

## Acquisition and Disruption of Category Specificity in the Ventral Visual Stream: The Case of Late Developing and Vulnerable Face-Related Cortex

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### 18.1 Introduction

The discrimination and recognition of individual visual objects, including faces, words, and common objects, are among the most taxing perceptual challenges confronting observers in their day-to-day life. Not only does the observer need to derive precise information about the various objects under dramatically differing lighting conditions, scales, and vantage points, but the object must also be perceptually individuated from all other instances of that object so that identity can be assigned and the appropriate semantics (and phonology, where relevant) activated. Moreover, all of these processes must be executed accurately and rapidly, notwithstanding the ambiguity of the input arising from the commonality of input features (e.g., all faces have two eyes, a nose, and a mouth in the same spatial arrangement, and all words are made from the same relatively small set of letters). Despite the clear computational challenge associated with object recognition, human observers are remarkably efficient at assigning identity effortlessly and accurately, particularly for faces.

Much recent research has suggested that one way in which this efficiency is achieved is through a division of labor, that is, different classes of input are assigned to different underlying neural systems to mediate the representation of that object type (Downing et al. 2006). At present, there is clear consensus that segregated regions of human ventral cortex are activated differentially in response to different stimulus classes, although the extent to which these regional distinctions are truly domain-specific and exclusive is highly debated. Also, elucidating the nature of the underlying computations in these differing regions is highly challenging, and much remains to be done to understand the mechanisms supporting recognition. Controversial, too, is the means by which this segregated topography and coherent organization emerges in human cortex. This latter point is the focus of this chapter. We also consider the consequences for object perception when this selectivity pattern is disrupted, either in the course of development or as a consequence of brain damage in pre-morbidly normal individuals.

### 18.2 Category-Specific Topography of the Ventral Visual Pathway

In adults, the functional topography of the ventral cortex reflects an organized category-selective map with particular stimulus classes eliciting distinct patterns of cortical activation (Downing et al. 2006; Grill-Spector, Chap. 6; Grill-Spector and Malach 2004; Hasson et al. 2003). Converging neuropsychological and neuroimaging studies indicate that common objects activate medial portions of the posterior fusiform gyrus and a region of the lateral occipital cortex (LO) (Grill-Spector et al. 1999), whereas buildings and landscapes activate the collateral sulcus (CoS) (Aguirre, Zarahn, and D'Esposito 1998) and the parahippocampal gyrus ("parahippocampal place area" (PPA); Epstein and Kanwisher 1998). Faces consistently engage a lateral portion of the posterior fusiform gyrus ("fusiform face area" (FFA); Kanwisher, McDermott, and Chun 1997), a lateral region in the inferior occipital cortex separable from the object-related region ("occipital face area" (OFA); Gauthier et al. 2000), and the superior temporal sulcus (STS) (Hoffman and Haxby 2000). Much recent evidence suggests that these areas are not necessarily fully independent and, at least for face processing, a distributed network of these nodes make up a core network that then interfaces with other relevant areas of cortex (Ishai 2007; Fairhall and Ishai 2007; Gobbini and Haxby 2007; Thomas et al. 2009).

Recently, researchers have begun to employ high-resolution neuroimaging techniques to evaluate how this functional topography develops in children's brains. Some progress has been made in elucidating the developmental trajectory by which this cortical organization emerges. We already know from decades of behavioral studies that there is a differential maturational trajectory associated with different visual stimulus classes. For example, children's recognition skills for face identity and expression do not mature until late childhood and lag behind recognition skills for other categories of visual objects. Specifically, children do not exhibit mature recognition skills for facial identity (Carey and Diamond 1977; Carey, Diamond, and Woods 1980; Ellis, Shepard, and Bruce 1973; Flin 1985; Mondloch et al. 2003, 2004) or facial expressions (Herba and Phillips 2004; Thomas et al. 2007) until early adolescence, although their recognition skills for houses and objects appears to mature much earlier (Carey and Diamond 1977; Golarai et al. 2007; Teunisse and de Gelder 2003). Indeed, children continue to show improvements in their abilities to recognize unfamiliar faces until 12 years of age, and this delayed developmental trajectory may be related to changes in the neural substrate for face processing (Diamond, Carey, and Black 1983).

Given the different developmental trajectories for recognition skills across different object categories, one might expect that the functional specialization of face-, object-, and place-selective patterns of brain activation also follows different developmental trajectories that coincide with the ages at which recognition skills become adult-like. This pattern of functional brain development is consistent with the "interactive specialization" model, which suggests that specialization is dependent on learning processes and interrelations among brain regions (Johnson 2001; Johnson and Munakata 2005). Alternatively, given the importance of object recognition, and face recognition in particular, one might expect that this category-specific organization is architecturally innate and functionally organized from an early age (Farah et al. 2000). In this case, one

