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Social Interest and the Development of Cortical Face Specialization: What Autism Teaches Us About Face Processing

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ABSTRACT: *Investigations of face processing in persons with an autism spectrum disorder (ASD) inform upon theories of the development of "normal" face processing, and the story that emerges challenges some models of the nature and origin of cortical face specialization. Individuals with an ASD possess deficits in face processing and a lack of a fusiform face area (FFA). Evidence from studies of ASD can be conceptualized best using an expertise framework of face processing rather than models that postulate a face module in the fusiform gyrus. Because persons with an ASD have reduced social interest, they may fail to develop cortical face specialization. Face specialization may develop in normal individuals because they are socially motivated to regard the face, and such motivation promotes expertise for faces. The amygdala is likely the key node in the system that marks objects as emotionally salient and could be crucial to the development of cortical face specialization.* Dev Psychobiol 40: 213–225, 2002. DOI 10.1002/dev.10028

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INTRODUCTION

Autistic Disorder (commonly referred to as autism) is a Pervasive Developmental Disorder (PDD) characterized by deficits in language, the presence of stereotypic or repetitive behaviors, and social impairments (American Psychiatric Association, 1994; World Health Organization, 1992). Of these three areas of difficulty, deficits in social reciprocity and

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social cognition are generally considered the most compelling. Individuals with autism have significant difficulty with social interactions; they can be somewhat unaware of social norms and have difficulties establishing social relationships with others (Volkmar et al., 1994). Autism is the archetypal PDD and shares many clinical characteristics with other PDDs such as Asperger syndrome and Pervasive Developmental Disorder-Not Otherwise Specified (PDD-NOS), but people with a particular developmental history and the most severe social disability are diagnosed with autism (Cohen & Volkmar, 1997). The shared phenotype of these disorders suggests common neurobiological and genetic mechanisms (Schultz, Romanski, & Tsatsanis, 2000b; Volkmar, Klin, & Pauls, 1998). Frequently, a dimensional approach as opposed to the categorical approach of the Diagnostic and Statistical Manual of Mental Disorders (DSM-IV; American Psychiatric Association, 1994) is used in this field, encapsulating all autism spectrum disorders (ASD).

At this time, there is no quantitative means, such as a blood test or genetic screening, to ascertain if a child has an ASD. Rather, diagnosis is established by an expert clinician (Filipek et al., 2000), often times using standardized interviews such as the Autism Diagnostic Interview–Revised (ADI-R; Lord, Rutter, & Le Couteur, 1989), and a standardized, semistructured assessment using the Autism Diagnostic Observation Schedule (ADOS; Lord, et al., 1989). There is no known cause of ASD, but current consensus suggests that the various forms of ASD may result from combinations of genetic and environmental factors (Fombonne, 1999; International Molecular Genetic Study of Autism Consortium, 1999; Lombroso, Pauls, & Leckman, 1994). A recent report suggests that ASD affects more people than once thought—as many as 16.8 children per 10,000 may have autism and 45.6 children per 10,000 may have some form of ASD (Chakrabarti & Fombonne, 2001).

The intent of this article is to reconcile many of the claims associated with face-processing research of "normal" individuals with what is known of face processing in individuals with an ASD. The study of a population with little or no social interest may teach us a great deal about normal social interest and its correlate, face specialization. Individuals with an ASD, because of their social impairments, provide an interesting contrast to most people whose interest in the face is ubiquitous but often not recognized as such. From the earliest descriptions of individuals with autism, it was noted that people with autism fail to make appropriate eye contact and are inattentive or indifferent to the faces of others (Kanner, 1943). Subtle deficits in face recognition and memory accompany lack of interest in the face, and suggest that individuals with an ASD may lack the expertise that typically developing individuals have with faces. The deficits in face processing for individuals with an ASD are likely related to their social disability (Klin et al., 1999; Schultz et al., 2000b). These data must be reconciled with normative accounts of the neural specialization and behavioral expertise for faces.

