

5

PERCEIVING AND ACTING ON THE SOCIAL WORLD

Cognitive neuroscience studies in adults have revealed a network of structures involved in the perception and processing of social stimuli, including interpreting the thoughts and intentions of other humans. However, considerable debate remains about the developmental origins of this brain network. Perhaps the most basic aspect of the visual social brain is the perception of faces. One extreme view is that there is an innate cortical module for face processing (maturational view). At the opposite extreme is the view that expertise for faces is acquired in the same way as visual expertise for non-social stimuli (skill learning view). By considering evidence from an animal model (chicks), behavior, and neuroimaging, I argue that a primitive bias ensures that infants orient frequently to faces. This early exposure to faces allows this stimulus to capture dedicated regions of neural tissue. This process of specialization for faces appears to take months or years. The remainder of the chapter addresses other aspects of social cognition such as perceiving and acting on information from the eyes, and attributing intentions or goals to other humans. Evidence from two developmental disorders, autism and Williams syndrome, initially appears to provide support for a social module that can be selectively impaired (autism) or spared in the face of other deficits (Williams syndrome). On closer inspection, however, it becomes apparent that such a clean dissociation is not borne out by the evidence, and that social information processing emerges as a result of constraints from interactions with other conspecifics, initial biases toward social stimuli, and the basic architecture of the brain.



5.1 THE SOCIAL BRAIN

One of the major characteristics of the human brain is its social nature. As adults, we have areas of the brain specialized for processing and integrating sensory information about the appearance, behavior, and intentions of other humans.

Sometimes this processing is also extended to other species, such as the family cat, or even to inanimate objects such as our desktop computer. A variety of cortical areas have been implicated in the “social brain,” including the superior temporal sulcus (STS), the “fusiform face area” (FFA – see further below), and orbitofrontal cortex (for recent review see Adolphs 2003) (see figure 5.1). One of the major debates in cognitive neuroscience concerns the origins of the “social brain” in humans, and theoretical arguments abound about the extent to which this is acquired through experience. Mentalistic understanding of others’ behavior (“theory of mind”) has been associated with various neural structures, including the amygdala and the temporal pole, the superior temporal gyrus and the temporo-parietal junction, and parts of the prefrontal cortex (mainly orbitofrontal and medial areas). According to Frith and Frith (2003), the neural activity in these regions may reflect different aspects of mental state understanding: the amygdala is involved in understanding emotions through empathy; parts of the temporal lobe represent biological motion and actions; and regions of the frontal cortex play a role in understanding “intentional” referential mental states, including mental states of the self. The question I will address in this chapter is how these regions develop their functionality and become parts of the human social brain.

The three perspectives on human functional brain development discussed in chapter 1 lead to different expectations about the origins of the social brain.

Superior Temporal Sulcus/Gyrus (1)



Left Frontal Operculum (2)

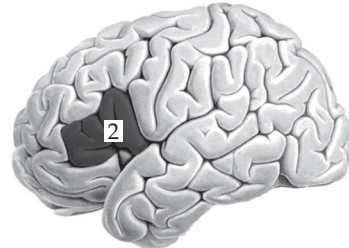
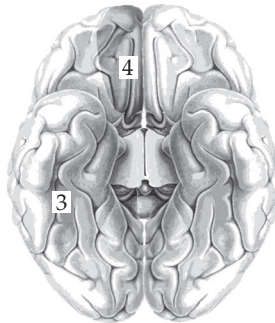

 Fusiform Gyrus (3)
 Orbitofrontal Cortex (4)


Figure 5.1 Some of the regions involved in the human social brain network.



According to the maturational view, through evolution, specific parts of the brain and areas of cortex have become dedicated to processing social information. Plausibly, some of the circuits are present and functioning at birth, while other components of the network become available through maturation later in development. For example, prefrontal areas associated with “theory of mind” computations may be the last component of the social brain to mature. While the maturational timetable may be accelerated or decelerated by experience, the sequence of maturation and the domain-specific wiring patterns are not. According to the skill learning view, at least some parts of the social brain are engaged by social stimuli because these tend to be the visual inputs with which we are most experienced. In other words, we tend to develop a higher level of perceptual expertise for socially relevant visual inputs. By this view we would not expect newborns to have any specific responses to social stimuli, and we should observe parallels between the development of face processing in infancy and the acquisition of perceptual expertise for other stimuli in adults. The third view, interactive specialization, predicts that the social brain will emerge as a network that becomes increasingly finely tuned to relevant stimuli and events in an activity-dependent manner. We should anticipate interactions between more primitive brain systems, cortical areas, and the environment, to produce the end result of a social brain.

In this chapter we initially examine these issues with perhaps the most fundamental visual function of the social brain – the perception and processing of faces. In later sections we go beyond this to examine some of the evidence available on more dynamic aspects of social cognition, such as interpreting eye gaze and the actions of other humans.

5.2 FACE RECOGNITION

The ability to detect and recognize faces is commonly considered to be a good example of human perceptual abilities, as well as being the basis of our adaptation as social animals. There is a long history of research on the development of face recognition in young infants extending back to the studies of Fantz more than forty years ago (e.g. Fantz, 1964). Over the past decade numerous papers have addressed the cortical basis of face processing in adults, including identifying areas that may be specifically dedicated to this purpose (Kanwisher, McDermott, & Chun, 1997; but see Haxby et al., 2001). Despite these bodies of data, surprisingly little remains known about the developmental cognitive neuroscience of face processing.

Face recognition skills may be divided into a number of components, including the ability to recognize a face as such, the ability to recognize the face of a particular individual, the ability to identify facial expressions, and the ability to use the face to interpret and predict the behavior of others. In a review of the

available literature in the late 1980s, Johnson and Morton (1991) revealed two apparently contradictory bodies of evidence: while the prevailing view, and most of the evidence, supported the idea that infants gradually learn about the arrangement of features that compose a face over the first few months of life (for reviews see also Maurer, 1985; Nelson & Ludemann, 1989), the results from at least one study indicated that newborn infants, as young as 10 minutes old, will track a face-like pattern further than various “scrambled” face patterns (Goren, Sarty, & Wu, 1975). Evidence that newborns showed a preferential response to faces was used by some to bolster nativist views of infant cognition (maturational view). In contrast, the evidence for the graded development of face processing abilities over several months tended to be cited by theorists who believed that such skills need to be learned, and result from experience of the world (skill learning view). To translate these views into the framework introduced in chapter 1, while some believed that the brain possesses innate representations of faces, others took the view that face representations resulted from the information structure of the environment.

Since the study with newborn infants remained controversial for methodological reasons, my colleagues and I attempted to replicate it (Johnson, Dziurawiec, Ellis, & Morton, 1991). As in the original study, newborn infants (this time around 30 minutes old) were required to turn their head and eyes to keep a moving stimulus in view. This measure contrasts with more standard procedures in which the infant views one or more stimuli in static locations and the length of time spent looking at the stimuli is measured. In the first experiment we conducted, three of the four stimuli used in the original Goren et al. (1975) study were used: a schematic face pattern, a symmetric “scrambled” face, and a blank face outline stimulus. While we were unable to replicate preferential head turning to follow the face pattern, we did successfully replicate the preferential response to the face using a measure of eye movements (see figure 5.2).

This experiment confirmed that the brain of the newborn human infant contains some information about faces. Several more studies on face preferences in newborns have been published since 1991. While there are some differences reached in the conclusions of these authors, all of the studies found some evidence for sensitivity to face-like patterns. These have led to three hypotheses about the basis of this newborn preference behavior. Further, these three hypotheses may be associated with the three perspectives on functional brain development mentioned earlier.