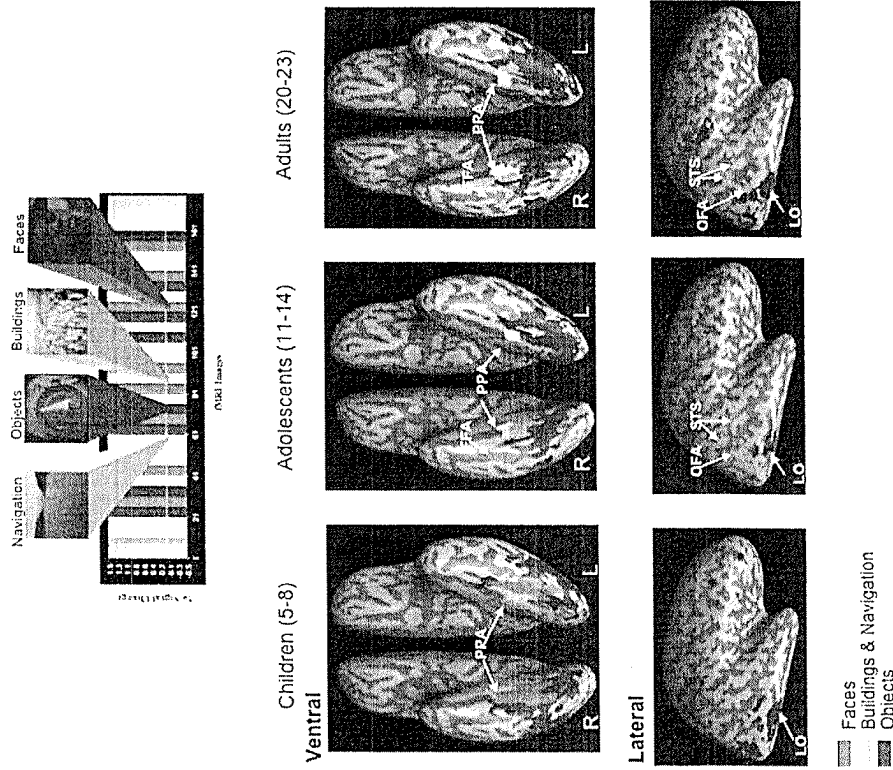
would expect to see adult-like patterns of face-selective activation even in very young children. Because the functional topography in the adult ventral visual pathway is so well characterized, studying the development of this system and the consequences for object perception that ensue when this selectivity pattern is disrupted provides a unique opportunity to evaluate models of the neural basis of object perception and of functional brain development more broadly.

### 18.3 Typical Development of Face-Related Cortex

Several neuroimaging studies have begun to explore the emergence of face-related activation in the developing brain, particularly in the fusiform gyrus. Although a PET study with infants suggested that face-related activation may be present in 2-month-old infants (Tzourio-Mazoyer et al. 2002), fMRI studies, which have better spatial resolution, are providing converging results that children less than 8 years of age, as a group, do not consistently activate the FFA and that FFA activation continues to mature through early adolescence (Aylward et al. 2005; Gathers et al. 2004; Golarai et al. 2007; Passarotti et al. 2003; Passarotti et al. 2007).

As an example of one such a study, Figure 18.1 presents data from a recent fMRI experiment conducted with observers aged 5 to 8, 11 to 14, and 20 to 23 years of age (Scherf et al. 2007). Participants viewed naturalistic, real-time movies of unfamiliar faces, buildings, navigation through open fields, and objects in a blocked fMRI paradigm (Fig. 18.1(a)). The movie clips were organized into 32 blocks of 15-s duration, each containing a single stimulus category. This task has been used successfully to map category-selective activation in the ventral visual cortex in adults (Hasson et al. 2004; Avidan et al. 2005). There were no specific task demands associated with this paradigm (by design), so performance differences between the different age groups could not account for different levels of functional activation. Also, the groups did not differ in the amount of motion throughout the scan, which was limited to 2 mm in any direction. Figure 18.1(b) shows the average activation maps for the different age groups in this experiment. Note that we group together the building and scene-related activation, as both typically activate the PPA in the collateral sulcus (CoS) (Avidan et al. 2005).

A number of important findings emerge from this study. As is evident in the group map for the adults shown in Figure 18.1(b), there is clear topographic organization in ventral visual cortex, replicating the numerous studies of this sort conducted with adults. Of greater interest for the present work is the apparent adult-like cortical profile in adolescents and the absence of face-related activation in the youngest age group. Statistically, there were no age differences in activation profiles for areas PPA or LO, which are building- and object-selective regions, respectively. However, children show significantly less face-selective activation than adolescents or adults, and this was true for both the right and left hemispheres. That face-selectivity emerges late and after the selectivity associated with other classes is interesting and has been taken to suggest that there is a protracted neural trajectory underlying the maturation of face processing. Note that the failure to observe face-related activation in the young children cannot be attributed to differences in motion or a lack of statistical power



**Figure 18.1.** Ventral stream category-specific topography within each age group. Contrast maps for each object category ( $p < .05$  corrected) from the group-level random-effects (GLM) mapped onto the ventral projection, and the lateral right hemisphere of a single representative inflated brain in order to show consistency, or lack thereof, across the age groups in category-selective activation. FFA, fusiform face area; OFA, occipital face area; STS, superior temporal sulcus; LO, lateral occipital object area; PPA, parahippocampal place area. (See color plate 18.1.)

given the robust and comparable activation for the other stimulus classes across the age groups.