NORMAL FACE PROCESSING IS NOT ESPECIALLY SPECIAL

It has long been suspected that "normal" face recognition is an exceptional process. Although faces may appear to be quite different from one another, features of the face and their placement are actually remarkably uniform compared to those of other common objects. It is important to be able to differentiate friends, foes, and strangers during social interactions, and typically developing individuals have developed strategies to distinguish between faces with extraordinary skill. Most people, however, are not as experienced in making such fine discriminations on other objects such as dogs, birds, or cars (Archambault, O'Donnell, & Schyns, 1999; Diamond & Carey, 1986). Because the difference between how we process faces and other objects appears to be a qualitative one, many researchers conclude that the way in which we process faces is "special" (Farah, Rabinowitz, Quinn, & Liu, 2000; Moscovitch & Moscovitch, 2000; Yin, 1969).

An important distinction between faces and most other categories of objects is the level of categorization at which the objects are spontaneously and most easily recognized—what has been called the "basic-level" or more recently "entry-level" (Jolicoeur, Gluck, & Kosslyn, 1984; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). Typically developing persons individuate a face much more quickly and efficiently than most other nonface objects; these processing differences can be attributed to their expertise for faces. For most nonface objects, on the other hand, people are more likely to categorize objects as a "chair or car or bird" than as a "Barcalounger or Ford Explorer or robin." The entry-level is one at which objects maximally differ in terms of their parts, and to categorize objects at more subordinate levels (e.g., "beagle or Snoopy") requires additional perceptual processing effort and time (Jolicoeur et al., 1984). For faces, people more spontaneously utilize a subordinate level of processing and categorize faces at the individual level (e.g., Bill and Hillary Clinton) as fast as they categorize them as "faces," despite having common parts and configuration (Tanaka, 2001). However, this does not imply something unique to faces because experts of other object categories, such as bird watchers or dog experts, also can categorize the individual level as fast as the entry-level (e.g., robin and bird; Tanaka & Taylor, 1991). Moreover, face-selective areas are part of a ventral temporal cortical region that is more engaged by subordinate-level than entry-level judgments on nonface objects (Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Gauthier, Tarr, Moylan, Anderson, & Gore, 2000b).

In addition, typically developing individuals use holistic or configural perceptual processing to inspect a face unlike feature-based processing used to inspect most nonface objects, but this processing strategy is also common to objects of expertise. Inverting a face impairs processing much more than inverting objects for which the observer has no particular expertise (Yin, 1969; see Rossion & Gauthier, in press; Valentine, 1988). Inversion appears to hinder face processing by disturbing the local relational information between face parts (e.g., the distance between the eyes, the nose, and the mouth); in contrast, the effect of inversion on the processing of individual features appears to be null or much more limited (Leder & Bruce, 2000; Le Grand, Mondloch, Maurer, & Brent, 2001). Further, the recognition of face parts is sensitive to changes in their natural configuration whereas this is not the case for common objects (Tanaka & Sengco, 1997). Experts with nonface objects, however, also show a large inversion effect for the objects of their expertise (Diamond & Carey, 1986), and their part recognition becomes highly dependent on part configuration (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). Moreover, configural processing in people trained in the laboratory to become experts with nonface objects is correlated with changes of activity in face-selective areas of the ventral temporal lobe during the process of expertise acquisition (Gauthier & Tarr, in press). As individuals become sensitive to the precise configuration of exemplars from a class of objects, functional magnetic resonance imaging (fMRI) reveals that they recruit their FFA in the processing of these objects.

Thus, a large part and perhaps all of the difference between faces and nonface objects can be attributed to a difference in the preferred level of categorization (subordinate) and the automatic processing strategy (configural). Both effects change with level of expertise. Although it is tempting to suggest that our ability to recognize and process faces is innate (even written into the human genome; Farah et al., 2000), the similarities between face expertise and expertise for other objects is such that a common mechanism in the perceptual systems of the brain would seem to be at work rather than some more specialized, endowed process distinct for faces.

