neurotransmitter norepinephrine) resulted in a severe impairment of preference in birds trained on the red box, but only a mild impairment in birds trained on the stuffed hen (Davies et al., 1985). In contrast to this, levels of testosterone correlated with preference for the stuffed hen, but not preference for the red box (Bolhuis et al., 1986).

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

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

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

There are several different ways in which the predisposition could constrain the information acquired by the IMM system. For example, the information in the predisposition could act as a sensory 'filter' or template through which information had to pass before reaching the IMM system. However, the currently available evidence is consistent with the view that the input to the IMM system is selected simply as a result of the predisposition biasing the chick to orient toward any hen-like objects in the environment. Given that the species-typical environment of the chick includes a mother hen in close proximity, and that the predisposition includes adequate information to pick the hen out from other objects in the early environment, the input to the learning system will be highly selected.

3. The two-process theory of face processing.

In 1991 Morton and Johnson published a two-process theory of the development of face processing in humans (Johnson and Morton, 1991; Morton and Johnson, 1991). 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 toward faces (termed *Conspec*; 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 Conspec served to bias the input to the developing cortical circuitry over the first weeks and months of life. In this way, Conspec 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 & 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 & 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 Figure 1).

Figure 1 about here

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 Conspec 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., 2000; Slater et al., 1998), 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., 1999; Farroni et al., 2005).

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 figure 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 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 Figure 2). At a distance, or in the periphery, a mechanism activated by these stimuli would direct attention toward 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 (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.

3.3 Emerging specialization of cortical face processing areas

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

In the absence of research on the neural basis of face processing at the time of writing their original 1991 paper, Johnson and Morton described Conlern in simple functional terms as "a system that acquires and retains specific information about the visual characteristics of conspecifics". As evidence has accrued over the years, Johnson (2010) has provided a more mechanistic account in which cortical specialization for face processing gradually emerges as a result of accumulating experience, but it is also constrained by intrinsic biases associated with cortical architecture and inter-regional connectivity. This emerging specialisation account can explain evidence that has previously been taken to support either domain-specific (e.g. Kanwisher, 2010) or domain-general (Gauthier and Nelson, 2001; Slater et al., 2010) views of cortical organization of face processing. For example, a series of studies on macaque monkeys which were reared from birth without visual experience with faces has been interpreted as providing support for a innate domain-specific view (Sugita, 2008). Despite their selective visual deprivation the animals still showed clear face preference over objects but did not show greater preference for monkey over human faces, a pattern of preference consistent with the human sub-cortical route (see Johnson 2010 for further discussion). However, a group of previously deprived macaques exposed to human faces for only one month showed rapid experience-dependent perceptual narrowing in their face processing skills: they discriminated between individual human faces far better than monkey faces. A reverse effect was observed for animals exposed to monkey rather than human faces. The process of perceptual narrowing, i.e. the narrowing of the class of visual face-like stimuli that are processed more rapidly and/or efficiently has been demonstrated in infants under 12 months of age in several studies (see Anzures et al., 2013), and is entirely consistent with *Conlern* involving processes of emerging specialization.

Reviews of the now extensive literature from neuroimaging studies with children indicate that adult-like organisation of face-sensitive cortical areas does emerge until after the age of 10 years (e.g. Cohen Kadosh et al., 2011; Cohen Kadosh et al., 2013; for reviews see Johnson, 2011; Johnson et al., 2009). The Interactive Specialization framework describes the developmental process of emerging functional specialization in terms of both intra- and inter-regional cortical connectivity. The same mechanisms have been used to account for the effects of training on faces, and associate with individual differences in face processing skills (Huang et al., 2014).

4. Sub-cortical route in the adult brain

Since Johnson and colleagues (Johnson et al., 1991) demonstrated 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 indirectly. This view was consistent with work in adults at the time apparently showing no “special attention” for faces, or faster detection 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 conspecifics has come from animal research and studies with human neonates. The relative scarcity of human adult data on sub-cortical face processing has lead 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 projections 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 activity 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 toward, face-like stimuli may reflect partially different 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 significant 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 et al., 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 Yukie, 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 toward 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. Firstly, the orienting bias was found in temporal but not in the nasal visual hemifields, consistent with the collicular mediation hypothesis (Tomalski et al., 2009b). Secondly, when viewing naturalistic scenes adults show extremely rapid saccades toward 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 and colleagues (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 & 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., 2007; Ward et al., 2005).

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 Conspec 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 toward 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 dependance 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; Vlamings 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., 2008; Senju et al., 2005), 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 & Johnson, 2009b).