#### 18.3.1 Mechanisms of Functional Brain Development in Fusiform Gyrus

Although this study and others like it have provided some indication about when face-related activation in the fusiform gyrus begins to mature, there is little consensus on how

this occurs. There are several candidate mechanisms for the maturation of face-related activation in the fusiform gyrus. They are not mutually exclusive and may occur along different developmental timelines, which may help explain the discrepancy in findings among the existing studies. For example, several reports suggest that the fusiform face area matures via an increase in the amount of face-selective activation within the gyrus, particularly in the right hemisphere (Aylward et al. 2005; Gathers et al. 2004; Golarai et al. 2007) but perhaps also bilaterally (Scherf et al. 2007). In one study, the size of children's (ages 7–11) right FFA was one-third the size of the adult's FFA (Golarai et al. 2007). Other findings reveal a shift in the locus of the face-selective activation from a more posterior portion of the ventral visual pathway to the more anterior region of the fusiform (Aylward et al. 2005; Gathers et al. 2004) and/or from a distributed to a more localized pattern of activation within the fusiform gyrus (Passarotti et al. 2003). Additionally, the emergence of the location of face-related activation in a group of individuals might arise via an increase in the consistency of the location of activation across individuals in these regions of cortex. It has been reported that there is more variability in the individually defined locus of face-related activation in young children, preventing the ability to detect group-level regions in a whole-brain analysis (Scherf et al. 2007). Finally, two studies reported a developmental increase in the magnitude of face-selectivity in the classic adult FFA region, particularly in the transition from childhood to early adolescence (Golarai et al. 2007; Scherf et al. 2007). In other words, during development there appears to be an increase in the number of neurons in the fusiform gyrus, particularly those near the classical FFA region, that are becoming selectively tuned for faces over other visual categories.

Importantly, these findings converge to indicate that face-related cortex is clearly immature in young children, which is not consistent with the strong version of the innately specified model of functional brain development in the ventral visual pathway. Furthermore, the consistency in findings that the transition from childhood to early adolescence appears to represent an important time for the development of face specificity, particularly in the fusiform gyrus, overlaps a great deal with that observed in behavioral performance on face-processing tasks. This suggests that experience plays an important role in influencing the course of functional specialization in the ventral visual pathway, which is consistent with the predictions of the interactive specialization model (Cohen Kadosh and Johnson 2007).

A large literature supports the notion that the ability to encode and recognize unfamiliar faces (Carey and Diamond 1977; Carey, Diamond, and Woods 1980; Ellis, Shepard, and Bruce 1973; Diamond and Carey 1986; Mondloch et al. 2004) and facial expressions (Herba and Phillips 2004) continues to improve into late childhood, and, in some cases, into adolescence. Many of these groups have argued that the ability to recognize individual faces continues to improve as children develop expertise in configural encoding. This involves recognizing faces on the basis of subtle metric variations between their constituent features, and is thought to reflect the acquisition of expertise. Several neuroimaging studies with adults have shown that both the FFA and the OFA are involved in recognizing individual faces (e.g., Gauthier et al. 2000). Also, expertise for classes of perceptually homogenous novel objects and objects of expertise produces increased activation in the classically defined FFA region (e.g., Gauthier et al. 1999). Thus, the apparent transition in the development of face-selective activation

may be related to the acquisition of expertise for individual face recognition and the subsequent fine-tuning of large populations of neurons in the adult face-related regions.

### 18.3.2 Relating Developmental Changes in Face-Processing Behavior and Face-Related Activation

A prerequisite in determining how experience influences the development of functional specialization in the brain is evidence of a relation between improvements in face-processing behavior and changes in the functional organization of the ventral visual pathway. Unfortunately, very few studies have been able to report developmental changes in such brain-behavior correspondences. Golarai and colleagues (2007) found a relation between the size of the right FFA and the accuracy of recognition memory for faces, but not places or objects, in children (ages 7–11) and adolescents (ages 12–16), but not in adults. They did not report whether a developmental increase in *face selectivity* in the right FFA was related to recognition memory performance.

Two studies employed the classic *face inversion* task as a means of evaluating the relation between changes in brain function and face-processing ability. Children and adults are slower and less accurate in their ability to recognize an inverted face (Yin 1969; Gilchrist & McKone 2003; Sangrigoli and de Schonen 2004), and developmental increases in the magnitude of the face-inversion effect have been interpreted to reflect more sophisticated use of face-recognition strategies, particularly in terms of improved configural processing (Carey and Diamond 1977). Aylward and colleagues (2005) found that the magnitude and extent of activation in both the right and left fusiform gyri correlated significantly with the magnitude of the face inversion effect (tested after the scanning session) in children (ages 8–10) and adolescents (ages 12–14). However, the authors did not report whether there was a developmental increase in the face inversion effect from childhood to adolescence, so it is possible that the brain-behavior correlations could have been mediated by individual differences, regardless of age. Finally, Passarotti and colleagues (2007) engaged children, adolescents, and adults in an emotion expression detection task while viewing upright and inverted faces during an fMRI scan. These authors did report a developmental increase in the magnitude of the behavioral face inversion effect. They further found that in the right lateral fusiform gyrus, there were significant positive correlations between age and the magnitude of the neural face inversion effect (e.g., activation upright > inverted faces) and between the magnitudes of the behavioral and neural face inversion effects. However, the relation between the behavioral and neural face inversion effects was present across the age groups. In other words, the correspondence between face-related activation and face-processing behavior did not change with age.