FURTHER READING: DE HAAN, 2001

The sensory hypothesis: This is the hypothesis that the visual preferences of newborns, including face preferences, are determined by low-level psychophysical properties of the stimuli. This hypothesis is consistent with the skill learning

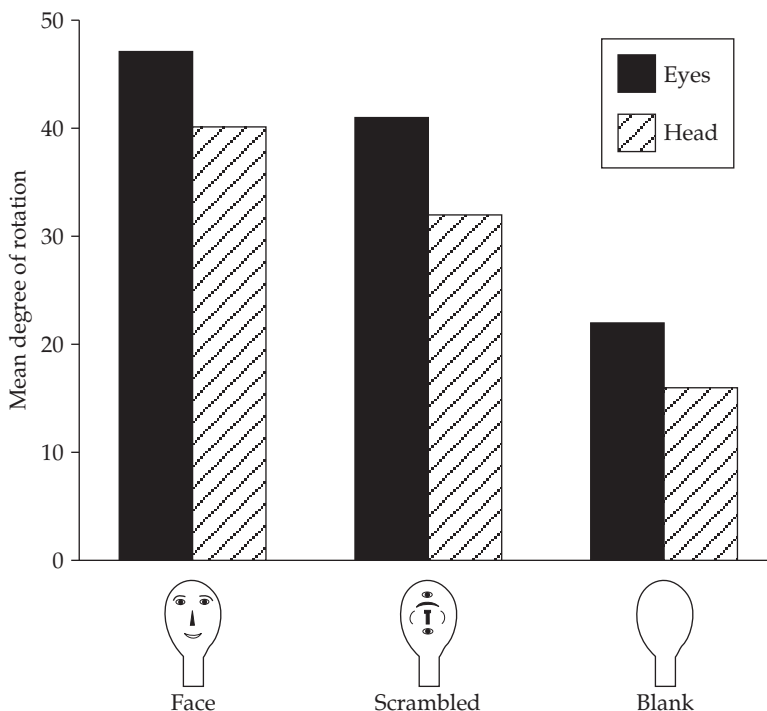


Figure 5.2 Data showing the extent of newborns' head and eye turns in following a schematic face, a scrambled face, and a blank (unpatterned) stimulus. The infants tracked the face significantly further than the other stimuli (Johnson & Morton, 1991).

perspective since it does not assume any domain-specific bias early in life. The hypothesis that face patterns are preferred due to their amplitude spectrum better suiting the infants' visual system (Kleiner, 1993) was initially rejected since face patterns always fare better than would be predicted on the basis of amplitude alone (Johnson & Morton 1991). However, Acerra, Burnod, and de Schonen (2002) recently suggested that minor differences in the exact schematic face stimuli used in critical experiments could regenerate the sensory hypothesis. Most recently, Bednar and Miikkulainen (2003) have criticized this analysis, and suggested that the overall pattern of data better fits a face-biasing system (see below for details).

Newborns have complex face representations: Empirical results have led some to the hypothesis that newborns already have complex representations of faces. This hypothesis is most consistent with the maturational view of functional brain development, since it presumably requires domain-specific circuits to be established prior to experience. These findings include the preference for attractive

faces, and data indicating that newborns are sensitive to the presence of eyes in a face (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2001), and prefer to orient toward faces with direct (mutual) eye gaze (Farroni, Csibra, Simion, & Johnson, 2002). However, inspection of images of such stimuli through the appropriate spatial frequency filters for the newborn visual system reveals that a mechanism sensitive to low-spatial frequency components corresponding to the spatial arrangement of a face (below) could account for these seemingly more complex preferences.

Face-biasing system ("Conspec"): These hypotheses argue that the newborns' brain contains a system that biases it to orient to faces. Johnson and Morton (1991) referred to such a system as "Conspec." This hypothesis is most consistent with the interactive specialization view. In contrast to the last hypothesis, the functioning of a cortical face module is not assumed. Rather, the bias is presumed to be close to the minimum necessary for picking out faces from a natural environment. In contrast to the sensory hypothesis, the spatial relations between face features are thought to be important, even though the representation underlying this preference may not exactly map on to a face (Simion, Macchi Cassia, Turati, & Valenza, 2003). In one variant of this hypothesis, Johnson and Morton (1991) argued that their "Config" stimulus (see figure 5.3) was the minimal sufficient representation to ensure this preference. In recent neural network simulations, Bednar and Miikkulainen (2003) found that such a representation could account for the vast majority of documented newborn preferences between schematic and realistic face stimuli (see figure 5.3).

In conclusion, it appears that a primitive face-biasing system (Conspec) can, at present, account for the vast majority of data currently available on face preferences with newborns. While this does not rule out some influence of sensory factors, it does mean that a simple version of the skill learning view is an unlikely explanation for the development of face processing.

Surprisingly, many other studies which used more conventional infant testing methods have not found a preference for face patterns over others until 2 or 3 months after birth (for review see also Maurer, 1985; Nelson & Ludemann, 1989). For example, Maurer and Barrera (1981) used a sensitive "infant control" testing procedure, in which participants view a series of singly presented static stimuli, and established that while 2-month-olds looked significantly longer at a face-like pattern than at various scrambled face patterns, 1-month-olds had no such preference. Using the same method, Johnson, Dziurawiec, Bartrip, and Morton (1992) replicated this result and extended the original findings by including in the stimulus set the "de-focused" face arrangement stimulus used in the newborn studies earlier. The results replicated entirely the previous findings: the face was looked at longer than any of the other stimuli by 10-week-olds, but a group of 5-week-old infants showed no preference. This evidence was consistent with the

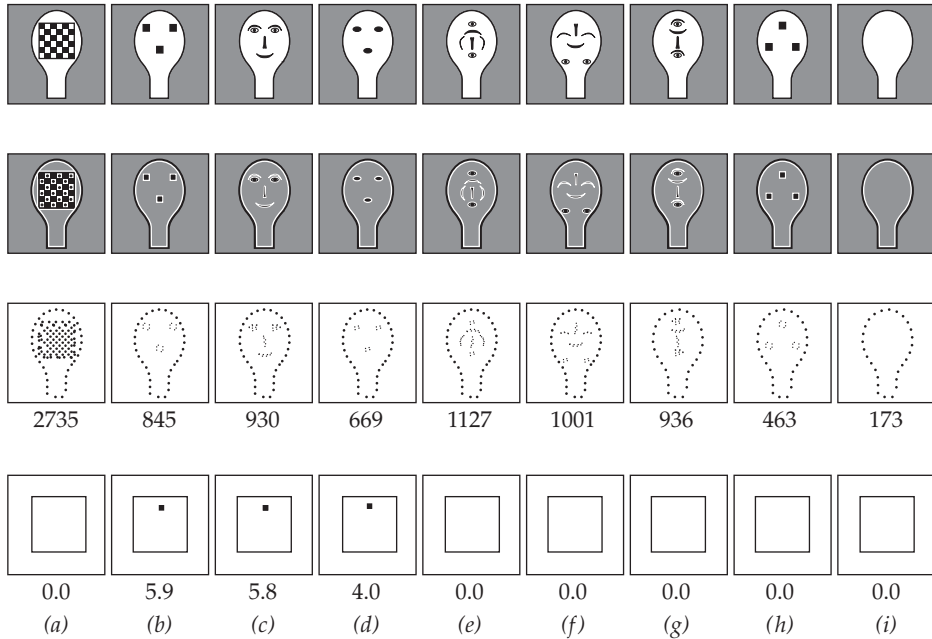


Figure 5.3 A summary of human newborn and model responses to schematic images. The top row represents some of the schematic patterns presented to both newborns and the “retina” of the neural network model. The next two rows illustrate the LGN and visual cortex stages of the models processing. The bottom row indicates the output of the model, with the preferred stimuli being *b*, *c*, and *d*. The preferences of the model correspond well to the results obtained with newborn infants.

alternative claim that infants gradually construct representations of faces as a result of repeated exposure to them over the first few months of life (Gibson, 1979). Clearly, these apparently contradictory findings raised a problem for theories of the development of face recognition that involved only one process (either learning or innate face representations). In an attempt to interpret this apparently conflicting behavioral data, Johnson and Morton (1991) turned to evidence from two areas of biology: ethology and brain development.

The primary source of evidence from other species (ethology) that Johnson and Morton used to interpret the human infancy results concerned filial imprinting in the domestic chick. Imprinting in chicks was selected because it is well studied both in terms of behavior and in terms of its neural basis. 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; Johnson & Bolhuis, 1991). While imprinting has been reported in the young of a variety of species, including spiny mice, guinea pigs,

chicks, and ducklings, only in precocial species (those that are mobile from birth) can we measure it using the conventional measure of preferential approach.



5.3 FILIAL IMPRINTING IN CHICKS

In the laboratory, 1-day-old domestic chicks will imprint onto a variety of objects such as moving colored balls and cylinders. After even a few hours of exposure to such a stimulus, chicks develop strong and robust preferences for the training object over novel stimuli. 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.

