Seeing the face through the eyes: A developmental perspective on face expertise

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Abstract

Most people are experts in face recognition. We propose that the special status of this particular body part in telling individuals apart is the result of a developmental process that heavily biases human infants and children to attend towards the eyes of others. We review the evidence supporting this proposal, including neuroimaging results and studies in developmental disorders, like autism. We propose that the most likely explanation of infants' bias towards eyes is the fact that eye gaze serves important communicative functions in humans.

Humans are experts at face processing

Almost all of us are experts in face processing by the time we reach adulthood. We can recognize thousands of individuals in diverse conditions of distance, luminosity or orientation (Maurer et al., 2002), a performance not yet attained by any automatic face recognition system (Zhao et al., 2003). Experimental studies have also shown that these perceptual capacities are not applied to all object categories: while we can tell apart new faces that are very similar to each other even if they are presented for a very short time (Lehky, 2000), we cannot do the same for other objects (Bruce et al., 1991). This extraordinary face expertise is thought to reflect specialized perceptual and neuronal mechanisms. For example, for faces, as opposed to other visual stimuli, we encode not only the composing elements (features) but also their relative distances. This type of encoding is referred to as *configural* (as opposed to *featural*) processing, and its impairment can have dramatic consequences on face recognition (for a review see Maurer et al., 2002). Face perception is also thought to engage a selective network of brain areas, most notably within the fusiform face area (Kanwisher et al., 1997; Haxby et al., 2001).

While there is still controversy on whether people can develop similar expertise for other classes of objects (McKone and Kanwisher, 2005; Bukach et al., 2006), it is widely accepted that faces are the most common and probably the earlier developing domain of expertise. From a functional point of view, the special status of face perception makes sense because only the recognition of individuals allows us to identify our kin, to keep track of friends and enemies, and to maintain group structure and hierarchy. Acquiring specialized face processing mechanisms, either by natural selection during phylogeny, or by intensive learning during ontogeny, seems to be a necessity.

This conclusion appears to be trivial, but it tacitly relies on the intuition that faces provide the main source of perceivable individual differences to be employed in recognition of others. People differ from each other in a number of non-visual characteristics (e.g., voice, odor), but also in a number of non-facial visual aspects. We have differently proportioned bodies and body parts (e.g., hands), and we also move in very distinct ways. Why do we then rely so much on the face in telling people apart? One possible reason could be that faces provide the richest cues of identity. Faces can differ in the morphology of their internal elements, and also in the relative distance among these elements and between the elements and the face contour. Faces also differ in complexion, and in eye and hair color. It is possible that human bodies and body parts simply do not offer as much variability as do faces, and that we would not be able to tell apart as many people on the basis of bodily cues as we can discriminate based on faces.

One way to demonstrate that other body parts can also be used for recognition of individuals is to show that humans succeed in determining a person's identity based on non-facial cues when they are explicitly asked to do so. Addressing this question, researchers have focused on both dynamic and structural properties of bodies. Bodily motion is rich in information, as people can tell someone's identity, gender or age only from point light displays of his or her movement (Hill & Johnston, 2001). Other kinds of information, like kinship, are probably poorly encoded in movement and, more importantly, motion cues are useless when the person is stationary. When focusing on the structural aspects, studies have shown that the human body configuration is processed in a similar way to the configuration of a human face (Reed et al., 2003), and recruits similar brain mechanisms (Stekelenburg & de Gelder, 2004; Gliga & Dehaene-Lambertz, 2005). Brain areas

specialized for processing body structure or motion have been described in the vicinity of face-specific cortical areas (Downing et al., 2001; Astafiev et al., 2004). These areas seem to encode subtle structural differences in a selective manner (for example, discriminating between two different hands but not between two motorcycle parts or noses), just as face-selective areas do (Urgesi et al., 2004). None of these studies, however, addressed directly the question of individual recognition from structural bodily cues. Thus, it is not yet known whether people could use non-facial body-related information for identification, if necessary.

Another way of comparing facial and bodily information for the purpose of individual recognition is to use automatic systems of artificial intelligence. Automatic detection and identification of people from visual scenes is a very active domain of research, mainly because of increased interest in visual surveillance systems. The level of performance of these systems, when using either faces or bodies, could tell us whether one provides potentially more information than the other. Unfortunately, this question is unanswered for the moment, as most of these systems concentrate on face recognition. It is not clear whether this imbalance represents an objectively verified superiority of faces in individual recognition or just the bias of the creators of these systems, who, being human, intuitively turn to the source that they predominantly use for identifying their conspecifics.

Although there is little evidence that body structure is used for identification by people, the potential to do that seems to exist, at least at a neuronal level, as shown by the above mentioned studies (Stekelenburg & de Gelder, 2004; Gliga & Dehaene-Lambertz, 2005). In parallel, studies have shown that, following a long and intense training, people can develop various kinds of expertise: they can recognize individuals of other species: dogs, birds, sheep (Diamond & Carey, 1986; Tanaka &

Taylor, 1991; McNeil & Warrington, 1993), or other classes of objects like cars or artificially created "Greebles" (Gauthier & Tarr, 1997; Gauthier et al., 2000). Thus, the question remains: if it is plausible that people become body experts, why does this expertise not develop? What makes faces so special that they become the primary source of recognition of individuals in humans?

In the following sections, we shall offer a developmental answer to this question. We propose that people become face experts because, from birth, children pay more attention to, and hence get more experience with, faces than with other body parts. This preferential treatment of face, we shall suggest, is due to a special interest in the eyes, which, in humans, function as an important communication device.