These findings are a promising first step toward understanding the relation between developmental changes in face-related cortex and face-processing skills, but they also reflect the difficulty in evaluating such brain-behavior correspondences. Part of the difficulty may be related to the focus on the fusiform gyrus, the use of face inversion as a measure of face-processing behavior, and the need to understand potential developmental changes in the computational properties of cortical regions comprising the face-processing network. We also note that, to date, there is no longitudinal study

more amygdala activation to fearful faces; Thomas et al. 2001), and (3) a pattern of increasing right lateralization in amygdala activation to fearful faces in females but not males during adolescence (Killgore, Oki, and Yurgelun-Todd 2001).

These findings are especially interesting in light of the evidence in adults that the amygdala is part of a subcortical system that receives rapid (<100 ms) low-spatial-frequency information about faces (and potentially other visual objects) that is sufficient to develop a coarse or "quick and dirty" representation of a face and that can modulate face processing in the fusiform gyrus through direct feedback connections (for review, see Vuilleumier and Fourtots 2007). By some accounts, this subcortical component of face processing is primary in development and ultimately bootstraps the development of cortical face processing (Johnson 2005). In future studies, it will be critical to understand whether and how developmental changes in amygdala function are related to developmental changes in other parts of the face-processing network (e.g., the more posterior fusiform, OFA, and STS) and to developmental changes in face-processing behavior. Ultimately, the ability to understand how developmental changes in face identification, recognition, and expression recognition are related to changes in functional organization in the developing brain may require a broader systems-level approach that evaluates both the "core" and the "extended" regions in the face-processing network.

Relating developmental changes in face-processing behavior and functional brain organization may also require the use of more fine-grained tests of face-processing behavior that are sensitive enough to observe differences through adolescence, when face-related activation continues to change. Most of the existing studies attempting to relate behavior and brain activation have relied on the face inversion effect (AyIward et al. 2005; Passarotti et al. 2007). Although several groups have reported that the behavioral face inversion effect increases from ages 6 to 12 as children's representations of upright faces improve (Carey and Diamond 1977; Schwarzer 2000), many studies have also found adult-like sensitivity to inversion effects in children of the same age (e.g., Gilchrist and McKone 2003; Lewis 2003; Tanaka et al. 1998). Furthermore, there is great debate about what mechanisms of face processing are being measured and, therefore, evaluated for developmental change in face inversion (see Maurer et al. 2002; Ashworth et al. 2008).

Another, potentially more fruitful approach for studying the relation between changes in face-processing behavior and face-related brain activation is to employ behavioral tasks that tax the visuo-perceptual and emotional components of face processing simultaneously, which may be more sensitive to developmental changes across a broader age range and may activate both the core and extended regions in the face-processing network more successfully. Previous work has shown that recognition memory for emotional expressions improves from late childhood through adolescence (Herba and Phillips 2006; Thomas et al. 2007), particularly for fear and disgust (Herba and Phillips 2004; Herba et al. 2006). Employing behavioral tasks that require participants to discriminate and/or recognize perceptually homogenous faces (e.g., similar-looking females) across changes in facial expressions may be more sensitive for measuring developmental changes in face-processing behavior that continue through adolescence and that could be linked with specific changes in brain function.

that directly assesses functional changes in brain organization and its relationship to behavior.

First, in order to truly understand how changes in brain function are related to children's emerging abilities to represent and recognize faces, developmental changes in face-related activation *throughout the face network*, which includes a widely distributed set of cortical and subcortical regions that extends beyond the ventral temporal lobe, will need to be evaluated in the context of children's performance on tests of face processing. Only two of the previously described fMRI studies investigated developmental changes in other face-selective regions within the ventral visual processing stream (e.g., OFA or STS). Scherf and colleagues (2007) found developmental increases in the size and selectivity of both of these regions bilaterally through adolescence; however, Golarai and colleagues (2007) did not observe similar developmental changes in the right STS in their study, and they did not evaluate changes in the OFA.

In addition to understanding how the maturation of individual regions within the face-processing network is related to changes in behavior, it will be important to evaluate how *dynamic interactions* among these distributed regions changes developmentally and how these interactions relate to improvements in face-processing behavior. Recent evidence suggests that in adults there is a hierarchical feedforward flow of information from the OFA to the FFA and separately to the STS supporting face perception (Fairhall and Ishai 2007). To date, there are no investigations of developmental changes in functional and/or structural connectivity between these "core" face-processing regions (Ishai 2007). One possible prediction is that the flow of information, or the functional coupling of activation, between the OFA and FFA, is weak in children, and this might significantly reduce the quality of face representations in this distributed network. Similar predictions might also be made with respect to the structural circuitry: the structural connections between cortical face-processing regions may be less organized in children, degrading the quality of the face representations. We have obtained preliminary evidence to this effect using diffusion tensor imaging studies with individuals of the same ages as those in the fMRI study shown in Figure 18.1 (Doyle et al. 2008). Understanding functional and structural specialization for faces in ventral visual cortex, and brain development more broadly, will require that all three of these potential mechanisms of change be investigated.