A particular region of the chick forebrain (thought to correspond to mammalian cortex) has been shown to be critical for imprinting, a region known as the intermediate and medial part of the hyperstriatum ventrale (IMHV) (for reviews see Horn, 1985; Horn & Johnson, 1989). Lesions to IMHV placed before or after training on an object severely impair preference for that object in subsequent choice tests, but do not affect several other types of visual and learning tasks (McCabe, Cipolla-Neto, Horn, & Bateson, 1982; Johnson & Horn, 1986, 1987). Similar size lesions placed elsewhere in the chick forebrain do not result in significant impairments of imprinting preference (McCabe et al., 1982; Johnson & Horn, 1987).

The next step in analyzing the neural basis of imprinting was to study the microcircuitry of the region involved. Although the bird forebrain lacks the laminar organization of mammalian cortex, the relation of the forebrain to subcortical structures is similar following the basic higher vertebrate brain design (chapter 2). Evidence from a variety of vertebrate species supports the suggestion that the avian forebrain is a site of plasticity, and not the location of inbuilt, automatic, types of behavior which are located in other structures (MacPhail, 1982; Ewert, 1987).

Figure 5.4 illustrates the location of IMHV within the chick brain. It is worth noting that this region corresponds to, or overlaps with, regions critical for auditory imprinting and song learning (e.g. Maier & Schiech, 1983). The area occupies about 5 percent of total forebrain volume. Its main inputs come from visual projection areas (hyperstriatum accessorium and the optic tectum), and some of its projections go to regions of the bird brain thought to be involved in motor control (such as the archistriatum). Thus, the area is well placed to integrate visual inputs and motor outputs.

After identifying features of the basic microcircuitry of IMHV, the next step was to take a synthetic approach and build a computational model of the circuit concerned (Bateson & Horn, 1994; O'Reilly & Johnson 1994). In one of these models, Randall O'Reilly and I constructed a connectionist model based on two

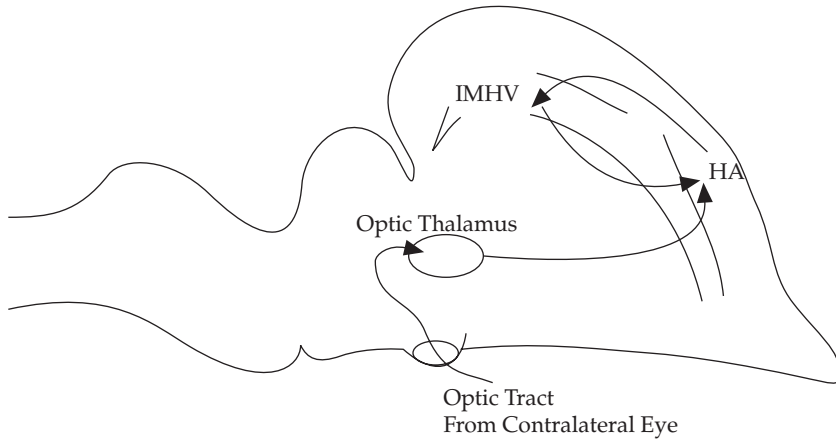


Figure 5.4 Outline sagittal view of the chick brain showing the main visual pathway to IMHV (HA, hyperstriatum accessorium). There are other routes of visual input to IMHV which are not shown in this figure (see Horn, 1985). The brain of a 2-day-old chick is approximately 2 cm long.

characteristics of the cytoarchitectonics of IMHV: the existence of positive feedback loops between the excitatory principle neurons, and the extensive inhibitory circuitry mediated by the local circuit neurons. The detailed architecture of the model is shown in figure 5.5. (For further details of the model and neuroanatomy, see O'Reilly & Johnson, 2002.)

FURTHER READING: O'REILLY & JOHNSON, 2002

In the laboratory a wide range of objects, such as moving red boxes and blue balls, are as effective for imprinting as are more naturalistic stimuli, such as a moving stuffed hen. However, in the wild, precocial birds such as chicks invariably imprint on their mother, 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.

An answer to this question became evident from the results of a series of experiments in which stimulus-dependent effects of IMHV lesions were observed (Horn & McCabe, 1984). Groups of chicks trained on an artificial stimulus such as a rotating red box were severely impaired by IMHV lesions placed either before or after training on an object. However, groups of chicks exposed to a stuffed hen were only mildly impaired in their preference. Other neurophysiological manipulations also show differences between the hen-trained and box-trained birds (see

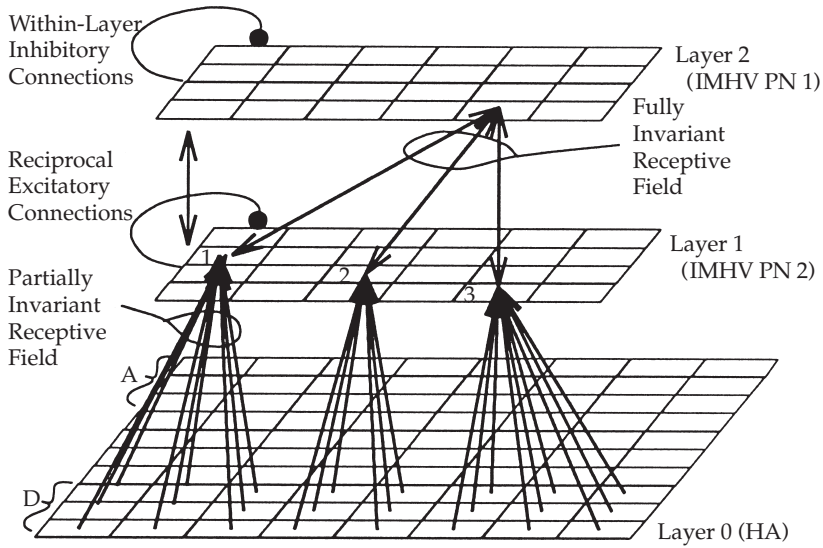


Figure 5.5 The detailed architecture of the model is designed around the anatomical connectivity of IMHV and its primary input area, the hyperstriatum accessorium (HA). The model is based on a set of layers, each of which has lateral inhibition within it. The “input” layer of the network, layer 0, represent HA. HA then projects to one subpopulation of IMHV projection neuron (PN) cells, which we assume to be type 1 PNs (see O’Reilly & Johnson, 2002). This is layer 1 of the IMHV component of the model. Note that the laminar distinction in the model between these two component cells of IMHV is not intended to suggest that the cells are arranged as such in the IMHV itself, but rather serves to reflect the functional distinction between the two types of PN. The axons from the type 1 neurons project to the type 2 projection neurons, as well as onto the local inhibitory neurons. This comprises the second layer of the model’s “IMHV” component. The type 2 PNs then send a bifurcating axon both back to the type 1 PNs and the inhibitory cells (layer 2), and to other areas, which are not modeled. Within each layer of the model, strong lateral inhibition exists in the form of relatively large negative weights between all units in the layer. This reflects the presence of a large number of GABAergic inhibitory interneurons in IMHV (Tombol et al., 1988), and its relatively low levels of spontaneous activity. The strong inhibition in this layer of the model resulted in only one unit in each layer becoming active at any time.

table 5.1). For example, administration of the neurotoxin DSP4, which depletes forebrain levels of the neurotransmitter norepinephrine (see chapter 2), 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, Horn, & McCabe, 1985). In contrast, plasma levels of the hormone testosterone correlate with preference for the stuffed hen, but not preference for the red box (Bolhuis, McCabe, & Horn, 1986).

These results led Johnson and Horn (1988) to seek experimental evidence for an earlier suggestion (Hinde, 1961) that naturalistic objects such as hens may be more effective at eliciting attention in young chicks than are other objects. A



Table 5.1 Stimulus-dependent effects of neurophysiological manipulations

<i>Treatment</i>	<i>Hen-trained chicks</i>	<i>Box-trained chicks</i>
Bilateral IMHV lesions	Mild impairment	Severe impairment
DSP4 treatment	Mild impairment	Severe impairment
Plasma testosterone levels	Correlated with preference	No correlation with preference
Multicellular recording in IMHV	No correlation	Correlated

series of experiments were therefore conducted in which dark-reared chicks were presented 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) concluded from these experiments that chicks have an untrained tendency, or predisposition, to attend toward features of the head and neck region of the hen. While this untrained preference seemed to be specific to the correct arrangement of features of the face/head, it was not specific to the species. For example, the head of a duck was as attractive as that of a hen.