It is difficult to test the origins of face processing when most studies include people who share a lifelong interest in the face. Although some studies suggest that infants show a preference for the face beginning very soon after birth (Simion, Valenza, Umilita, & Dalla Barba, 1998), this preference could be due to more general constraints in the newborn visual system (Kleiner, 1987; Kleiner & Banks, 1987; Simion, Macchi Cassia, Turati, & Valenza, 2001). It may be that humans are biologically prepared to acquire expertise for any class of objects provided there is sufficient motivation and practice to do so, and the brain systems which mediate this process may be genetically prescribed. Social interest, or the interest that primes people to want to be with others, to look at others, and to relate to others on a personal level, may provide such motivation. In the context of the development of cortical face specialization, the idea of social interest encompasses the preference of most young children to regard the face.

HOW FACE PROCESSING DIFFERS IN ASD

In the context of such research on face recognition and expertise, it would seem logical to begin the study of abnormal face processing in ASD by asking whether people with an ASD differ in the level of categorization and configural processing used for faces. However, the study of face processing in ASD has been proceeding in parallel with most of the work in normal face recognition, and links are only beginning to emerge between the two literatures. A diminished inversion effect for faces in these populations as discussed later is indicative of less expertise with faces or being a "face novice" despite no tests of the level of categorization in these populations. Assessing the level of categorization that individuals with an ASD apply to a face presents challenges because current tests of level of categorization play to weaknesses of people with an ASD (such as the use of linguistic cues and reliance on naming people). Nonetheless, face-processing abnormalities of individuals with an ASD suggest that they are less expert at face processing than individuals who do not have the social disorder.

Even at an early age, children with an ASD differ from normal children in interest in others and social behavior. In a retrospective study of the first birthday parties of 11 children with autism and 11 typically developing children, the children with autism showed significantly less interest in the faces of other persons and were less likely to show objects to other people, point to objects, or orient to a person calling their name (Osterling & Dawson, 1994). These social deficits characterized 10 of the 11 children with autism in the group. The failure to orient to a person calling their name also distinguished the children with autism (children with ''late-onset'' autism were excluded in the comparisons) from typically developing children earlier than 1 year of age (Werner, Dawson, Osterling, & Dinno, 2000). It is evident from early on that children with an ASD do not value social stimuli such as the face in the same way that typically developing children do (Dawson, Meltzoff, Osterling, Rinaldi, & Brown, 1998; Volkmar, Cohen, & Paul, 1986; Wing, 1969). This developmental abnormality is likely to place an obstacle in the developmental path of normal face-processing strategies in these children.

People with an ASD, who are arguably face novices compared to typically developing individuals, can nonetheless discriminate between faces (Boucher & Lewis, 1992; Hauck, Fein, Maltby, Waterhouse, & Feinstein, 1998; Ozonoff, Pennington, & Rogers, 1990) and have performed as well as controls on certain tests of face processing (Celani, Battacchi, & Arcidiacono, 1999; Teunisse & de Gelder, 1994). When the demands of the task are increased or elements of emotion are included, however, performance is impaired for persons with an ASD (Davies, Bishop, Manstead, & Tantam, 1994; Tantam, Monaghan, Nicholson, & Stirling, 1989). Moreover, delayed memory of faces is impaired (Boucher & Lewis, 1992; de Gelder, Vroomen, & Van der Heide, 1991; Klin et al., 1999), and recognition memory may be equivalent for faces and objects whereas normal children show a memory advantage for faces (Hauck et al., 1998). The differences in face processing probably arise out of reduced social interest in individuals with an ASD who do not regard the face as socially important (Klin et al., 1999).

Probably one of the most elegant and revealing studies of face processing in ASD was also the first. In a well-controlled study of two groups of children with autism (ages 9 and 14 years), Langdell (1978) demonstrated abnormalities in the way that autistic children process faces by showing them pictures of their classmates' faces with different features occluded by a mask. Both groups of children with autism were better at recognizing their classmates from pictures of their classmates' mouths than the children in the control groups. Whereas the group of children with autism at age 9 had difficulty recognizing their classmates from the upper part of the face (including the eyes), children with autism by age 14 were as good at recognizing their classmates from the upper part of their classmates' faces. In fact, the older group of children with autism was so efficient at identifying particular features of faces that they showed little inversion effect typical of the younger children with autism and the control groups. Children with autism adopted a more feature-based strategy for face recognition and focused more on the mouth than the whole face, in sharp contrast to the preference for eyes demonstrated by normal children (Langdell, 1978). Face-processing deficits may be more pronounced in younger children with autism because older children may have developed compensatory strategies for face identification (Klin et al., 1999; Langdell, 1978). Many of these findings have been replicated: a less pronounced inversion effect (Hobson, Ouston, & Lee, 1988; Tantam et al., 1989), an increased identity recognition ability from the mouth (Joseph, 2001), and a dramatically increased time focused on the mouth (Klin, Jones, Schultz, Volkmar, & Cohen, in press).