In addition to the "core" ventral temporal face-related regions, limbic regions including the amygdala, insula, and medial prefrontal cortex and regions in the anterior paracingulate cortex make up the "extended" face-processing network and process more changeable aspects of faces (Ishai 2007), such as facial expressions (for review, see Phan et al. 2002; Phillips et al. 2003) and associating "person knowledge" with faces, including personal traits, attitudes, mental states, and intentions (see Gobbi and Haxby 2007 for review). Although, to our knowledge there are no existing developmental studies investigating changes in the medial prefrontal or paracingulate cortices related to face processing, there are reports of developmental changes in amygdala function related to face processing. Researchers investigating developmental changes in the neural basis of affect regulation often use fearful faces as stimuli and have found (1) increasing amygdala responses during facial recognition tasks through adolescence (Baird et al. 1999), (2) a transition from late childhood to adulthood in amygdala function (i.e., children show more amygdala activation to neutral faces and adults show

To date, the existing studies have implicated several potential mechanisms of developmental change in face-selective activation that could be related to changes in face-processing behavior. However, an additional possibility is that the specific nature of the computations being performed within individual face-related regions may change through the course of development, and these may be highly correlated with changes in face-recognition performance. For example, there is a growing consensus that face recognition can be divided up into different subprocesses such as those required to detect the presence of a face and those required to categorize or identify the face (Bowers and Jones 2008; Mack et al. 2008). Similarly, the adult face-processing network can be parcellated into regions that detect a face (i.e., posterior FFA, OFA) versus regions that identify an individual face (i.e., anterior FFA and posterior STS) versus regions that link semantic and biographic information with the perception of a face (i.e., inferior temporal gyrus). There are no existing studies evaluating whether these kinds of computations change developmentally in the face-processing network. Given that children are less accurate at unfamiliar face recognition, one might predict that the identity computations in the anterior FFA may be much weaker than in adults and may be highly correlated with accuracy in face recognition tasks (Scherf et al., under review).

As is evident, much remains to be done to elucidate, in detail, the developmental manifestations of face selectivity both at a neural and at a psychological level, as well as the interrelations between these two levels. In parallel, there is much to be done on the developmental emergence of category specificity for other non-face objects, too, in order to uncover fully the topographic organization of ventral visual cortex and its functionality. This work will be critical for evaluating the predictions of the interactive specialization model of functional brain development in the ventral visual pathway and will provide the basis for beginning to understand the computations supporting efficient object perception.

#### 18.4 Atypical Development of Category-Specific Topography in Ventral Visual Cortex

As reviewed in the preceding section, it takes many years to attain the adult profile of category-selective face activation in ventral visual cortex, and this protracted development is likely correlated with the difficulties children experience in face processing. Another way of understanding how experience with visual objects influences functional brain organization in the ventral visual pathway is to study individuals who experience lifelong difficulties in face processing. Identifying the atypicalities in the face-processing behavior and structural and functional organization in such individuals can cast light on how the system might normally emerge.

One group of individuals who meet this criterion includes those with autism spectrum disorder (ASD). Autism spectrum disorder is a neurodevelopmental disorder in which individuals exhibit marked deficits in social interaction, verbal, and nonverbal communication and have restricted or stereotyped patterns of behaviors (Baron-Cohen and Belmonte 2005; Frith and Happe 2005; Behrmann, Thomas, and Humphreys 2006b). Impairments in face processing are a relatively recent discovery in ASD, but

have quickly become a widely accepted aspect of the behavioral profile (Behrmann et al. 2006b) and undoubtedly are related to the social difficulties experienced by these individuals, even in adulthood. The impairment in these individuals goes beyond face recognition, and involves difficulty in remembering faces (Boucher and Lewis 1992), processing facial expressions (Ashwin et al. 2007; Humphreys et al. 2007), and knowing which components of faces convey especially important communicative information (Joseph and Tanaka 2003). Despite the growing empirical evidence, the origin of the face-processing deficits in autism remains unknown.

One view suggests that individuals with autism have decreased motivation to attend to social stimuli, which limits the ability to gain expertise in face processing (Dawson et al. 2002; Grelotti, Gauthier, and Schultz 2002). In support of this hypothesis, several groups have reported that individuals with autism spend less time looking at the eye region of faces (Klin et al. 2002; Adolphs et al. 2008; Spezio et al. 2007), which is critical for identity recognition in typically developing individuals. Furthermore, this atypical fixation pattern may be related to aberrant activation in the fusiform gyrus (Dalton et al. 2005). This social motivation impairment is not predicted to affect the recognition of nonsocial objects.

An alternative hypothesis is that the face-processing deficits result from atypical perceptual processing (e.g., enhanced processing of local features; Happé and Frith 2006; Mottron et al. 2006). On the basis of a fundamental perceptual difficulty (and/or bias to process features preferentially), individuals with ASD may be limited in the ability to develop expertise with any class of visual objects (Behrmann et al. 2006a; Behrmann et al. 2006b) that are perceptually homogeneous, like faces. This is because fine-grained discrimination and representation of the configural properties of these stimuli (Diamond and Carey 1986) is required to differentiate these similar objects. In this framework, the limited time spent fixating the eye region has been interpreted in a different way. The eye region of a face is especially laden with configural information. Additional evidence for atypical visuo-perceptual processing in ASD is the finding that children with autism are not sensitive to configural properties in the eye region of faces (Joseph and Tanaka 2003), perhaps because of increased reliance on local features (Klin et al. 2002; Lahie et al. 2006). This failure to encode the face in a typical fashion may hamper their ability to master visuo-perceptual expertise that is critical for face recognition.