The results of these and several other experiments led to the proposal that there are two independent brain systems that control filial preference in the chick (Horn, 1985; Johnson, Bolhuis, & Horn, 1985). The first of these controls a specific predisposition making newly hatched chicks orient toward objects resembling a mother hen. In contrast to non-specific color and size preferences in the chick (see Johnson & Bolhuis, 1991), this predisposition system appears to be specifically tuned to the correct spatial arrangement of elements of the head and neck region. While the stimulus configuration triggering the predisposition is not species- or genus-specific, 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. Although the neural basis for this predisposition is currently unknown, the optic tectum, the homolog of the mammalian superior colliculus, is one likely candidate.

The second brain system acquires information about the objects to which the young chick attends and is supported by the forebrain region IMHV. In the natural environment, it has been 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 IMHV impair preferences acquired through exposure to an object, they do not impair the specific predisposition (Johnson & Horn, 1986).

There are, of course, a number of different ways in which the predisposition could constrain the information acquired by the IMHV 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 IMHV system. The evidence available at present is consistent with the view that the two systems influence the preference behavior of the chick independently, that is, there is no internal informational exchange between them. Instead, it appears that the input to the IMHV 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.

One benefit of this well-studied animal model for developmental cognitive neuroscience is that it allows us to examine the plausibility of the three perspectives on human functional brain development (while bearing in mind the possibility of species differences). The chick imprinting story is inconsistent with the skill learning view in that the predisposition is present without prior training, and the learning involves self-terminating plasticity. The chick model is also somewhat inconsistent with the maturational view in that the IMHV is relatively unconstrained in its learning, and appears to emerge from surrounding tissue as a result of experience. The evidence suggests that the emergence of a simple vertebrate social brain is consistent with the interactive specialization view as brain plasticity was constrained by simple biases, neural architecture, and the early environment.



5.4 BRAIN DEVELOPMENT AND FACE RECOGNITION

The other source of biological data that Johnson and Morton used to generate an account of human infant face recognition came from the postnatal development of the cerebral cortex. As previously mentioned (chapter 3), both neuroanatomical and neurophysiological data indicate that visually guided behavior in the newborn infant is largely (though not exclusively) controlled by subcortical structures such as the superior colliculus and pulvinar, and that it is not until several months of age that cortical circuitry comes to completely dominate subcortical control over behavior. Consistent with these arguments is the position that visually guided behavior in human infants, like that in domestic chicks, is based on activity in two or more distinct brain systems. If these systems have distinct developmental time courses, then they may differentially influence behavior in infants of different ages.

There is much evidence that the recognition of individual faces in adults involves cortical areas and pathways. This evidence comes from three main sources: (i) neuropsychological patients with brain damage who are unable to recognize faces (prosopagnosia); (ii) neuroimaging studies of face perception; and (iii) single- and multi-cellular recording studies with non-human primates. To briefly review this literature, prosopagnosia commonly results from damage to the region of cortex



that lies between the temporal and occipital (visual) cortex, although the exact neuropathology required is still controversial and may vary between participants. Some cases have suggested that only a right-hemisphere lesion is necessary, while others suggest bilateral lesions are required (see Farah, 1990, for a review). The deficit resulting from these lesions can be fairly specific. Although prosopagnosic patients have difficulty recognizing individual faces, they sometimes seem to be able to identify other objects. Of course, exceptions to this have been noted, with some patients having difficulty identifying other complex objects. However, not all face processing is entirely abolished in these patients. For example, some prosopagnosic patients seem to have intact facial emotion processing (e.g. Bruyer et al., 1983), and many show “covert” recognition of familiar faces as indicated by sensitive measures such as galvanic skin responses (Tranel & Damasio, 1985).

Evidence from neuroimaging studies of human adults has demonstrated the involvement of a number of regions of cortex. A range of cortical regions within the social brain, including regions of the fusiform gyrus, lateral occipital area, and superior temporal sulcus, have all been implicated in neuroimaging studies as being face-specific regions involved in encoding or detecting facial information. The stimulus specificity of response has been most extensively studied for the “fusiform face area” (FFA), a region which is more activated by faces than by many other comparison stimuli, including houses, textures, and hands (Kanwisher et al., 1997). While the greater activation of the FFA to faces than other objects has led some to propose it is a face module (Kanwisher et al., 1997), others call this view into question. In particular, investigations demonstrating that (a) the distribution of response across the ventral cortex may be more stimulus-specific than the strength of response of a particular region such as FFA (Haxby et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; but see Spiridon & Kanwisher, 2002), and (b) that activation of the FFA increases with increasing expertise in discriminating members of non-face categories (Gauthier et al., 1999), together suggest that the region may play a more general role in object processing. However, the observations do remain that faces more than any other object activate the FFA, and that the distribution of activity over the ventral cortex for faces differs from other objects in that it is more focal and less influenced by attention (Haxby et al., 2001).

Thus, there is considerable evidence for specific cortical involvement in face processing among adults. However, there is also evidence for a face preference in newborn infants, whose behavior, as discussed in the previous chapter, is thought to be guided largely by subcortical sensorimotor pathways. Consideration of this evidence led Morton and myself to propose a two-process theory of infant face preferences analogous to that in chicks. We argued that the first process consists of a system accessed via the subcortical visuomotor pathway (but possibly also involving some of the deeper, earlier developing, cortical layers) that is responsible for the preferential tracking of faces in newborns. However, the influence of this system over behavior declines (possibly due to inhibition by developing cortical circuits) during the second month of life. The second brain system

depends upon cortical maturity, and exposure to faces over the first month or two, and begins to control infant orienting preferences from around 2 or 3 months of age. By extension with the evidence on chicks, we (Johnson & Morton, 1991) argued that the newborn preferential orienting system biases the input set to developing cortical circuitry. This circuitry is configured in response to a certain range of input, before it starts to gain control over the infant's behavior. Once this occurs, the cortical system has acquired sufficient information about the structure of faces to ensure that it continues to acquire further information about them. Like in the chick, the proposal is that a specific, early developing brain circuit acts in concert with the species-typical environment to bias the input to later developing brain circuitry. While this theory is far from proven, a number of strands of evidence are consistent with it. First, let us consider evidence about the neural basis of the face bias in newborns.

Johnson and Morton (1991) speculated that the face bias ("Conspec") was mediated largely, but not necessarily exclusively, by subcortical visuomotor pathways. This proposal was made for several reasons: (a) that the newborn preference declined at the same age as other newborn reflexes assumed to be under subcortical control; (b) evidence from the maturation of the visual system indicating later development of cortical visual processing, and (c) evidence from another species (the domestic chick). Owing to the continuing difficulty in successfully using functional imaging with healthy awake newborns, this hypothesis has, as yet, only been indirectly addressed. First, de Schonen and colleagues examined face preferences in a number of infants with perinatal damage to regions of cortex. Even in cases of damage to the visual cortex, the bias to orient to faces remained (Mancini et al., 1998). The second line of evidence used the fact that the nasal and temporal visual fields feed differentially into the cortical and subcortical visual pathways. Specifically, Simion and colleagues predicted that the face bias would be found in the temporal visual field, but not the nasal visual field. This prediction was confirmed (Simion, Valenza, Umiltà, & Dalla Barba, 1998). A third line of indirect evidence comes from adult neuropsychological studies, and specifically evidence from adult patients with spatial neglect and extinction. Vuilleumier and colleagues (Vuilleumier, 2000; Vuilleumier et al., 2001) report that these patients extinguish (fail to detect) a face much less often than other stimuli. While a variety of explanations of this phenomena are possible, one view is that damage to cortical circuits in adults releases inhibition of a subcortical face bias. Finally, functional imaging studies in adults that include subcortical structures in their analysis have observed activation of a range of subcortical structures in addition to the well-known areas of cortical specialization (Adolphs, 2002).

While Johnson and Morton (1991) identified the superior colliculus as a major visuomotor structure that could be involved in determining Conspec preferences, another candidate structure is the pulvinar. Our knowledge of this brain structure has increased dramatically over the past decade, and the description of its function now makes it a candidate for involvement in newborn visual preferences. Specifically, portions of pulvinar receive input directly from the superior colliculus



(as well as from the retina and, at least in adults, striate and extrastriate visual cortex). Additionally, in adults there are reciprocal connections to frontal, temporal, and parietal regions and to the anterior cingulate and amygdala. The advent of new technology suitable for studying the neural correlates of behavior in newborns may allow further investigation of this issue.