The failure of individuals with an ASD to orient to the eyes speaks to social aspects of the face and may serve as a guide to our understanding of normal face processing. Individuals not only identify their families and friends by regarding the face but also how their friends and family are feeling emotionally. While individuals free of social disability orient to the eyes for information regarding the mental states of others, people with an ASD have been shown to have difficulty extracting the ''language'' of complex emotional states from the eyes (Baron-Cohen, Wheelwright, & Jolliffe, 1997).

In an elegant study, eye-tracking technology measured the visual fixations of 15 males with an ASD and 15 matched controls viewing social scenes from the movie, *Who's Afraid of Virginia Woolf* (Klin et al., in press). While the control group monitored the interactions of the actors by regarding the actors' eyes, people with an ASD were much more focused on the mouth in the movie. Greater attention to the mouth may explain why this feature is a perceptual strength of individuals with an ASD. Klin and colleagues (in press) argued that persons with an ASD, unlike typically developing individuals, do not find the eyes meaningful or informative. The authors suggest that whereas most people attend to the eyes to follow social interactions, individuals with an ASD look at the mouth in an attempt to obtain more verbal information about the exchanges.

Face-processing deficits are at the core of the findings presented earlier that individuals with an ASD fail to receive social information from the face. Whereas deficits in face processing detrimentally affect face recognition, these processing deficits also may disrupt processing of social information from the face. Therefore, exploring abnormalities in face perception at the neurofunctional level might help us to contextualize some of the face-related aspects of the social disorder (such as emotion discrimination and eye gaze detection) as well as characterize normal face processing.

WHAT THE BRAIN THINKS OF FACES

Research of patients with brain injuries suggests that the areas subserving face processing are segregated at a cortical level from those important to the processing of objects (Moscovitch, Wincour, & Behrmann, 1997). Prosopagnosia, an impairment in face recognition which results from lesions of ventral temporal cortex in the area of the fusiform gyrus (FG), has provided a road map for investigation of the neural substrates of face processing using other methodologies (Damasio, Damasio, & Van Hoesen, 1982). In some rare cases, object recognition is argued to be intact (De Renzi, 1986) or the face impairment appears to be disproportionate with deficits with objects (Farah, Levinson, & Klein, 1995). Despite the rarity of these cases, the great variability between them, and important methodological limitations of many studies (Gauthier, Behrmann, & Tarr, 1999a), research on prosopagnosia has convinced some that part of the cortex is solely devoted to the recognition of faces.

Intracranial recordings in the human temporal lobe, a technique used preoperatively in cases of intractable epilepsy, have also implicated the ventral temporal cortex in the processing of faces (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999). A negative potential around 200 ms is selective for faces compared to other objects. Using scalp electrodes, a similar negative potential is recorded at 170 ms, which has been called the N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Its amplitude is larger to faces than to most other objects, although there also can be significant differences in amplitude between other categories (e.g., shoes, cars, and chairs; Rossion et al., 2000). However, it is the effect of inversion on the N170 which most reliably distinguishes face and nonface object recognition. Whereas inversion has no effect on the N170 for objects, it increases the amplitude of the N170 for faces and also causes a very robust delay of about 10 ms in the peak of the potential (Linkenkaer-Hansen et al., 1998; Rossion et al., 2000).