The interest in faces develops early

The first signs of a specialization for face processing can be seen very early, during the first days of life. In an influential study, Johnson et al. (1991) showed that, only a few hours after birth, infants follow a face-like schematic pattern more persistently than other patterns. This preference decreased between 1 and 2 months of age, but reappeared later under different presentation conditions. The movement of the face stimulus was not necessary at this later age, and photographs of faces were better at triggering the preference than were schematic faces (Johnson et al., 1991; Mondloch et al., 1999). These results led Morton and Johnson (1991) to propose the CONSPEC-CONLEARN model. The model hypothesized that innate orienting mechanisms are responsible for the initial face following in neonates (the CONSPEC mechanism), which were possibly implemented in sub-cortical structures (the superior colliculus, the pulvinar, or the amygdala). The sub-cortical origin of this

face preference is supported by the special conditions in which it can be triggered –

the stimuli have to be in motion in the periphery or presented in the temporal visual

field (Simion et al., 1998). A couple of months later, the visual cortex would start

playing more and more of a role in face processing, allowing finer face encoding and

thus better face recognition (the CONLEARN mechanism).

This interpretation of the visual properties that drive newborns' face

preference has recently been challenged. Macchi Cassia and colleagues (2004)

showed that the exact positioning of the facial elements is not important in triggering

a preference, as long as the display is symmetric and there are more elements in its

upper part (the "top-heavy" hypothesis). Moreover, a general preference for "top-

heavy", compared to "bottom-heavy" stimuli, even in the absence of any

resemblance to faces, was found in the newborn. These authors concluded that a

non-specific bias, induced by an upper-visual-field advantage in visual sensitivity,

drives the initial face preference. Having more elements in their upper part, faces

take advantage of this initial bias by capturing newborns' attention. Interestingly, this

bias seems to be still present in adulthood, as the fusiform face area is activated

more by "top-heavy" stimuli, similar to those used in the infant studies (Caldara et al.,

2006).

However, one can also argue that this bias evolved specifically for face

processing. Whether or not a visual mechanism acts as a face-preference bias

depends not on a goodness-of-fit function to an ideal face template, but on its

efficiency in drawing infants' attention to faces in a natural environment. If a bias

toward "top-heavy" stimuli successfully selects faces in the species-typical

environment of a human newborn without generating too many false alarms, then it

is as domain-relevant as a preference for stimuli matching a face template, and they

share a common function. Note also that, as we shall see later, "top-heaviness" in a purely geometrical sense does not explain all aspects of newborns' preferences for face-like patterns (Farroni et al., 2005).

Whatever the exact "filters" that assist newborns in finding faces, these innate (or early functioning) biases have always been seen as being beneficial for the infant. Because they bring and maintain human faces in the infant's central visual field, they could be responsible for increasing his/her visual experience with human faces, and thus boosting the perceptual and cortical specialization for this class of objects. A direct influence on the cortical processes, through direct neuronal connections from the sub-cortical structures, might also be involved in the initial face tracking. These connections would allow the cortex to receive the relevant visual information before the cortical pathways are fully developed (Johnson, 2005).

The speed with which infants acquire knowledge about face structure contrasts with their human body knowledge. It is well established that infants can quickly learn the visual properties of various objects. They can group together different exemplars of an animal category based on both facial and bodily features (Quinn et al., 2001). Surprisingly, however, infants manifest very little knowledge of the human body (Slaughter et al., 2002). If they do display some knowledge, it is when the face is removed from the body (Gliga & Dehaene-Lambertz, 2005). What is in the face that captures infants' attention from the start?

Face expertise is driven by an early interest in eyes

There is one particular feature of faces that seems to be exceptionally effective in triggering young infants' attention – the eyes, especially when they appear to look directly at the infant. Newborns are shown to prefer faces with eyes

open to faces with closed eyes (Batki et al., 2000) and, when the eyes are open, they prefer a direct gaze to an averted one (Farroni et al., 2002). In addition, faces with direct gaze are more thoroughly processed, as suggested by the stronger neuronal responses they evoke (Farroni et al., 2002, 2004) and by the better recognition they produce (Farroni et al., 2006a).

Based on these and other findings that will be reviewed in the following sections, we propose that it is the interest in eyes, and especially in eye gaze, that triggers newborns' orientation towards faces and infants' continuing fascination with this particular body part. Knowing how plastic the face processing neural networks are in the first months, we expect that the consequences of spending more time exploring the eyes and the surrounding area are long lasting, leading to the preferential use of the face for identification in later life. We believe that there is enough evidence to support this hypothesis, and we shall devote the rest of this chapter to reviewing the relevant findings.