We now turn to the neurodevelopment of face processing during infancy and childhood. To re-cap, the three perspectives on human functional brain development discussed earlier make differing predictions about how this specialization arises. By a maturational view we expect to see the gradual addition of new brain modules relating to aspects of face processing ability. From a skill learning perspective, the fusiform face area should become active as the perceptual skill of face processing is acquired. From an interactive specialization view, we expect to observe the increasing neural specialization and more restricted localization of face processing with development. With these different predictions in mind, let us review some of the evidence from developmental cognitive neuroscience.

Several labs have examined changes in event-related potentials (ERPs) as adults view faces. In particular, interest has focused on an ERP component termed the “N170” (because it is a negative-going deflection that occurs after around 170 milliseconds), which has been strongly associated with face processing in a number of studies on adults (see de Haan, Johnson, & Halit, 2003, for review). Specifically, the amplitude and latency of this component vary according to whether or not faces are present in the visual field of the adult volunteer under study. An important aspect of the N170 in adults is that its response is highly selective. For example, the N170 shows a different response to human upright faces than to very closely related stimuli such as inverted human faces and upright monkey faces (de Haan et al., 2001). While the exact underlying neural generators of the N170 are currently still debated, the specificity of response of this component can be taken as an index of the degree of specialization of cortical processing for human upright faces. For this reason de Haan and colleagues undertook a series of studies on the development of the N170 over the first weeks and months of postnatal life.

The first issue addressed in these developmental ERP studies was when does the face-sensitive N170 emerge? In a series of experiments a component in the infant ERP that has many of the properties associated with the adult N170, but that is of a slightly longer latency, was identified (240–90 ms; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003; Halit, Csibra, Volein, & Johnson, 2004). In studying the response properties of this component at 3, 6, and 12 months of age we have discovered that (1) the component is present from at least 3 months of age (although its development continues into middle childhood), and (2) the component becomes more specifically tuned to human upright faces with increasing age. To expand on the second point, we found that while 12-month-olds and adults showed different ERP responses to upright and inverted faces, 3- and 6-month-olds did not (de Haan et al., 2002; Halit et al., 2003). Thus, the study of this face-sensitive ERP component is consistent with the idea of increased

specialization of cortical processing with age, a result also consistent with some behavioral results (see below).

While we still await definitive functional imaging studies on face processing in infants and young children, evidence for increased localization of cortical processing of faces comes from a recent fMRI study of the neural basis of face processing in children compared to adults (Passarotti et al., 2003). As illustrated in figure 5.6, in this study, even when children and adults were equated for behavioral ability (in a face-matching task), children activated a larger extent of cortex around face-sensitive areas than did adults. Similar conclusions can be drawn from a PET study conducted on 3-month-old infants, in which a large network of cortical areas were activated when infants viewed faces as compared to a moving dot array (Tzourio-Mazoyer et al., 2002). This study involved the “subtraction” of the activation resulting from a complex dynamic stimulus from that elicited by photographs of a female face. The resulting areas of activation corresponded to those regions activated by face processing in adults, namely bilateral activation of the superior and middle temporal gyrus (though the regions activated in infants may be more anterior than those in adults). Despite a low baseline of overall metabolic activity in the frontal lobes (in agreement with the Chugani et al. study [2002] reviewed in chapter 2), there was a significant increase in activity in the left orbito-frontal cortex and Broca’s area in the face condition.

Converging evidence about the increasing specialization of face processing during development comes from a behavioral study that set out to test the intriguing idea that as processing “narrows” (Nelson, 2003) to human faces, then infants will lose their ability to discriminate non-human faces (Pascalis, de Haann, & Nelson, 2002). Pascalis and colleagues demonstrated that while 6-month-olds could discriminate between individual monkey faces as well as human faces, 9-month-olds and adults could only discriminate the human faces. These results are particularly compelling since they demonstrate a predicted competence in young infants that is not evident in adults.

The three lines of evidence reviewed above are hard to reconcile with a strictly maturational view that posits the addition of new components of processing with development. Rather, the evidence available to date suggests “shrinkage” of the cortical activity associated with face processing during development. While increased specialization and localization are specifically predicted by the interactive specialization view, these changes are not necessarily inconsistent with skill learning (Gauthier & Nelson, 2001). Thus, with regard to face perception, the available evidence from newborns allows us to rule out the skill learning hypothesis, while the evidence on the neurodevelopment of face processing over the first months and years of life is consistent with the kinds of dynamic changes in processing expected from the interactive specialization, and not the maturational, approach.

Before leaving the topic of face and individual face recognition, I should note that there is some evidence that infants in the first week of life are able to identify their mother (e.g. Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995). At first sight this evidence seems to conflict with the view that cortical face

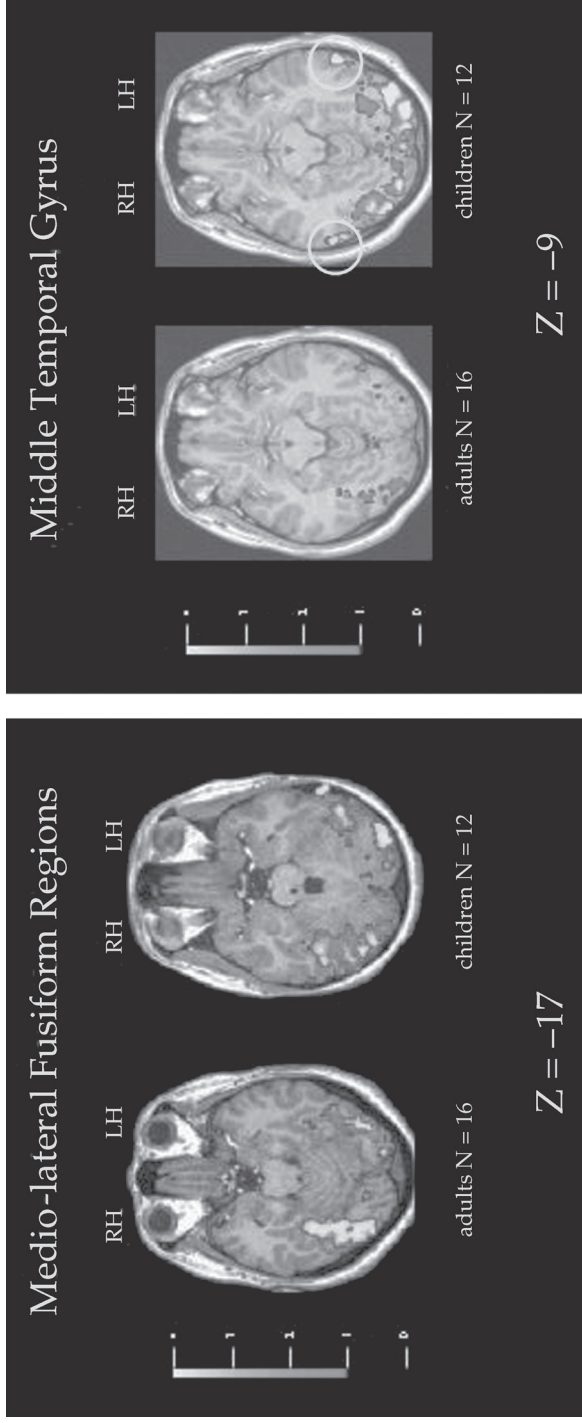


Figure 5.6 Face-matching task. (A) Significant clusters of functional activation in medio-lateral fusiform regions for the face-matching task, in 16 adults (BA 21) and 12 children (right-hand side). (B) Significant clusters of functional activation in the middle temporal gyrus (BA 21) in adults (left-hand side) and children (right-hand side). Circled in yellow is the bilateral middle temporal gyrus activation, which is present only in children, not in adults. Note that posterior activation is within the middle (BA 19) and inferior (BA 18) occipital gyrus. The Z coordinates refer to the distance in mm of the axial slices (e.g. brain slices according to a superior-to-inferior axis) from the intercommissural (anterior commissure–posterior commissure) plane. The colored bar to the left represents the percent increase in intensity of activation in the experimental task, as compared to the control task. Note that according to the radiological convention the left side of the brain represents the right hemisphere (RH), and the right side of the brain represents the left hemisphere (LH).

processing does not emerge until at least the second month. However, this discriminative ability in newborns is based only on the general shape of the head and hair, and not on facial configuration or features. De Schonen and Mancini (1995) argue that this “third system” is a non-specific visual pattern learning ability which has also been evident from studies with visual patterns of many other kinds. Johnson and de Haan have modified the original two-process theory to take account of early hippocampal-based learning (see chapter 6).