Positron emission tomography (PET) and fMRI also have been used extensively to study systems involved with face recognition. The superior spatial resolution of these techniques has allowed the precise localization of several face-selective areas in the human brain. The best known is the fusiform face area (FFA; Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995; Puce, Allison, Gore, & McCarthy, 1995), which shows more activity to faces than most other objects (Figure 1). More recently, attention has been drawn to a second face-selective area in the lateral occipital cortex, an ‘‘occipital face area’’ (OFA; Gauthier et al., 2000c; Halgren et al., 1998; Haxby et al., 1999). Its response is not as robust as that of the FFA, and it is still not clear what role it plays vis-à-vis the FFA in face perception. Other areas along the superior temporal sulcus respond selectively to facial movements, eye gaze, and gesture (Puce, Allison, Bentin, Gore, & McCarthy, 1998). This region seems involved in the decoding of nonverbal communications expressed through the face and body.

Recently, attention has been turned to the reasons underlying cortical specialization for face processing. Select regions of the FG and occipital cortex provide the neural substrate that preferentially responds to faces over other objects, but is it possible to say that this is so because faces are ‘‘special?’’ According to some, evidence for the special perceptual effects found with faces places them among very few categories (perhaps with scenes and body parts) whose processing is highly modular. In a recent review, Kanwisher (2000) stated ‘‘that many studies show that [the FFA] is not only activated when subjects view faces but activated at least twice as strongly for faces as for a wide variety of nonface stimuli, including letter strings, assorted objects, animals without heads, and the backs of human heads’’ (p. 759). Evidence such as this has led her and others to believe that the FFA is domain specific or a ‘‘module’’ for faces in the human brain, and more specifically that the FFA may be dedicated to the *detection* of the face geometry (Kanwisher, Downing, Epstein, & Kourtzi, 2001).

Just as in behavioral studies, neural effects which have been at some point deemed ‘‘face-specific’’ can, under the right circumstances, be demonstrated for nonface objects of one’s expertise as well. First, as described earlier, fMRI studies associate factors such as subordinate-level processing and expertise with activity in face-selective areas (Gauthier et al., 1997; Gauthier, Skudlarski, Gore, & Anderson, 2000a; Gauthier, Tarr, Anderson, Skudlanski, & Gore, 1999b; Gauthier et al., 2000b; Gauthier et al., 2000c). For instance, the right FFA and OFA of car experts activates more for cars than for birds whereas the reverse is true for bird experts (Gauthier et al., 2000a).