Early interest in eyes

Infants are sensitive to eye gaze from birth. Farroni et al. (2002) have shown that three-day-old newborns look longer, and reorient more frequently, to a face with direct gaze than to a face with averted gaze when these stimuli are shown side by side. The salience of direct gaze could be partly explained by the unique morphology of the human eye. Human eyes are wider in the horizontal direction, expose much higher proportion of sclera than the eyes of other primates, and the sclera is completely white (Kobayashi & Koshima, 1997). Accordingly, direct gaze in a front view face creates an area of high contrast, which could attract infants' attention (Figure 1b). Further experimental findings suggest that newborns are indeed

sensitive to the specific luminosity contrast that consists of dark regions on a white background. Farroni et al. (2005) demonstrated that the preference for the upright schematic face pattern is lost if a contrast-reversed stimulus is presented (white dots on a dark background), but regained if eye-like elements are used instead of the simple white dots (Figure 1a). When the head is oriented to one side, direct and averted gaze are hardly distinguishable on the basis of the contrast pattern within the eyes only (Figure 1c). As expected, in this case no preference is recorded in newborns (Farroni et al., 2006b). Simple sensitivity to a white-dark-white pattern is nevertheless not sufficient to explain the initial advantage of direct gaze because inverting the face disrupts this preference (Farroni et al., 2006b). Thus, a complex interplay between gaze perception and structural face perception drives infant's preferences from the very beginning (see Farroni et al., 2005, for a detailed discussion).

A few months later, the sensitivity to the mutual eye gaze is still preserved but it is further refined. Faces with direct gaze, compared to faces with averted gaze, elicit a stronger neurophysiological response (the N290, the event-related potential component that is the likely precursor of adults' face-specific N170) in 4-month-old infants (Farroni et al., 2002). At this age, the same result was also obtained when a three-quarters view of the face was used (Farroni et al., 2004a). Considering the absence of preference for the direct gaze in newborns when presented on 3/4 view faces, the results obtained in 4-month-old suggests that by this time infants have developed the non-trivial capacity of "reading" gaze direction on the basis of both eye and head orientation. The direct gaze in a frontal-view face is nevertheless still privileged, as only this condition, but not the three-quarters view, evokes a frontal

burst of gamma-band oscillatory activity[1] (Grossmann et al., 2007). Frontal activity (especially in the right dorsal medial prefrontal cortex) is associated in adults with processing social signals directed to the self (direct gaze, calling their name, see Kampe et al., 2003). Together these studies suggest that while 4-month-olds already recognize the equivalence between direct gaze configurations, whether they are located in a frontal or averted face, the latter stimulus has not yet gained the same social significance for them as the canonical eye-contact pattern.

Studies around the same age reveal not only excellent gaze discrimination capacities but also a positive emotional response to establishing mutual gaze. Infants remain engaged for longer, and smile more, when their conversation partner is looking at them (Hains & Muir, 1996; Symons et al., 1998). They do not only "enjoy" mutual gaze but also try to elicit it. According to Blass (2001), in the presence of an actor who looks away or does not interact with them, 12-week-old "infants made considerable efforts, including smiling, gurgling, and flirting, to establish contact" (p. 771). Direct gaze is an extremely powerful stimulus, which, we believe, attracts infants' attention to faces (1) directly through perceptual salience and (2) indirectly through positive feedback mechanisms mediated by emotional systems. Additional behaviors, like infant-directed speech ("motherese"), facial expressions and movements produced in contingency with infant's own vocalizations or with his own movements accompany the establishment of a the mutual gaze during mother-infant interactions and further strengthen the saliency of the face (Werker & McLeod, 1989; Cooper & Aslin, 1990; Striano et al., 2005)

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[1] Induced gamma-band (>24 Hz, characteristically around 40 Hz) oscillations have been used for studying infants' brain responses to complex visual stimuli (Csibra, Davis, Spratling, & Johnson, 2000; Kaufman, Csibra, & Johnson, 2003); For more details, see (Csibra & Johnson, 2007).

It is not only mutual gaze that infants are interested in during their first year of life. When an object is present in the visual scene, 9-months-olds prefer, and show enhanced electrophysiological responses to, gaze shifts towards the object (Senju et al., 2006, 2007). Although this preference makes older infants look towards the object and thus away from the face, such a tendency could also contribute to the developing face expertise by motivating them to search for such object-directed cues on others' face. This argument will be discussed at length in the last section of the paper.

Earlier neuronal specialization for eye processing

Five-month-old infants can discriminate direct gaze from gaze averted by only 5 visual degrees, i.e., when a person is looking at the infant's ear instead of her eyes (Symons et al., 1998). Strikingly, at around the same age, infants' face recognition capacities are by far not as spectacular, as we will see later. Do face-processing mechanisms develop slower than gaze processing mechanisms in the first months of life?

Starting around 4 months, the eyes are the face elements that evoke the strongest event-related potentials (ERPs) response (Gliga & Dehaene-Lambertz, 2006), and this specific signature accompanies eye processing along further development (Taylor et al., 2004). ERP studies comparing the correlates of eye and face processing have brought evidence for an earlier specialization of the eye-processing networks compared to those processing face-general properties. The maturation and/or specialization of neuronal networks is generally associated with a decrease in response latency in different modalities (Taylor & Baldeweg, 2002). This effect could be either due to a general improvement in neuronal conductivity or to

more efficient neuronal architectures (Nelson & Luciana, 1998). The shortening of latencies can also be observed for face-induced ERP components. In adults, face and eye perception are associated with a temporal-occipital negativity, at a peak latency of around 170 ms (N170). The generators of the whole-face-evoked and the eye-only-evoked responses are distinct, as suggested by their different topographies on the scalp, and by dipole source localization (McCarthy, 1999; Shibata et al., 2002). As we go back in time from adulthood to early infancy, the latency of the face-evoked "N170" increases by at least 120 ms (Taylor et al., 2004). In contrast, the latency of the eye-evoked response shifts much less (see Figure 2 and Gliga & Dehaene-Lambertz, 2006). Since these developmental differences are unlikely to be accounted for by general maturation of the brain, which would affect both face- and eye-evoked responses, they require a functional explanation. We suggest that the neural mechanisms responsible for gaze-processing, or at least those involved in detecting mutual gaze, develop earlier than the ones involved in general configural processing, probably because the second task requires more perceptual expertise to accumulate. Thus, by being active early enough in development, eye-orienting mechanisms could bias infants towards developing perceptual face expertise rather than perceptual body expertise.