A recent study evaluated whether individuals with autism have difficulty developing perceptual expertise and whether any such decrement is specific to faces or extends to other objects, too (Scherf et al. 2008). Children (ages 8–13) and adults with high-functioning autism (FSIQ > 80) and age- and IQ-matched control participants performed perceptual discrimination tasks, including a face inversion task and a classification-level task, which requires especially fine-grained discriminations between individual exemplars, on three classes of stimuli: faces, perceptually homogeneous novel objects, Greebles, and perceptually heterogeneous common objects. They found that by late childhood, individuals with autism do reveal some visuo-perceptual expertise for faces (as indicated by similar magnitude face inversion effect and similar success at exemplar-level discriminations as controls) but are, in general, less skilled at discriminating and recognizing faces than are typically developing individuals. Interestingly, children and adults with autism also evince poorer recognition for novel

perceptually homogeneous objects (see also Ashworth et al. 2008), especially at the exemplar level, suggesting that they have a generalized deficit in visuperceptual processing that may interfere with their ability to develop expert configural processing, which adversely impacts their recognition of any within-class perceptually homogeneous objects, and especially faces. These results suggest that even if a social aversion to faces contributes to limitations in the development of face expertise in autism, it may not be the primary factor, because processing of other nonsocial objects, specifically perceptually homogeneous objects, is also affected. These findings of limited development of visuperceptual expertise for faces in autism lead to clear predictions about disruptions in the development of functional specialization in the ventral visual pathway, particularly for face-related activation.

These predictions have begun to be tested in some recent studies. In one of these, children and adolescents with autism (ages 6–12) performed a 1-back task on faces of an adult stranger, their mother, a familiar child, an unknown child, and objects while in the scanner. A significant reduction in the number of active voxels was noted in the right and left fusiform for the autism group, specifically when they were observing an unfamiliar adult face, relative to the controls, although a similar reduction was noted during the object condition in the right fusiform, too. A whole brain voxelwise analysis revealed a similar finding. These findings led the authors to conclude that there is a selective hypoactivation of the fusiform region in response to unfamiliar adults. Of particular interest is whether there are any differences in the autism (and control) group as a function of age. Given that there is growing consensus that younger typical children are unlikely to evince normal fusiform activation, one wonders whether the major group difference emerges in the children in the higher age range in the autism group.

Several recent studies have begun to elucidate the category selectivity in ventral visual cortex in adults with autism, although there still remain inconsistencies between the findings. Using fMRI, many studies (Critchley et al. 2000; Schultz et al. 2000; Pierce et al. 2001; Hail, Szechtman, and Nahmais 2003; Hubl et al. 2003; Ogai et al. 2003; Piggot et al. 2004; Wang et al. 2004; Dalton et al. 2005; Grelotti et al. 2005; Deeley et al. 2007; Humphreys et al. 2008) have found reduced face selectivity in the fusiform face area (FFA), but five studies have failed to replicate this finding (Hadjikhani et al. 2004, 2007; Pierce et al. 2004; Bird et al. 2006; Kleinhans et al. 2008). It has also been proposed that FFA activation is normalized when people with autism look at the face stimuli (Hadjikhani et al. 2004), specifically the eye region (Dalton et al. 2005, 2007), although this does not always seem to be entirely the case (Hasson et al., submitted). The findings from the fMRI studies are also supported by a recent study using magnetoencephalography (MEG). In this study, the neural responses to images of faces, observed in right extrastriate cortices at approximately 145 ms after stimulus onset, were significantly weaker, less lateralized, and less affected by stimulus repetition than in control subjects (Bailey et al. 2005). Additionally, early latency (30–60 ms) responses to face images over right anterior temporal regions also differed significantly between the two subject groups in an image identification task. Interestingly, no such difference was observed for images of mugs or meaningless geometrical patterns, again pointing to a specific or more severe difficulty with face stimuli.

Far fewer studies have paid attention to other face-selective regions such as the superior temporal sulcus (STS) and the occipital face area (OFA). The existing results indicate that there is also weaker face-related activation in these regions (Pierce et al. 2001; Hadjikhani et al. 2007) and in the extended face-processing regions, including the amygdala, inferior frontal cortex, and face-related somatosensory and premotor cortex (Hadjikhani et al. 2007). There are also reports of increased face-related activation in individuals with autism bilaterally in the inferior temporal gyrus (Schultz et al. 2000) and atypical activation in the frontal and primary visual cortices (Pierce et al. 2001).

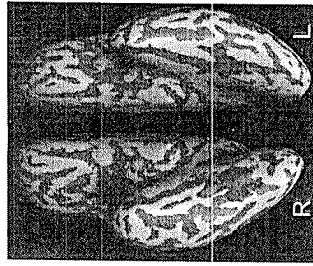
The inconsistency among these findings also applies to cortical responses to other visual object classes, although rather few studies have been conducted in this domain. One study found no consistent differences in cortical object activation in individuals with autism (Schultz et al. 2000), and another found no differences in activation for houses (Bird et al. 2006). In a MEG study, however, the sources of object-related signals were more variable in the autism group than in the typical group (Bailey et al. 2005). Finally, the LO object-related region apparently responds to both face and pattern processing in individuals with autism, and the superior parietal lobule, usually associated with visuospatial processing (Gitelman et al. 2000; Gitelman et al. 2002), is also more active.