To explain the neural mechanism underlying the eye contact effect, Senju & Johnson (2009b) proposed the fast-track modulator model, which extends the two-systems theory (Figure3). This model proposes that the eye contact effect is mediated by the subcortical face detection pathway discussed in the previous section. We (Senju &

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.

Figure 2 – about here

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 subcortical route mediates the detection of, and orienting toward, 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 & 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 sub-cortical pathway modulates the processing of direct gaze in the cortical pathway. Firstly, 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. Secondly, 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 Figure 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 & 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 centered 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 toward, 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 sub-cortical route not only detects the presence of faces and eye contact, and orients the newborn toward 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.

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Figure legends

Figure 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).

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

Figure 1
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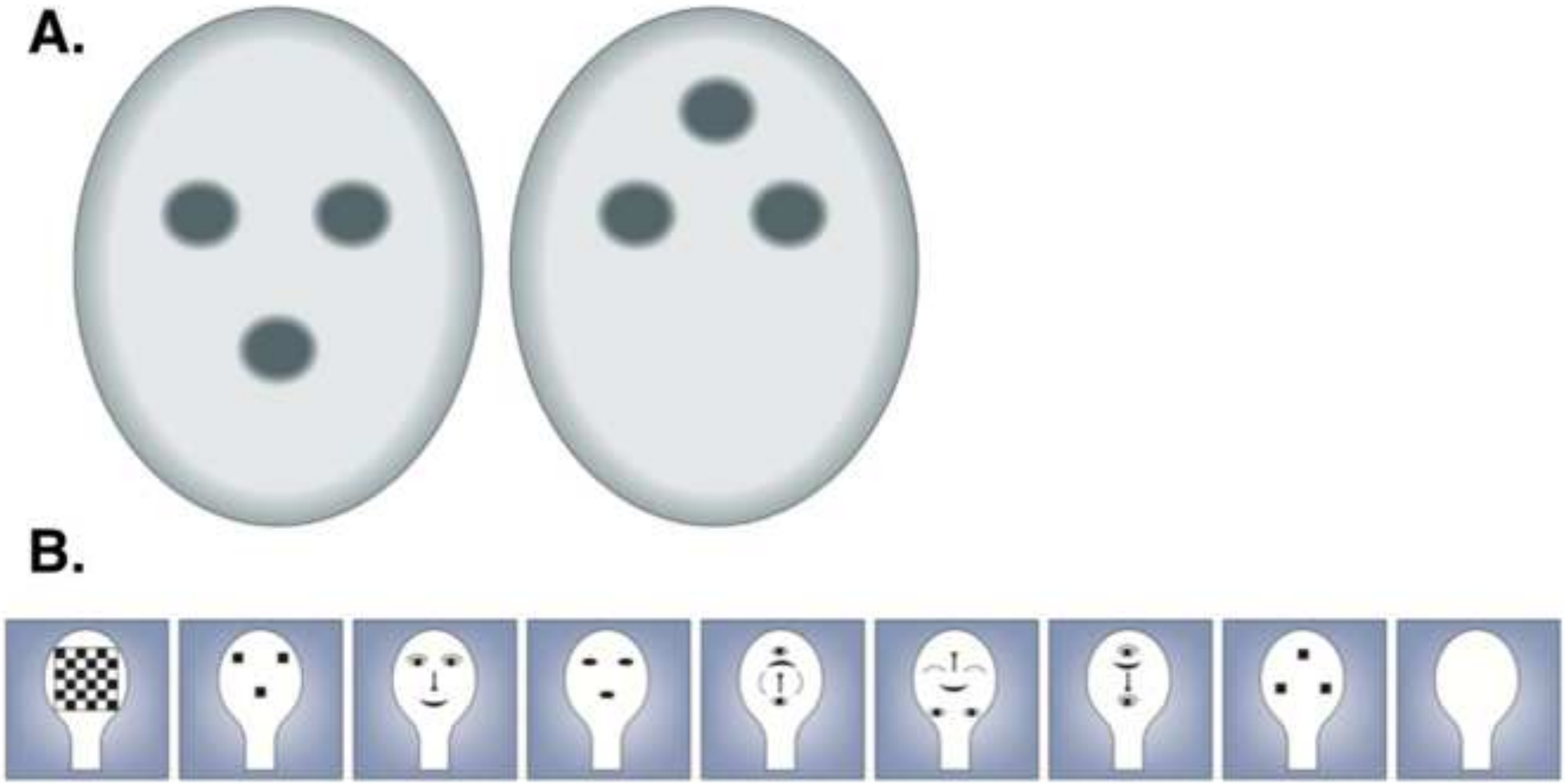

Figure 2
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