Direct evidence that eye-processing networks are in operation from the first months of life comes from a study using the repetition-priming paradigm. This paradigm is based on the observation that repetition of stimuli induces diminished activation in the cortical areas that encode their common property. When used with functional magnetic resonance imaging (fMRI), this approach gives access to a finer spatial delineation of the neuronal processes than traditional paradigms (Grill-Spector et al., 1998; Naccache & Dehaene, 2001). Repetition-induced ERP effects

are similar but occur in the temporal domain. Using this paradigm, Gliga and Dehaene-Lambertz (2006) found a suppression of the eye-evoked responses to the repetition of different human eyes, both in adults and in 3-month-old infants. The latency of the amplitude reduction (~ 200 ms) was strikingly similar in the two populations (Figure 2). On the other hand, the same study showed a different pattern of results when structural aspects of faces had to be processed. While adults process human heads in a view-invariant manner, 3-month-old infants do not, as shown by the absence of neuronal adaptation when different face views (front view and profile) are repeated (Gliga & Dehaene-Lambertz, 2006).

Eye detection mechanisms seem to be adult-like at 4 months of age, while processing structural aspects of faces are not. These results add to a number of others showing that "face expertise" (as opposed to "gaze expertise") develops slowly from infancy during childhood and through the teen-age years (Carey, 1992; Taylor et al., 2004). In a recognition memory task where 36 face photographs had to be memorized and retrieved a few minutes later, six-years-old children performed barely better than chance, while adults' performance was at ceiling (Carey, 1992). The slow improvement of face expertise depends not only on experience with human faces but also on the general improvement of basic visual skills up until adolescence. A recent study by Mondloch et al. (2006) showed that the discrimination among both human and monkey faces improves further between 8 years of age and adulthood.

The studies reviewed in this section indicate that recognizing people by their faces is not an easy task for children, while expertise in eye detection seems to start in early infancy. Because structural face processing is heavily experience-dependent, the emergence of this ability will be susceptible to be influenced by the early developing mechanisms that mediate orienting attention to faces, like the ones

that govern eye detection. These studies, however, do not provide a proof for a direct effect of looking for eyes (and especially eyes with direct gaze) on learning about face properties. The next section will offer such evidence.

Learning about faces when looking at the eyes

To demonstrate that infants' interest in eyes and eye gaze has a modulatory effect on face perception, one has to show that facial features are encoded better when the person's eyes are open, and even better when she looks directly at the observer. Such evidence for the role of direct gaze in face recognition has recently been provided. Farroni et al. (2006a) showed that 4 to 5-month-old infants memorize a stranger's face better if they are presented with direct gaze during the encoding phase. Interestingly, when the experiment started with the presentation of faces with direct gaze, face recognition was better even for the faces with averted gaze presented in a subsequent block. This suggests that direct gaze does not simply induce a local increase in the efficiency of encoding but has a more general and longer lasting attentional effect. In this respect, direct gaze could act similarly to "physiological" learning enhancing factors, like sucrose intake. Blass (2001) found a strong interdependence between sucrose intake and mutual gaze, showing that infants learn better a stranger's face only when both factors were present.

While the study by Farroni et al. (2006a) shows that mutual gaze has a direct effect on face recognition, it also leaves a lot of questions unanswered. One such question concerns the spatial and temporal extent of these facilitatory effects. Does the direct gaze enhance the encoding of the whole face (thus contributing to the development of configural processing, for example) or would the eyes be privileged? In a habituation paradigm, 4- and 6-month-old infants showed dishabituation when

the upper half face changed but not when lower half of the face changed, whereas 8-month-olds detected changes in both conditions (Zauner & Schwarzer, 2003). It is thus possible that the interest in eyes biases further face recognition towards using the upper part of the face, at least in the first months of life. More facial information will be incorporated later on as a result of more exposure or of improved face scanning mechanisms.

There is nevertheless evidence that the eyes are used for recognition more than other face elements even in adulthood. The relative weight given to eyes or any other face part for individual recognition can be estimated by masking various face regions and assessing whether the removal of a region reduces recognition performance drastically. Using this approach, researchers found that, in adults, the head outline, the eyes and the mouth are the most relevant features for face recognition (Shepherd et al., 1981). A new and more precise masking technique (called 'Bubbles') was designed by Gosselin and Schyns (2001) for the same purpose. The procedure involves covering faces with an opaque layer with randomly distributed "holes" in it. The intersection of the stimuli that resulted in successful recognition would highlight the face regions that observers primarily use for identification. The results of a study employing this technique (Vinette et al., 2004) pointed again to the eyes as the primary features used by adult participants when performing a recognition task. Furthermore, these authors were also interested in whether the reliance on eyes was due to the fact that they carry more structural information than other face elements — the question that we asked earlier for faces with respect to the rest of the body. When an automatic template-matcher was presented with the same images as the human observers, it used both the eye region and the outer head contour for recognition. Thus, people seem to be

preferentially guided by the eyes even if they could have also used other face regions for identification. The 'Bubbles' technique was recently employed in a study of 7-month-old infants' recognition of familiar and strangers' faces (Humphreys et al., 2006). Consistent with the results obtained with adults, infants manifested a preference for their mother's face only when the eyes were visible in the masked faces.