In an attempt to map out the large-scale organization of ventral visual cortex in adults with autism, we used the movie localizer paradigm (Fig. 18.1) to contrast face-, place-, and object-selective activation in ASD adults, and age- and IQ-matched controls (Humphreys et al. 2008). Figure 18.2 shows the group maps averaged over ten typical individuals (Fig. 18.2(a)) and ten individuals with autism (Fig. 18.2(b)). The autism group consisted of individuals who were in the high functioning range (FSIQ < 75), with a group mean in the average range (VIQ=103, PIQ=106). The diagnosis of autism was established using the Autism Diagnostic Interview Revised (ADI-R) (Lord et al. 1994), the Autism Diagnostic Observation Schedule (ADOS) (Lord et al. 2000), and expert clinical diagnosis. Potential participants were excluded if they had an associated neuropsychiatric disorder or a history of birth asphyxia, head injury, or seizure disorder. Exclusions were based on neurological history and examination, chromosomal analysis, and, if indicated, metabolic testing.

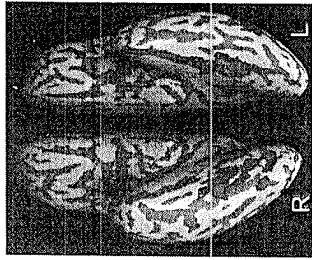
The findings from the typical group largely replicate the adults maps in Figure 18.1 (and other similar studies in the literature), except that building/scene-related activation (green) in PPA appears somewhat reduced, especially in the left hemisphere. Others have observed similar PPA variability in the left hemisphere, too (Avidan et al. 2005). The most marked feature in the maps for the autism participants is the clear reduction in face-related activity. In fact, the only face-related activity at this threshold for the autism group is in the right OFA. In contrast, object-related activity in object-related LO appears more extensive for the autism group than the comparison group, a pattern that has been noted previously as well.

In common with many previous studies, in this study, there is a reduction in FFA activity in response to faces in adults with autism. In contrast to the group differences in face-related regions, there were no consistent BOLD differences between the groups in place-related (building- and scene-related) activation, across any of the dependent measures or analyses. This replicates the absence of a group difference for activation to house stimuli (Bird et al. 2006). The selective activity in place-related cortex was fairly

### Typical Adults



b.



Faces  
 Buildings & Navigation  
 Objects

**Figure 18.2.** Group map reflecting average activation for faces, buildings, scenes, and objects for (a) typical adults and (b) adults with autism. Maps are inflated and shown from the ventral view (upper panel) and the lateral view of the right hemisphere (lower panel). For both groups, the maps were computed using a random effects general linear model and are thresholded at  $P = .006$ . (See color plate 18.2.)

low for both groups relative to other regions sampled, so it is possible that this result represents a floor effect. If any atypicalities exist for place-related activation in autism, they are much more subtle than those affecting face-related activation. It does not, however, seem that differences in functional organization of the ventral visual pathway in autism are limited to face-related regions, as there was evidence of differences, albeit subtle, affecting the representation of common objects as well.

How should we interpret the broad pattern of results, of markedly reduced activation and selectivity in face-related cortex in the group of adults with autism, but with fairly typical levels of activation in object and place areas? Notably, as we discussed, studies with typically developing children have shown that activation in place and object areas is adult-like even in early childhood, whereas the development of the face-related regions (FFA, OFA, STS) is much more protracted, becoming more selective and responsive to faces with age, but not reaching adult-like activation until early adulthood (Colzani et al. 2007; Scherf et al. 2007). One rather obvious possibility, then, is that visual category-selective organization in autism reflects an early plateau in development, rather than deviance, with the category selectivity resembling that of younger, typically developing children. Studies comparing individuals with autism

and typically developing children of different ages would be useful to evaluate this possibility.

Alternatively, a number of authors propose abnormalities of neural connectivity in autism (Belmonte et al. 2004; Frith 2003; Courchesne and Pierce 2005a,b; Rippon et al. 2007), specifically underconnectivity between different functional regions (long-range) and over-connectivity at a more local level (short-range) (Markram, Rinaldi, and Markram 2007). These findings are evident even intrinsically when the brain is at rest (Kennedy and Courchesne 2008). Along with previous authors (e.g., Johnson et al. 2002), we speculate that the longer a particular function takes to mature, the greater the cascading effects of differences in the development of neurons and synapses. This may explain how differences in face-related cortex are much more pronounced in autism than are those affecting the earlier maturing place- or object-related cortices. The refinement in selectivity of later-developing cortex may be impeded as a result of overconnectivity at a local level, giving rise to a face-processing system prone to crosstalk and noise, resulting in reduced functional specificity (see Rippon et al. 2007). This framework would also predict that greater typical/autism group differences would be evident in other, later-developing brain functions. For example, we would expect to find greater differences on tasks that engage secondary and tertiary visual cortex compared to those relying on primary visual cortices (Hasson et al. submitted). These predictions are consistent with findings of greater divergence between the groups on tasks tapping frontal functions (e.g., Luna et al. 2002; Takarae et al. 2007).