FURTHER READING: DE HAAN, 2001



5.5 PERCEIVING AND ACTING ON THE EYES

Moving beyond the relatively simple perception of faces, a more complex attribute of the adult social brain is processing information about the eyes of other humans. There are two important aspects of processing information about the eyes. The first of these is being able to detect the direction of another person’s gaze in order to direct your own attention to the same object or spatial location. Perception of averted gaze can elicit an automatic shift of attention in the same direction in adults (Driver et al., 1999), allowing the establishment of “joint attention” (Butterworth & Jarrett, 1991). Joint attention to objects is thought to be crucial for a number of aspects of cognitive and social development, including word learning. The second critical aspect of gaze perception is the detection of direct gaze, enabling mutual gaze with the viewer. Mutual gaze (eye contact) provides the main mode of establishing a communicative context between humans, and is believed to be important for normal social development (e.g. Kleinke, 1986; Symons, Hains, & Muir, 1998). It is commonly agreed that eye gaze perception is important for mother–infant interaction, and that it provides a vital foundation for social development (e.g. Jaffe, Stern, & Peery, 1973; Stern, 1977).

With regard to the social brain network, the superior temporal sulcus (STS) has been identified in several adult imaging studies of eye gaze perception and processing (for review see Adolphs, 2003). As with cortical face processing above, in adults the response properties of this region are highly tuned (specialized) in that the region responds only to non-biological motion (Puce, Allison, Bentin, Gore, & McCarthy, 1998). While we cannot directly capture the functioning of STS in infants, my colleagues and I have conducted a series of behavioral experiments to ascertain the specificity or otherwise of gaze cueing in infants.

Several studies have demonstrated that gaze cues are able to trigger an automatic and rapid shifting of the focus of the adult viewer’s visual attention (Friesen & Kingstone, 1998; Driver et al., 1999; Langton & Bruce, 1999). All these studies used variants of the spatial cueing paradigm (see chapter 3), where a central or



peripheral cue directs attention to one of the peripheral locations. When the target appears in the same location where the cue was directed (the congruent position), the participant is faster to look at that target compared to another target at an incongruent position relative to the previous cue. Human infants start to discriminate and follow adults' direction of attention at the age of 3 or 4 months (Vecera & Johnson, 1995; Hood, Willen, & Driver, 1998). In our studies we examined further the visual properties of the eyes that enable infants to follow the direction of the gaze. We tested 4-month-olds using a cueing paradigm adapted from Hood et al. (1998). Each trial began with the stimulus face eyes blinking (to attract attention), before the pupils shift to either the right or the left for a period of 1,500 ms (see figure 5.7). A target stimulus was then presented either in the same direction as the stimulus face eyes were looking (congruent position) or in a location incongruent with the direction of gaze. By measuring the saccadic reaction time of infants to orient to the target we demonstrated that the infants were faster to look at the location congruent with the direction of gaze of the face.

In a series of experiments using this basic paradigm, we have established that it is only following a period of mutual gaze with an upright face that cueing effects are observed. In other words, mutual gaze with an upright face may engage mechanisms of attention such that the viewer is more likely to be cued by subsequent motion. In summary, the critical features for eye gaze cueing in infants are (1) lateral motion of elements and (2) a brief preceding period of eye contact with an upright face.

Evidence from functional neuroimaging indicates that a network of cortical and subcortical regions are engaged in eye gaze processing in adults. This network of

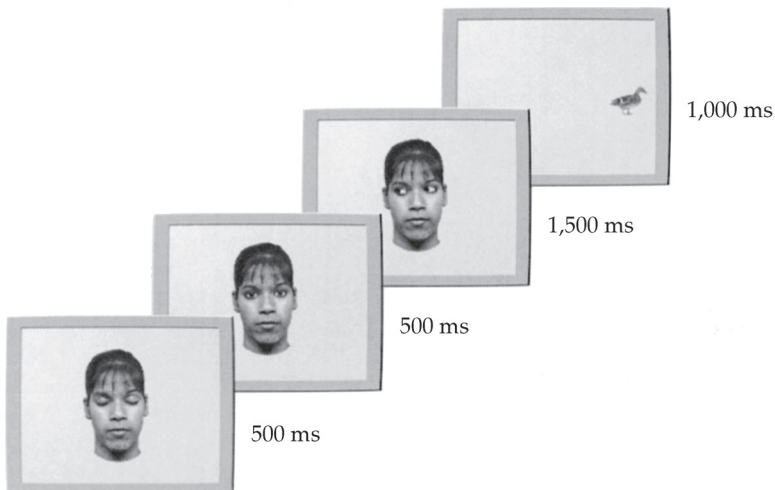


Figure 5.7 Example of the edited video image illustrating the stimulus for Experiment 1 in Farroni et al. (2000). In this trial the stimulus target (the duck) appears on the side incongruent with the direction of gaze.

structures overlaps with, but does not completely duplicate, the patterns of activation seen in the perception of motion, and the perception of faces in general. While it may be important to activate the whole network for eye gaze processing, one region in particular, the “eye area” of the superior temporal sulcus, appears to be critical. The finding that infants are as effectively cued by non-eye motion (Farroni, Johnson, Brockbank, & Simion, 2000) provides preliminary evidence that their STS may be less finely tuned than in adults.

Following the surprising observation that a period of direct gaze is required before cueing can be effective in infants, my colleagues and I investigated the developmental roots of eye contact detection. It is already known that human newborns have a bias to orient toward face-like stimuli (see earlier), prefer faces with eyes opened (Batki et al., 2001), and tend to imitate certain facial gestures (Meltzoff & Moore, 1977). Preferential attention to faces with direct gaze would provide the most compelling evidence to date that human newborns are born prepared to detect socially relevant information. For this reason we recently investigated eye gaze detection in humans from birth. We (Farroni et al., 2002) tested healthy human newborn infants by presenting them with a pair of stimuli, one a face with eye gaze directed straight at the newborns, and the other with averted gaze (see figure 5.8). Videotapes of the baby’s eye movements throughout the trial were analyzed by the two recorders. The dependent variables we used

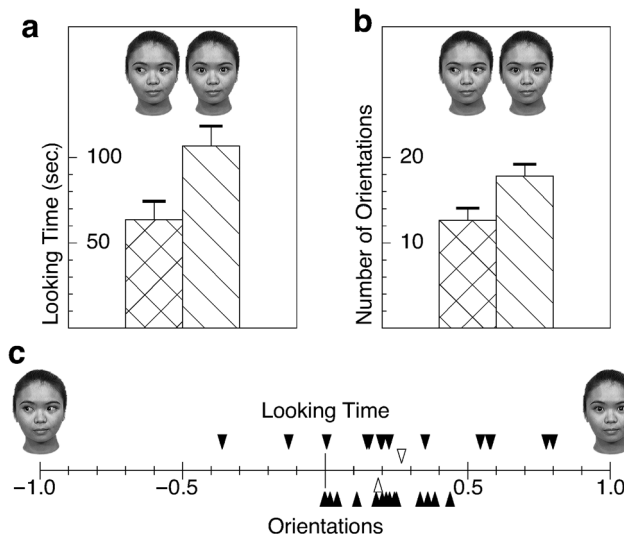


Figure 5.8 Results of the Farroni et al. (2000) preferential looking study with newborns. (a) Mean looking times (and Standard Error) spent at the two stimulus types. Newborns spent significantly more time looking at the face with direct gaze than at that with averted gaze. (b) Mean number of orientations toward each type of stimulus. (c) Filled triangles = reference scores for the direct gaze over the averted gaze for each individual newborn. Open triangles = average preference scores.



were the total fixation time and the number of orienting responses. Results showed that the fixation times were significantly longer for the face with the direct gaze. Further, the number of orientations was higher with the straight gaze than with the averted gaze.

In a second experiment, we attempted to gain converging evidence for the differential processing of direct gaze in infants, by recording event-related potentials (ERPs) from the scalp as infants viewed faces. We studied 4-month-old babies with the same stimuli as those used in the previous experiment with newborns, and found a difference between the two gaze directions at the face-sensitive component of the infant ERP discussed earlier (Farroni et al., 2002). Our conclusion from the second study is that direct eye contact enhances the perceptual processing of faces in 4-month-old infants.