Another prediction derived from the increased interest in direct gaze on a frontal view face is that the frontal orientation should be the easiest to encode into memory. The opposite prediction could also be made based on the richness of information present in different face orientations. It is generally accepted that the 3/4 view of the face conveys much more identity information than the profile or the frontal-view because it makes both the configuration of the internal elements and the 3D shape properties visible (Baddeley & Woodhead, 1983; Vuilleumier et al., 2005). When these two predictions were contrasted, no advantage of the 3/4 view over the frontal view was found in a recognition task (Liu & Chaudhuri, 2002). While this result does not support one hypothesis over the other, it nevertheless suggests that our face processing system is not only driven by the available information content and optimal bottom-up strategies. Similar studies should also be performed with infants, where we would predict better recognition of front-view faces compared with other orientations.

Further studies will have to explore the impact of the eye preference on learning face properties, and also to address the question of whether the eye preference in early infancy has the potential to shape a life-long face expertise. It is known that the first year of life is a period of increased activity-dependent plasticity in face processing. The variability within the physiognomies of the faces that infants

encounter tunes their face representations, allowing them to better recognize those types of faces that they are most likely to come across in the first months of life. Infants gradually become better at processing their own species' faces while losing their ability to tell faces of other species apart (Pascalis et al., 2002). Three-month-old infants brought up amongst Caucasian caregivers are better at discriminating Caucasian than Asian faces (Sangrigoli and De Schonen, 2004), and they prefer to look at their own race faces (Kelly et al., 2005). This own-race preference appears to be a robust phenomenon since it has been replicated and extended under various conditions (Kelly et al., 2005; Bar-Haim et al., 2006), though this advantage disappears if the infants are given a brief "training" with faces of another race (Sangrigoli & De Schonen, 2004). Also, infants have been shown to exhibit an early face gender preference, depending on who their primary caregiver is – the mother or the father (Ramsey-Rennels & Langlois, 2006). Further evidence on the impact of early experience with faces on life-long face processing capacities is provided by studies of children having suffered from congenital cataract during their first year of life. These individuals, years after the cataracts have been removed, are still impaired at face recognition (Le Grand et al., 2003).

We have seen that the interest in eyes facilitates face processing at an age where visual experience actively shapes the perceptual space. Brain imaging studies that target the neural structures involved in eye-gaze processing during development might also shed light on the nature of the link between gaze preference and face expertise. For the time being, no such studies have been carried out in infants. Nevertheless, in the following paragraphs, we will consider a number of studies with adults and children, which, we think, are extremely important for interpreting the findings regarding the early development of face and gaze processing.

The role of the amygdala in face and eye perception

In adults, the amygdala has repeatedly been associated with gaze processing and also with emotion perception from faces and eyes (Adolphs et al., 2002; Adams et al., 2003; Vuilleumier & Pourtois, 2006). Both the fusiform gyrus and the amygdala increase their activity when people look at a face with a direct gaze compared with a face with averted gaze (Kawashima et al., 1999; George et al., 2001, but see Hoffman & Haxby, 2000, for absence of modulation of the fusiform gyrus by the direction of the gaze). Similarly to infants, adults are also faster when having to make judgments about faces with direct gaze, even when their attention is directed away from the gaze information (Macrae et al., 2002; Hood et al., 2003). This effect is not due to increased contrast of the eyes with direct gaze, as it is present, and even stronger, when faces are presented with averted head orientation (Vuilleumier et al., 2005). Moreover, George et al. (2001) did not find an activation difference at occipital areas between the faces with direct and averted gaze, suggesting that direct gaze in adults does not facilitate general visual processing.

More interestingly, an increased coupling between the activation of the amygdala and the fusiform gyrus was also observed in the above studies (Kawashima et al., 1999; George et al., 2001). However, these results cannot inform us about the directionality of this coupling. An involvement of the amygdala in the modulation of fusiform gyrus activation, if shown, would be very interesting from a developmental point of view. Could the amygdala play a role in face processing in infancy? Its selective sensitivity to low spatial frequencies (Vuilleumier et al., 2003) suggests that the poor visual acuity in infancy would not be a limiting factor. Moreover, a recent study (Whalen et al., 2004) showed that a subtle difference in the

dark versus white proportion of the eye region, as in the contrast between fearful or surprised and happy facial expressions, can modulate amygdala activity. As we have seen, newborns pay a special attention to high-contrast elements and their contrast polarity within face-like patterns (see Figure 1a, Farroni et al., 2005). Indeed, the amygdala, together with other sub-cortical structures, is thought to be involved in enhancing infants' attention to socially relevant stimuli and in modulating the activity of cortical structures that process these stimuli (Johnson, 2005).

The exact role played by this structure in face processing is still under debate. A case study of a patient with amygdala damage, who showed impaired fear recognition but performed as well as controls when she was explicitly instructed to look at the eyes, suggests that the amygdala helps orienting the attention towards the eyes without being necessary for further processing (Adolphs et al., 2005). The amygdala, together with other subcortical and cortical structures, among which are the medial and orbital parts of the prefrontal cortex, is also known to be involved in stimulus-reward learning (Baxter & Murray, 2002). Within this circuit, the amygdala might thus mediate the establishment of the positive feedback loop that makes infants enjoy and seek mutual gaze.