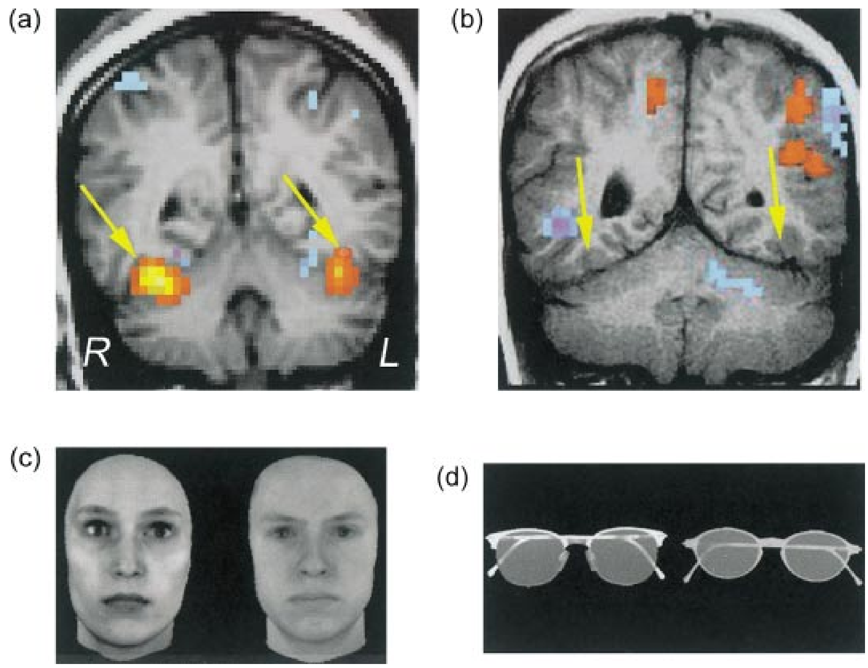

FIGURE 1 fMRI *t* maps of the brain during face perception. Activation of the fusiform gyrus to faces is shown in red/yellow and identified by arrows in a typically developing young adult (a). Note the clear focus of face-related activation bilaterally in the fusiform gyrus. In contrast, a young adult with autism shows a lack of activation (b). Images are in a coronal orientation, with right and left reversed by convention, and functional data are superimposed on anatomical images for localization. fMRI data are from a blocked experiment comparing face perception (c) to nonface object perception (d) during a "same/different" discrimination task on a 1.5 Tesla system. The threshold for displaying activations is set at $t = 1.5$. Object activations are shown in blue on the fMRI maps (adapted from Schultz, Grelotti, & Pober, 2001).

Second, effects of expertise are found on the first face-sensitive event-related potential component; for example, experts show larger amplitude N170s for the object of their expertise than for other objects (Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, in press; Tanaka & Curran, 2001). Moreover, specialization for different categories seems to be a relatively general phenomenon in the visual system which can be obtained for many different categories (Haxby et al., 2001; Kreiman, Koch, & Fried, 2000) including the case of letter specialization, the development of which necessarily implicates learning rather than evolutionary mechanisms (Gauthier et al., 2000c; Puce, Allison, Asgari, Gore, & McCarthy, 1996).

Another model of cortical face specialization was inspired by the role of level of categorization and expertise in face processing and the facelike activations in experiments of level of categorization and expertise in nonface objects. Tarr and Gauthier (2000) argued that a "process map" in ventral temporal lobe (as opposed to the idea of a "feature map" first proposed by Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999) better accounts for the experimental data on neural activity in this area. According to this hypothesis, different parts of the visual system are best suited for different object-recognition strategies (e.g., feature detection or configural processing). Through practical experience with objects, different categories of objects become associated with particular recognition strategies (e.g., faces need to be recognized rapidly at the individual level, a problem which appears to be solved at least partly through the use of relational information). It is believed that the repeated association of a category's geometry with a processing strategy and the repeated advantage in processing of certain parts of visual cortex for this strategy eventually lead to a direct link between object geometry and activity in this part of the brain. This hypothesis offers an explanation for the origins of the observed feature map in ventral temporal cortex, which may arise through the repeated mappings between features and localized brain processes.

The results of neuroimaging studies in ASD support the idea that expertise underlies face-processing strategies and activation in the FFA. In the first neuroimaging study of face recognition in ASD, Schultz and colleagues (2000a) discovered that the slight face deficits characteristic of ASDs have significant neurofunctional implications. In a study of 14 individuals with an ASD, subjects were asked to make same/different judgments for faces and objects. Normal controls showed typical activation of the FG for faces, but individuals with an ASD showed no activation in the FG (Figure 1). Instead, individuals with an ASD seemed to use areas that normal controls used to process objects, specifically the inferior temporal gyrus. The finding that individuals with an ASD show little or no face specialization in the FG now has been confirmed by other studies (Critchley et al., 2000; Dierks, Bolte, Hubl, Lanfermann, & Poustka, June, 2001).

The expertise model provides an account of the neural deficit for face processing in individuals with an ASD. It is not clear how other theories of face processing may explain these findings in ASD. Individuals with an ASD have no difficulty detecting a face. A face-detection theory of the FFA is therefore not supported by evidence from ASD. People with an ASD are reasonably accurate at distinguishing faces and, compared to typical individuals, show small to moderate face deficits under many but not all experimental setups. There is certainly no deficit as severe as that found in most cases of prosopagnosia (Damasio et al., 1982). In addition, it is interesting to note that studies of prosopagnosics do not report that the patients experience major social impairments other than that of face recognition. Nevertheless, persons with an ASD have no FFA. It is not known whether the neurobiology of the FG of individuals with an ASD is abnormal; however, neuroradiologists did not see any structural abnormality in the FG on anatomical scans of the subjects of one study (Schultz et al., 2000a). While it is possible to use a modular view of face processing to explain these results, this approach would have to explain why only the face module or the face part of the feature map failed to develop properly, coincidental to deficits in other systems that support social cognition. As such, the process map model, with its consideration of the role of experience in category specialization, offers the most parsimonious explanation for this finding by putting activation in the FFA in the context of a broader network of social processing.