## 18.5 Conclusion

Object perception, and face perception more specifically, is a highly complicated process at both the visuo-perceptual/cognitive and neural levels. Recent neuroimaging work indicates that children exhibit adult-like patterns of activation for the perception of places and objects, but that face-related activation continues to develop into adolescence and early adulthood. These findings converge with behavioral reports of early maturation of house and object recognition skills compared to later-developing face recognition skills.

An important question to consider is why different object categories develop at different rates, with specialization for faces developing particularly late. Given their social significance, one might have expected faces to be amongst the very first visual classes mastered by young children, but it turns out that faces are an especially difficult stimulus for the visual system. First, compared to other classes of objects, faces are remarkably perceptually homogeneous and are typically distinguished at the individual level (e.g., Jane's versus Sally's face). This requires sensitivity to differences in facial features and in the subtle metric differences in spacing or configuration among the features, which are especially difficult to detect. Objects, on the other hand, are typically identified at the basic level (e.g., pencil versus paper), and it may well be the case that there are sufficient featural differences to support identification without having to engage the more difficult configural processing to converge on the identity of the object. In fact, despite all the experience with faces, typically developing adults and young adolescents (ages 10–13) are both less accurate with faces than common

objects when performing a simple forced choice recognition task (Scherf et al. 2008). Furthermore, to a far greater extent than is true for any other visual class, faces are dynamic stimuli from which we typically extract many different kinds of information simultaneously (e.g., identity, expression, eye gaze). It is the case, though, that the dynamic information in faces is probably highly salient to young infants and may initiate the long developmental process of acquiring the neural and behavioral foundations for sophisticated face processing. However, learning to perform many computations (e.g., extracting invariant qualities of a face for individual recognition versus abstracting categories of emotional expressions across individual faces) on the same dynamically changing input may contribute to the late trajectory for sophisticated face processing skills.<sup>1</sup> It has been argued previously that extracting these different kinds of computations on a single source of input may give rise to interference effects (Cohen Kadosh and Johnson 2007) and, we would like to argue, may make the system more vulnerable to disruption (as is seen in adults with autism).

On the other hand, visuo-perceptual and neural specialization for objects and place cortex may consolidate earlier in development as a result of the perceptual heterogeneity, and therefore ease of identification/recognition, and relatively more limited kinds of invariances that need to be extracted from such stimuli. The consequence of this earlier specialization may be that these mechanisms/specialized regions of cortex are less likely to be disrupted in developmental disorders. One caveat to this notion is that we still know very little about the computational properties of all of these regions and how they change developmentally.

Another important point that emerges from this work is that the transition from late childhood to early adolescence is especially important for the development of visuo-perceptual and neural specialization for faces. This transition appears to represent a sensitive developmental window in which a convergence of sufficient visual experience and experience-dependent influences on the plasticity of the developing brain lead to increasing visuo-perceptual and neural specialization for faces. The outcome of this developmental transition is computationally efficient and spatially organized regions of cortex that support fast and efficient face and object recognition processes. This may also represent a particularly vulnerable time for developmental disruptions to the functional organization of the ventral visual pathway, particularly for face-related cortex. Future studies investigating changing relations in brain-behavior correspondences in both typically developing children and those with developmental disorders that affect object recognition skills, including autism, congenital prosopagnosia, and developmental visual agnosia, will be critical for understanding more about early adolescence as a sensitive period for functional brain development.

Finally, there appear to be several mechanisms by which the neural specialization emerges within this sensitive period. One possibility is that there is a contingent progression among these mechanisms that ultimately leads to adult-like selectivity and computational properties within a particular region. For example, in the fusiform gyrus, it may be the case that initially some neurons must learn to respond preferentially to faces, particularly in the anterior part of the gyrus. Experience-dependent strengthening of the local connections among these neurons may then lead to a sufficiently large

<sup>1</sup> There is an alternative possibility that the dynamic nature of the faces may make it easier to extract identity information and facilitate individuation rather than contributing additional difficulty/variance to the problem.

number of such neurons that are in close enough proximity to collaboratively represent the complexity of faces, which ultimately allows the neurons to settle on the most efficient computations to represent faces in a fine enough grain to accomplish the task or tasks at hand (e.g., detection, recognition, categorization). Disruption to the more primary mechanisms earlier in the course of development may have catastrophic downstream effects, preventing the development of adult-like specialization. For example, one possible explanation for the hypoactivation in the FFA in adults with autism is that there are face-selective groups of neurons, but that intrinsic disruptions in the local connections among these neurons prevent a sufficiently large number of such neurons from working together to collaboratively represent the complexity of faces.

Taking all these findings into account, we suggest that the face- and object-perception systems are ideal for testing broad theories of functional brain development, including understanding the relation between experience-dependent learning and experience-dependent brain plasticity, and elucidating the consequences when development is disrupted as in cases like autism. Engaging computational models of vision will be enormously helpful in working through the different possible scenarios and in thinking about issues such as category specificity and its emergence and the mechanistic processes that drive the organization of ventral visual cortex. Understanding whether fine-tuning of category-selective organization emerges from tuning of initially non-selective neurons and/or through some competitive interaction between neurons across the entire ventral visual cortex will assist in elucidating the typical developmental trajectory as well as the mechanisms that are adversely impacted during altered neurodevelopment.

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