At present, there is no suitable neuroimaging technique to study amygdala activation in human infants. However, one particular condition – autism — offers a unique opportunity to assess the importance of eye gaze and the role of the amygdala during development.

Deficits of gaze and face perception

Another way of testing the potential link between the early tendency of orienting towards eye gaze and the later developing face processing expertise is to

look at populations in which the initial interest in eyes may not be present. In this case, one would expect a less developed face expertise or even the development of alternative kinds of expertise for identification of individuals. Children with autism provide a relevant case for this purpose.

Amongst the first signs of autism is the reduced time children spend looking at people's faces or engaging in mutual gaze (Osterling & Dawson, 1994). Based on retrospective analysis of home video recordings, the indifference towards faces and eyes is described as early as the first year of life, persists during the childhood (Dalton et al., 2005), and is still present in adults (Klin et al., 2002). In contrast to typically developing children, children with autism do not show an advantage in detecting faces with direct gaze versus averted gaze (Senju et al., 2005).

Despite a disinterest in faces and in mutual gaze, autistic individuals are not "blind" to eye direction. On the contrary, their physiological measures show a bias for mutual eye gaze, manifested as a stronger ERP or skin conductance response (Kylliainen et al., 2006a,b). Thus, the deficit may lie not in perceiving mutual gaze as a special stimulus but in attributing the correct social relevance (i.e., positive valence) to this stimulus. The lack of orienting to other social signals in autism supports this view. While they can discriminate voices, autistic children orient less to human voice or to infant-directed speech (Ceponiene et al., 2003; Kuhl et al., 2005), even when being called by their name (Lord, 1995; Werner et al., 2000), and are less distressed by a "still-face"[2] situation than typically developing children (Nadel et al., 2000). When asked to judge the emotional status of a face, they are slower than

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[2] When faced by a suddenly unresponsive social partner, young infants typically react by ceasing smiling and by gazing away. This procedure has been used to investigate a broad range of questions about early social and emotional development.

control subjects to detect an emotional expression or a direct gaze, while no such difference was found for neutral faces having averted gaze (Dalton et al., 2005).

Along with the defective processing of social-communicative cues, mild deficits in face discrimination and recognition have also been described in children with autism. By middle childhood, these children perform worse than mental and chronological aged-matched peers in face recognition tasks (Tantam et al., 1989; Gepner et al., 1996). On the other hand, children with autism are less impaired in recognizing inverted faces than control subjects (Langdell, 1978; Hobson et al., 1988). It is suggested that the superior performance with inverted faces is the result of relying less on holistic face encoding mechanisms and more on local information (Boucher & Lewis, 1992; Davies et al., 1994). In typically developing children, it is the holistic processing that develops slower, being highly dependent on exposure (Carey, 1992). It was also shown that toddlers with autism do not show an advantage for discriminating human faces compared with monkey faces at an age when typically developing children already show superior processing of human faces (Chawarska & Volkmar, 2006).

It is still a matter of debate whether a deficit in face processing mechanisms diminishes the interest of children with autism in the social cues conveyed by faces, or whether it is the indifference towards eyes that gives them less chance to learn about faces, as compared with the normal population (Grelotti et al., 2002). Keeping in line with the main hypothesis of this chapter and with the supportive evidence brought up to this point, we are inclined towards the second causal relationship: that it is the disinterest in eyes and in mutual gaze which lies at the origin of the face recognition deficit in this disorder (but see Behrmann et., 2006 for an alternative view). As of today, only a few studies have addressed this relationship directly.

Nevertheless those that show that children with autism can become experts in processing other facial features than eyes, or in processing face-like stimuli where the eyes are less salient (e.g., cartoon characters, see Grelotti et al., 2005), speak against the hypothesis of an initial face-processing deficit.

If autism can be characterized by the absence of the positive "eye bias" present in the normal population, it offers us the opportunity to see what alternative cues can be used for identification. Would individual recognition rely more on other face elements or on the body in this disorder? When scanning a face in a dynamic video scene, adults with autism spend less time on the eyes, but also more time on the mouth, than do control individuals (Klin et al., 2002). The same scanning pattern is found in children with autism in a face recognition task (Dalton et al., 2005). This scanning pattern suggests that, in contrast to typical population, individuals with autism would rely more on the lower part of the face for recognition. Indeed, it was shown that children with autism recognize the lower half of faces better, while typically developing children used more the upper part (Langdell, 1978). These findings have recently been replicated by Joseph and Tanaka (2003), who demonstrated not only better recognition performance in children with autism on the basis of the mouth region, but also better performance when the mouth region was upright as opposed to inverted. This suggests that children with autism also rely on holistic processing strategies in face recognition but, because they are not attracted to eyes, they end up focusing on other face regions when encoding identity-specific information. The reliance on body cues for identification was not tested in this population, but we would again expect them to perform better than typically developing individuals.