"WE DON'T KNOW WHO DISCOVERED WATER, BUT WE'RE CERTAIN IT WASN'T A FISH." attributed to Marshall McLuhan

Tim Langdell is known only to us by his landmark 1978 article on face processing in autism, but when discussing his research, we immediately begin to think of what he must be like as a person. We ascribe personal traits to him such as insight and compassion despite never having met him, and we think of what he must look like. Each of us, however, has a different mental image of his face: One of us may believe that he must be somewhat on the thin side, pale-skinned and dark-eyed, with bushy, expressive eyebrows and a thin nose and lips. People with an ASD are not as motivated to make such social attributions, and the face, to them, is not a repository of important information like it is for typically developing individuals. Because persons with an ASD have a social disability that leads them to have a different set of life experiences with people, it seems likely that their lack of social interest and emotional engagement with others leads to less expert face-processing strategies and underactivation of the FFA (Schultz et al., 2000a).

Our interest in faces is pervasive and often unnoticed, like water to fish. We are led to believe that the nature and origin of this face processing is so important that it is innate, specifically written in our genome, or otherwise contained in ventral temporal cortex. But we have no good control for interest in faces in experiments of normal individuals, and unlike geological formations on Mars, we have seen no face in our genome.

Individuals with an ASD, absent unspeakable studies of deprivation, provide our only control for the social interest that underlies or accompanies all processes that deal with the face. Evidence from ASD suggests that if one removes social interest, specialization in the cortex for faces does not develop. Social interest may or may not exert a direct influence on specialization in the visual system, but without this natural influence there is little to prime us to look at faces with any more frequency than other objects. Social interest could be necessary to the specialization for faces in the FG, or it is possible that it could be replaced by external sources of motivation such as the kind of supervised learning that one can encounter for letters and words and which appears to lead to similar specialization for letters in other parts of the visual system (e.g., Puce et al., 1996). Research in ASD suggests that the origin of social motivation is not contained in the FFA, but the result of another brain area (Schultz et al., 2000a; Schultz et al., 2000b).

THE CHICKEN OR THE EGG

The expertise model, as currently formulated, tells only part of the story of face specialization because it heretofore has not specified the necessary and sufficient forces behind the acquisition of this specialization. One question is whether there is some organizing principle in the brain that would influence one's motivation to individualize exemplars of a category and devote neural resources to configural processing of the object. For faces, it is likely that social interest provides the motivation to regard the face and individualize a person, from which expertise for faces and cortical face specialization develops. A job of this type is likely to make use of a structure that is limbic in nature, and the darling of current theories is the amygdala (Schultz et al., 2000a; Schultz et al., 2000b).

It is easy to understand that activities to which people devote a considerable amount of their time have special significance for them. Bird experts love birds, dog experts love dogs, and car experts love cars (At least one car expert known to us writes books of road poetry.) Experts organize social organizations to discuss their interests, devote Web sites to their interests, and probably choose to associate with others on the basis of mutual interests. Greeble experts also could be construed as forming a social bond with Greebles; they learn to make social attributions to Greebles by naming them and categorizing them into "families." There is a relationship between interest and objects of one's expertise. Whether expertise and cortical face specialization develop as a result of interest or whether interest becomes important as expertise develops is unknown.