The empirical evidence gathered on the development and neural basis of eye gaze processing in infants is consistent with the interactive specialization view. Specifically, the same primitive representation of high-contrast elements (“Conspec”) as underlies the face bias in newborns may also be sufficient to direct them toward faces with direct eye contact. Therefore, the more frequent orienting to the direct gaze in newborns could be mediated by the same mechanism that underlies newborns’ tendency to orient to faces in general. A face with direct gaze would better fit the spatial relation of elements in this template than one with gaze averted, suggesting that the functional role of this putative mechanism is more general than previously supposed. This primitive bias ensures a biased input of human faces with direct gaze to the infant over the first days and weeks of life.

According to the interactive specialization view, a network as a whole becomes specialized for a particular function. Therefore, I suggest that the “eye region” of the STS does not develop in isolation, or in a modular fashion, but that its functionality emerges within the context of interacting regions involved in either general face processing or in motion detection. Viewed from this perspective, STS may be a region that integrates motion information with the processing of faces (and other body parts). While STS may be active in infants, it may not yet efficiently integrate motion and face information. In other words, while the 4-month-old has good face processing and general motion perception, it has not yet integrated these two aspects of perception together into adult eye gaze perception. By this account, making eye contact with an upright face fully engages face processing, which then facilitates the orienting of attention by lateral motion. At older ages, eye gaze perception becomes a fully integrated function where even static presentations of averted eyes are sufficient to facilitate gaze.



5.6 THE ATYPICAL SOCIAL BRAIN

Beyond face processing and eye gaze detection there are many more complex aspects of the social brain such as the coherent perception of human action, and the

appropriate attribution of intentions and goals to conspecifics. One way in which these issues have been addressed is through behavioral studies with infants, toddlers, and children. A second way is through studying developmental disorders in which aspects of social cognition are either apparently selectively impaired (autism) or selectively intact amidst otherwise impaired cognition (Williams syndrome).

Autism is a relatively rare developmental disorder (with an incidence of around 5 in 10,000 births, see appendix). While there is evidence for some genetic contribution to the disorder, there may be several possible genetic “routes” to autism, and there is also clearly an interaction with environmental factors (see Frith, 2003, for review). Most of the core deficits of the developmental disorder of autism lie in the domain of social relations with others, though there are many non-social cognitive deficits as well. Major behavioral symptoms include avoidance of eye contact, an apparent unawareness of the existence and thoughts of others, a reluctance to be held or touched by others, repetitive behaviors such as rocking or hand flapping, and commonly a fascination for certain objects or other inanimate aspects of their environment. Alongside these deviant behaviors are often deficits in other cognitive and language skills, such as echolalia (repeating words and sentences heard previously). A related disorder, which shares many of the same symptoms, is Asperger’s syndrome, though these individuals have a normal verbal IQ (Happé, 1994; Pennington & Welsh, 1995).

Many different laboratories have attempted to locate specific brain deficits in autism. Applying the adult neuropsychology model (see the causal epigenesis view in chapter 1), it was initially assumed that there would be a focal structural deficit somewhere in the brain, and that this “hole” in the brain could be associated with a particular pattern of cognitive deficits. As we will see, although developmental deficits can result in seemingly quite specific profiles of cognitive deficit, the corresponding structural damage to the brain can be elusive, diffuse, and/or inconsistent across different individuals. In the case of autism, structural brain imaging and postmortem neuroanatomical studies have variously implicated the brain stem, cerebellum, limbic system, thalamus, and frontal lobes (for review see Happé & Frith, 1996). Several studies have reported enlargement of the ventricles, indicating atrophy in adjacent limbic and frontal structures (for review see Pennington & Welsh, 1995). However, like several of the brain atypicalities that have been reported in autism, ventricular enlargement is not specific to autism, since it is also observed in schizophrenia.

FURTHER READING: OZONOFF, 2001; TAGER-FLUSBERG, 2003

Another deficit observed in several studies on autism is in the cerebellum (e.g. Courchesne, Yeung-Courchesne, Press, Hesselink, & Jernigan, 1988). At present it is unclear whether this is a postnatal effect (recall from chapter 2 that cell migration in this region continues into postnatal life) or whether, as Courchesne



et al. (1988) argue, it is caused by atypical cell migration between 3 and 5 months of gestation. Some evidence for migrational failures in cortex has also been observed, though these do not appear to be restricted to any particular area (Piven et al., 1990). One problem in determining developmental brain damage is that it is difficult to ascertain which atypicalities are the root cause, and which are subsequent consequences of earlier atypical development. In general, it is likely that structures and areas that develop latest are most likely to be affected by earlier deviations from the normal developmental trajectory. For example, in autism the atypicalities sometimes observed in the cortex, hippocampus, and cerebellum could all possibly be the consequences of a primary deficit in the thalamus.

The latest region of the cortex to show structural changes in postnatal development, the frontal cortex, has been a favorite region of focus for studies of autism and other developmental disorders such as phenylketonuria (see appendix and chapter 8). While atypicalities in this region may be responsible for some of the cognitive deficits observed, this does not mean that people with autism can be equated with patients with acquired prefrontal cortex damage.

While the brain damage that gives rise to autism may be diffuse and variable, the resulting cognitive profile presents a clearer picture. Many social processes observed in infancy appear to be intact in children with autism. However, they show clear deficits in a later developing aspect of social cognition called “theory of mind”. Despite its grand title, theory of mind is a relatively basic and essential function for our understanding of, and interactions with, other people. Specifically, theory of mind refers to the ability most of us have to comprehend another person’s thought processes, such as their feelings, beliefs, and knowledge. One type of task that can be used to study theory of mind abilities is the so-called “false-belief” task. For example, the following scenario can be demonstrated with dolls, puppets, or human actors (example of procedure taken from Wimmer & Perner, 1983).

Sally has a marble that she puts in a basket. Sally then goes away for a walk. While Sally is away, Anne comes in and moves the marble from the basket to a box. The participant viewing this scenario is then asked “When Sally returns, where will she look for her marble?” If the participant simply tries to predict Sally’s response on the basis of their own personal knowledge, then he or she will answer “the box”. If, on the other hand, she predicts Sally’s response on the basis of Sally’s (false) belief, then the participant will correctly predict that Sally will look in the basket for the marble.

Another false-belief scenario involves showing the participant a container that normally holds candy well known to the child and asking the child what is in the container. The participant will reply with the name of the appropriate candy. The box is then opened and the child shown that it contains a pencil, and not candy. The child is then told that a friend will come in a moment and be shown the closed container and asked what is in it. The participant is asked what the friend will say. Once again, only if the child can infer the friend’s inevitable false belief will he or she reply with the name of the candy rather than a pencil.

Baron-Cohen, Leslie, Frith and their collaborators have shown in a series of studies that most individuals with autism, unlike those with Down's syndrome, fail these and other theory of mind tasks (for reviews see Happé, 1994; Baron-Cohen, 1995; Frith, 2003), while they are relatively unimpaired (compared to mental-age-matched controls) on a variety of related tasks. This pattern of deficit would explain why people with autism often seem to regard others as little different from inanimate objects. Thus, many believe that a deficit in theory of mind is a central cognitive deficit in autism. While there is some agreement on the nature of this cognitive deficit, there are a number of detailed variants of this view that are currently being tested.

Other theoreticians have proposed more developmental accounts, arguing that a lack of theory of mind arises from deficits in precursors such as the infants' capacity for imitation (Rogers & Pennington, 1991) or the perception of emotion (Hobson, 1993). Thus, these authors believe that a social-cognitive deficit from birth, or very shortly thereafter, results in the later deficit of theory of mind. However, whether children subsequently diagnosed as autistic show clear abnormalities before 18 months of age remains controversial. Recently, some laboratories have begun to use high-density ERPs to assess brain functioning in toddlers with a preliminary diagnosis of autism. For example, Dawson and colleagues studied effects of familiarity on face and object (toy) processing (Dawson, Carver, Meltzoff, McPartland, & Webb, 2002). While a control group of young children showed ERP evidence of recognition of both categories, the potentially autistic sample did not show evidence of recognizing the faces. This suggests some degree of specificity in their neural deficit. However, as the authors point out, this deficit is probably secondary to an earlier developmental cause such as failing to orient toward faces at birth. In a similar experiment, Grice and colleagues observed that the ERP correlates of eye gaze processing (as described earlier) appear to be developmentally delayed in young children with autism (Grice et al., in press).