The brain areas activated by face perception could also shed light on the

nature of face processing deficit in autism. One noteworthy discovery is that the neurons of the amygdala in people with autism are smaller and more densely packed than in the normal population (Bauman and Kemper, 2005; Munson et al., 2006). In addition, the amygdala tends to be less active in face processing tasks in this disorder (Baron-Cohen et al., 1999). As we have seen, the amygdala is associated with processing information from the eyes and thought to be involved in orienting the attention towards faces, in infancy. Accordingly, a failure to engage this system may lead to reduced exposure to faces. Baron-Cohen et al. (2000) proposed that a deficit in amygdala function is the basis of failing to engage in eye contact in autism. It is also interesting to note here that a striking similarity has been observed between the reliance on the mouth region in individuals with autism and in a patient with bilateral damage to the amygdala (Adolphs et al., 2005). Atypical functionning is also reported at other areas in the visual stream. The fusiform face area (FFA), one of the most important cortical regions for face identity processing, is only weakly activated by faces in individuals with autism, while a network of alternative brain regions - prefrontal and primary visual cortices - shows activity (Pierce et al., 2001). Dalton et al. (2005) showed that the FFA is activated in autism, but only in those individuals who spend more time with looking at the eyes. The time spent looking at the eyes was positively correlated with the right FFA activity. This result is compatible with the hypothesis that individuals who do not pay special attention to faces will not develop a neuronal specialization for face processing in the fusiform gyrus. This finding is nevertheless also compatible with the opposite hypothesis, according to which impairment in the FFA development could force people with autism to recruit alternative strategies for encoding identity. Looking at the early development of infants at high risk of autism, like the siblings of autistic children, will probably

provide us with valuable information regarding the directionality of these effects (see Elsabbagh & Johnson, this volume).

The interest in eyes is driven the social relevance of gaze

We embarked on this chapter with the goal of explaining the selective reliance on faces (in contrast to other equally informative body parts) for the recognition of individuals in humans. We took a developmental perspective and tried to construct an alternative account to what was previously proposed. Our central hypothesis has been that an interest not in facial patterns *per se* but in human eyes is the driving force of the development of face expertise. We have proposed that because infants are looking for mutual gaze, faces appear more often than other body parts in their central visual field.

Nevertheless, the explanation that infants spend more time looking at faces because the eyes and gaze constitute salient stimuli for them, provides only a partial answer to our question. This answer accounts for what perceptual mechanisms trigger newborns' and infants' bias but it does not explain what functional role this bias serves. What do infants gain by looking at the eyes? Eyes and gaze convey rich information: they have been associated with expressing emotions, mental states and communicative information. Eyes might even reflect physical health and fitness (subjectively perceived as "beauty") (Rhodes, 2006). Which of these aspects drives infants' tendency to look at the eyes?

Infants' development of understanding of emotional expressions is dependent on their exposure to a normal range of such expressions from their caregivers (de Haan et al., 2004). The straightforward conclusion - that infants must look at the eyes in order to extract this information - is weakened, nevertheless, by the fact that

only some of these expressions are conveyed by the eyes. Expressions like fear,

anger or surprise are accompanied by a clear widening or narrowing of the eyes.

While young infants can discriminate between the above expressions, none of them

invites them to explore the faces longer (anger has even the opposite effect,

Grossmann et al., 2006). It is instead the smiling expression that is preferred by

newborns (Farroni et al., 2006). However, when having to judge this expression,

adults explore the mouth and not the eye region (Schyns et al., 2002).

While eyes might not help infants understand emotional expressions, the

direction of the eye gaze can have an emotional effect on infants. Most episodes of

mother-infant interaction are accompanied by direct gaze from the mother (Watson,

1972). A few hypotheses have been put forward on what caregivers and infants gain

from such intense and emotionally rich interactions, amongst which the most obvious

one is the strengthening of the mother-infant relationship (Watson, 2001). It was

suggested that the amount of emotional affect and behavioral contingency during

these interactions has an impact on seeking, maintaining, and avoiding contact

during social interactions later in life (Volker et al., 1999). The preference for mutual

gaze might thus be needed for normal affective development in humans.

Note, however, that filial attachment in many non-human species is achieved in

the absence of extended face-to-face interactions between parents and infants,

which suggest that this end can be achieved without relying on mutual gaze. One

further factor that shapes the properties of the mother-infant relationship is bodily

contact. Chimpanzee mothers are in constant bodily contact with their offspring in

the first 3 months after birth, as the infant clings to the mother and the mother

embraces the infant (Matsuzawa, 2006). Human evolution, however, was

accompanied by an increasing tendency for physical separation, from which mothers

benefited because, having their hands free, they could engage in other activities. It is therefore possible that in exchange for bodily contact, communicative distal contact through facial (eye gaze), gestural and vocal signals between mothers and babies has proliferated. In this context, direct gaze may act as a substitute of bodily contact and will assure infants of being cared for and protected by their mother.

Finally, eyes carry important communicative information, which humans use extensively. In fact, two kinds of communicative information are embedded in eye gaze. Direct gaze (i.e., eye contact) is an ostensive stimulus (Csibra & Gergely, 2006), which signals that the accompanying or subsequent communication is directed to the other party. On the other hand, a gaze shift from direct to averted position may also signal referential information by specifying the direction or location where the referent of the communication can be found. Human newborns are sensitive both to the ostensive (Farroni et al., 2002) and to the referential (Farroni et al., 2004b) aspects of human gaze, and evidence suggests that the latter one depends on the former one (i.e., infants' attention shifts to the direction indicated by others' gaze only after mutual gaze has been established, see Farroni et al., 2003; Senju et al., 2007).