The amygdala, by virtue of its role in salience detection and because of its dense reciprocal anatomical connections to the ventral temporal cortex (Aggleton, 1993), is ideally positioned to influence and guide the acquisition of face expertise. It can flag the face as a meaningful object that requires further, more extensive processing, which may lead to the expertise effects that we measure experimentally. Normative studies have implicated the amygdala in emotional learning (Gaffan, Gaffan, & Harrison, 1988; Ono, Nishijo, & Uwano, 1995), signaling of the emotional salience of events (Aggleton, 1993; Ono et al., 1995), social behavior (Brothers & Ring, 1993; Kling & Steklis, 1976; Rosvold, Mirsky, & Pibram, 1954), social cognition (Castelli, Happe, Frith, & Frith, 2000), and the perception of facial expressions (Adolphs, Tranel, & Damasio, 1998; Breiter et al., 1996; Fried, MacDonald, & Wilson, 1997). Amygdala and FG activations to judging the intentionality of the movement of geometric shapes (compared to randomly moving shapes) in a study of social cognition (Castelli et al., 2000) accentuate the potential influence of the amygdala on the FG.

We believe that the amygdala plays an important developmental role in the acquisition of face expertise, such that it participates in signaling the emotional and social relevance of faces to the developing infant. This forces experience with faces and allows the development of expertise. Once face specialization occurs, amygdala damage does not seem to undo normal face perception (Broks et al., 1998), though there could be some role for amygdala processes in maintaining preinjury levels of expertise.

The amygdala could work to support cortical face specialization in one of two ways. The amygdala, possibly among other structures, may have a direct influence on the development of the FFA, demanding that the FG accommodate social interests such as faces with faster perceptual processing. On the other hand, it may orient an individual to the face out of social interest and indirectly shape visual cortex as a result of a repeated exposure to this visual stimulus. Both models may be related to the processes that engender expertise for other interests such as cars, birds, or dogs. Further, these models seem to fit evidence that direct gaze increases activation of the FG and correlations of fusiform activity with that of the amygdala (George, Driver, & Dolan, 2001). Thus, the lack of attention paid to the eyes in persons with an ASD (Klin et al., in press) is probably a reflection of their lack of social interest, and at the same time may partially explain the underactivation of their FG to faces.

Neuroimaging and histological studies have found abnormalities in the organization or function of the amygdala of individuals with an ASD. Neuroimaging studies of the perception of emotional expressions provide evidence to the hypothesis that the amygdala of individuals with an ASD is less active than those of typically developing subjects (Baron-Cohen et al., 1999; Critchley et al., 2000). Postmortem studies of the brains of individuals with autism have revealed structural abnormalities in their amygdala (Bauman & Kemper, 1995). Lesioning of the amygdala seems to provide the best animal model of ASD (Bachevalier, 1994). Ventral temporal areas of the cortex are plastic (Fujita, Tanaka, Ito, & Cheng, 1992; Löwell & Singer, 1992; Rolls, Baylis, Hasselmo, & Nalwa, 1989; Webster, Ungerleider, & Bachevalier, 1991) and may be shaped by their reciprocal connections to the amygdala (reviewed in Schultz et al., 2000b).

Amygdala dysfunction might disrupt social interest in individuals with an ASD in two ways. The inability to make appropriate social judgments about the face in individuals with an ASD and individuals with bilateral amygdala damage suggests that amygdala dysfunction impairs the ability to link social stimuli with their social meaning (Adolphs, Sears, & Piven, 2001). In addition, a general lack of social interest resulting from amygdala dysfunction might not spark the acquisition of face expertise. If the amygdala of individuals with an ASD is not geared to support social interest, it may not stimulate attention to faces. Without the amygdala signaling the salience of faces during infancy, face specialization would not occur.

CONCLUSIONS

Behavioral and neuroimaging evidence from studies of individuals with an ASD support the hypothesis that face processing is another example of expertise processing and that face specialization in the FFA is mediated by experience with faces. Future studies of face processing and expertise may take advantage of new paradigms to more directly address the role of the amygdala in the development of cortical face specialization. There also is a need for a better assessment of object processing in ASD, and it will become important to consider the results of behavioral intervention on the response of the FG to faces, and perhaps the response of the FG in individuals with an ASD to objects of their expertise. Histological or high-resolution structural neuroimaging data also may uncover heretofore unknown neuronal abnormalities in the visual system. By trying to account for abnormalities in face processing in people with an ASD as well as normal specialization for faces, the expertise model sets the bar higher and clearly defines the next challenge: to specify the role of social interest and the emotional circuitry of the brain in the development of face processing.

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