Given the somewhat mixed structural neuroimaging and neuroanatomical evidence, some research teams have tried to use the pattern of cognitive deficits to infer which brain pathways and structures are damaged in autism. Perhaps the most commonly held neuropsychological view is that the pattern of cognitive deficits observed is consistent with damage to the frontal cortex (e.g. Damasio & Maurer, 1978; Pennington & Welsh, 1995). For example, even high-functioning people with autism fail on a number of "executive function" tasks thought to be markers for frontal lobe functioning, such as the Tower of Hanoi planning task and the Wisconsin card sorting task (Ozonoff, Pennington, & Rogers, 1991). At present it is unclear whether these deficits are primary to those in theory of mind, independent of theory of mind, or dependent on the same underlying computations (see Pennington & Welsh, 1995).

The view that the deficit in theory of mind is one of several cognitive deficits which share common underlying computations is also held by those who argue for the importance of the atypicalities observed in the cerebellum (e.g. Courchesne,



1991). By this view, theory of mind is disrupted because the cerebellum is important for the processing of complex context-dependent sequential information that unfolds over time. It is likely that future studies involving functional neuroimaging will allow the dissociation between these different neuropsychological hypotheses.

In contrast to the specific social deficit seen in autism, Williams syndrome participants appear to have the putative “social module” intact. Williams syndrome (WS) (also known as infantile hypercalcemia) is a relatively rare disorder of genetic origin effecting approximately 1 in 20,000 to 50,000 births (Greenberg, 1990) (see appendix). The disorder can now be diagnosed in early infancy through genetic or metabolic markers, and is typified by a number of physical and cognitive characteristics.

Evidence from structural neuroimaging indicates that WS brains are only about 80–5 percent of the overall volume of typical brains, but there are no obvious gross atypicalities or lesions (Jernigan & Bellugi, 1994). Currently, the only evidence for a specific focus of damage is that they show a relative increase in volume in particular lobules on the cerebellum. This cerebellar atypicality contrasts with autism, in which the same lobules are relatively smaller than normal (Jernigan & Bellugi, 1994). At the cytoarchitectonic level, a preliminary analysis by Galaburda, Wang, Bellugi, and Rosen (1994) found disturbances within cortical layers and decreased myelination. Given the lack of evidence for any discrete focal lesions, the specificity of the neurocognitive profile that WS participants present is striking.

FURTHER READING: KARMILOFF-SMITH, 2002; TAGER-FLUSBERG, 2003

Alongside surprising linguistic abilities (see chapter 7), WS participants perform as well as controls in a face discrimination task (the Benton test; Bellugi, Bihrlé, Neville, Jernigan, & Doherty, 1992), and better than typical adults on the face recognition component of a standard memory test (the Rivermead Behavioral Memory Test; Udwin & Yule, 1991). This pattern of spared abilities suggests approximately the opposite of deficits described earlier for autism, and raised the initial hypothesis that people with WS have intact a functional brain system corresponding to a “social module.” Specifically, one preliminary hypothesis is that the social module remains intact in WS, while being specifically damaged in autism. As discussed earlier, one prominent account of the cognitive deficit in autism is that people with autism lack a theory of mind. Karmiloff-Smith and colleagues carried out a series of experiments with WS participants to test the hypothesis that there is “a broad cognitive module for representing and processing stimuli relevant to other individuals, including face processing, language, and theory of mind” (Karmiloff-Smith, Klima, Bellugi, Grant, & Baron-Cohen, 1995, p. 197). While only about 20 percent of autistic participants pass theory of mind tasks such as that described earlier, 94 percent of the WS participants passed these tasks, indicating that theory of mind is intact alongside aspects of language and

face processing. From this result, along with some others, it is tempting to portray WS as showing approximately the opposite neurocognitive profile to autism (while acknowledging that both groups may show some general retardation). This hypothesis is enhanced by the differential cerebellar atypicalities.

However, Karmiloff-Smith et al. (1995) cite evidence from other developmental disorders that is contrary to the simplest view of an impaired or intact prespecified module. For example, in Down's syndrome, a serious deficit in face processing and in the use of morphology in language can co-occur with relatively good performance on theory of mind tasks (Baron-Cohen, Leslie, & Frith, 1985, 1986). Conversely, in an individual with hydrocephalus with associated myelomeningocele, very competent language output co-exists with serious deficits in face processing and theory of mind (Cromer, 1992; Karmiloff-Smith, 1992). These different patterns of dissociation clearly challenge the notion of a predetermined social module in the brain.

An alternative view (Karmiloff-Smith, 2002) is that some degree of modularization is a result of postnatal development, and not a precursor to it (see also chapter 10). Specifically, domain-specific biases in the newborn (such as the face preference discussed earlier in this chapter and the speech discrimination abilities discussed in chapter 7) ensure that cortical circuits are preferentially exposed to socially relevant stimuli like language and faces. With prolonged exposure to such stimuli, plastic cortical circuits develop representations appropriate for processing these inputs, eventually giving rise to an emergent superordinate system for the pragmatics of social interaction in general.

FURTHER READING: KARMILOFF-SMITH, 2002

If this general view of the emergence of the social brain is correct, it implies that early sensory or social deprivation may have long-term consequences. Two lines of research have pursued this issue. In the first, Maurer and colleagues have studied people who suffered visual deprivation for varying periods of time following birth due to uni- or bilateral cataracts. These dense cataracts prevent structured visual input until they are reversed by surgery, usually within the first year. By studying aspects of face processing in this clinical population, this research group showed that even after years of normal experience of faces some deficits remained (Le Grand, Mondloch, Maurer, & Brent, 2001). In other words, visual deprivation over the first months has detectable life-long effects on face processing. Further, by examining cases of unilateral deprivation it has recently been shown that these effects are more due to right hemisphere (left eye) deprivation. Data such as these present a severe challenge for the "skill learning" approach to human functional brain development, and suggest propensity of the right hemisphere for face processing from the first months.

While the cataract population can inform us about sensory deprivation, other populations have been studied that suffered from social deprivation. For example,



samples of children raised in orphanages (e.g. during the Romanian communist regime) can subsequently have multiple social, cognitive, and sensorimotor problems (for review see Gunnar, 2001). While orphanage rearing can be variable in general care quality, at a minimum, stable long-term relationships with caregivers are missing (Rutter, 1998). The outcome from “good” orphanages can include problems with executive functions (see chapter 8) and social cognition, while other aspects of sensorimotor, cognitive, and linguistic development can recover well. At the other extreme, in a sample of children raised in Romanian orphanages for at least the first 12 months, 12 percent exhibited features of autism, although even here these symptoms tended to diminish over time (Rutter et al., 1999).

FURTHER READING: GUNNAR, 2001



5.7 GENERAL SUMMARY AND CONCLUSIONS

As discussed at the beginning of this chapter, the three viewpoints on functional brain development make different predictions about the development of the social brain. Evidence reviewed from the neurodevelopment of face processing appeared inconsistent with a maturational account. The long-term effects of early deprivation and the presence of face and eye gaze biases in the newborn discourage a strictly skill learning perspective. Thus, there is probably neither an innate module for social cognition, nor innate representations relating to these functions that “mature” in the cortex during postnatal life. Rather, complex representations for processing information about other people, their probable thoughts, and likely future actions emerge in the brain as a result of at least three sets of factors: initial biases to attend to socially relevant stimuli such as faces and language; complex interactions with other people; and the basic architecture of the cortex and relevant subcortical structures. Atypicalities in any of these factors could send the infant into a deviant path in which only components of normal social cognitive abilities develop.

A challenge for this interactive specialization view of the emerging social brain will be to generate hypotheses about the consequences of the network of social processing areas being initially intermixed with other cortical networks. Behavioral studies with infants have demonstrated that, from at least 9 months of age, they attribute goals to appropriately moving objects even when these objects do not physically resemble biological forms (see Csibra, 2003, for review). Indeed, some have suggested that infants and toddlers may over-extend their social cognitive abilities to physical objects that adults would not (Csibra, 2003). Whether this blurring of the boundary between social and non-social perception is a by-product of a social brain that has not yet fully emerged from the rest of the brain remains an interesting topic for future research.