The use of gaze signals in communication is widespread among humans, and it plays an even more important role in infants than in adults. Preverbal infants, who are unable to decode verbal reference, can use gaze information to comprehend non-verbal referential expressions. In fact, a whole body of literature demonstrates that understanding non-verbal reference may be a precondition of efficient word learning in infancy (Baldwin, 1993; Tomasello, 2001; Bloom, 2000). But words are not the only type of knowledge that infants can acquire by referential communication. Valence and function of objects and actions also represent the kinds of information

that are much easier to acquire via social than via individual learning. Generally, humans, unlike other animals, tend to acquire a big part of their knowledge through communication. It is thus plausible to assume that human infants' bias towards eyes reflect the functioning of a human-specific social learning system, which evolved to transmit useful cultural knowledge across generations via ostensive communication (Csibra and Gergely, 2006).

Whatever the exact function (or functions) of human infants' obsession with eyes, the evidence we reviewed in this chapter offers an alternative causal story for the development of face expertise in humans. Faces are not the carriers of identity because they are necessarily more informative about individuals or because infants are born with specialized face processing mechanisms, or at least not *only* for the above reasons. Becoming a *face* expert might in addition be a by-product of an increased interest in people as potential sources of valuable information during development. We believe that it is infants' interest in eye-mediated communication that makes them spend more time with looking at human faces, leading to the rapid improvement of face processing skills and eventually to the irreversible perceptual and neuronal specialization for individual recognition by faces.

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Figure Legends

Figure 1. The saliency of mutual gaze: **a.** Newborns prefer the pattern on the left within the top and the bottom pairs, but not within the middle one (Farroni et al., 2005); **b.** Mutual and averted gaze in a frontal face, as seen by a 4-months-old infant (Farroni et al., 2002) **c.** To distinguish between averted and mutual gaze in 3/4 view faces, gaze direction and head direction have to be integrated (Farroni et al., 2004) **d.** A bonobo face with averted gaze (left) and chimpanzee face with direct gaze (right). The absence of the white sclera makes it difficult to "read" the gaze direction.

Figure 2. Targeting eye-selective processing by repetition suppression. Thirty eye images were randomly presented amongst face or house images. The ERPs to eyes were reduced if presented in a face context but not in a non-related house context, in both adults and 4-month-old infants. The response suppression started at similar latencies in both ages. The voltage distribution over the scalp in the two conditions (left) is presented along with the curves recorded by the electrodes indicated by a white dot on the voltage maps (light grey – eyes/faces; black – eyes/houses). (Adapted from Gliga & Dehaene-Lambertz, 2006).
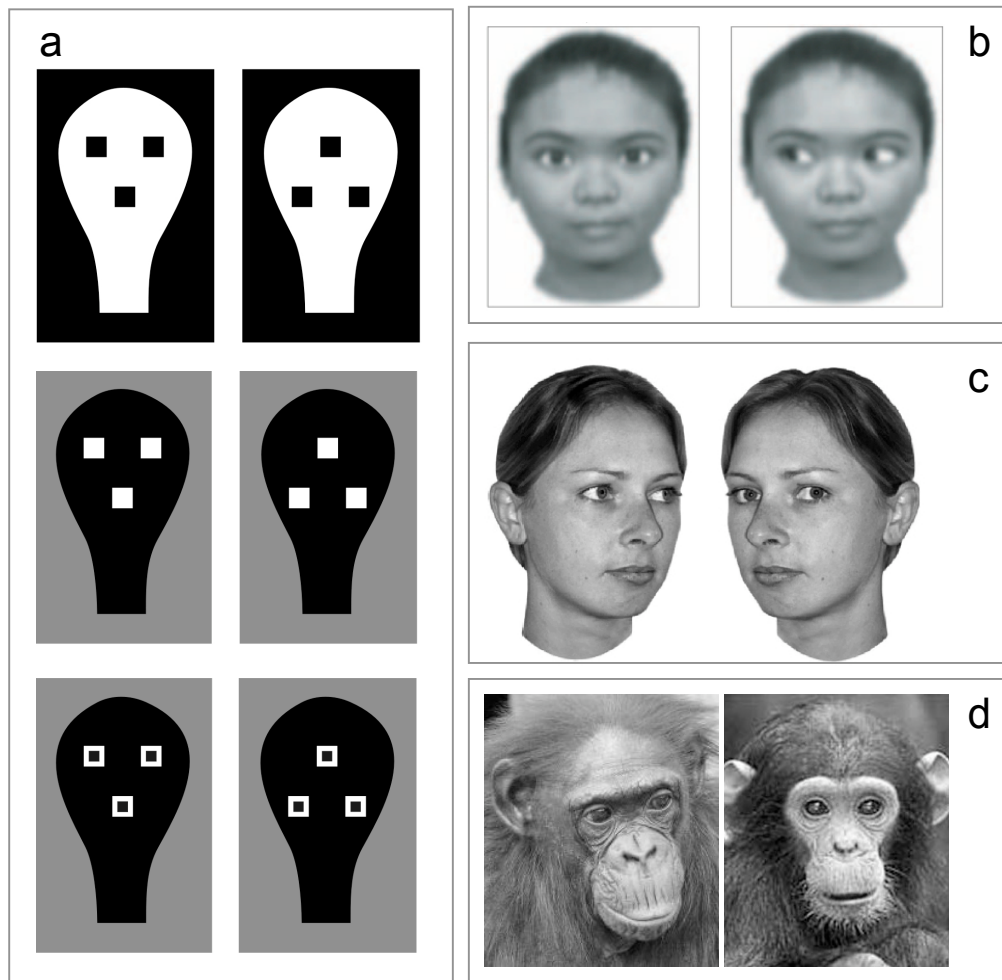
Figure1

Figure 2