

Mapping Functional Brain Development: Building a Social Brain Through Interactive Specialization

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The authors review a viewpoint on human functional brain development, interactive specialization (IS), and its application to the emerging network of cortical regions referred to as the *social brain*. They advance the IS view in 2 new ways. First, they extend IS into a domain to which it has not previously been applied—the emergence of social cognition and mentalizing computations in the brain. Second, they extend the implications of the IS view from the emergence of specialized functions within a cortical region to a focus on how different cortical regions with complementary functions become orchestrated into networks during human postnatal development.

Keywords: cognitive brain development, face processing, interactive specialization, social cognition

One of the most prominent, and to an extent unique, characteristics of the human brain is the ability to process stimuli in a social context (Adolphs, 1999; Brothers & Ring, 1992). That is, the brain not only assesses the outward appearance and behavior of other humans but also the setting of stimuli and events in their social context, thereby taking into account differing mental states, intentions, and desires. However, how these adult processing specializations emerge as a result of development remains largely unknown. Johnson (2001, 2005) reviewed three perspectives on how the neuroanatomical development of the brain could be related to the changes in motor, perceptual, and cognitive abilities observed during infancy and childhood: (a) a maturational perspective, (b) a skill-learning viewpoint, and (c) interactive specialization (IS). In the present article, we focus on advancing the IS view in two ways. First, we extend this approach into a domain to which it has not previously been applied—the emergence of social cognition and mentalizing computations in the brain. Second, we extend our exploration of the implications of the IS view from the emergence of specialization within a cortical region to a focus on how networks of collaborating cortical regions may emerge during human postnatal development.

The IS view assumes that postnatal functional brain development, at least within cerebral cortex, involves a process of organizing patterns of interregional interactions (Johnson, 2001, 2005). According to this view, the response properties of a specific region

are partly determined by its patterns of connectivity to other regions and, in turn, by their patterns of activity. During postnatal development, changes in the response properties of cortical regions occur as they interact and compete with each other to acquire their role in new computational abilities. From this perspective, some cortical regions may begin with poorly defined functions and are consequently partially activated in a wide range of different contexts and tasks. During development, activity-dependent interactions between regions tune up the functions of regions such that their activity becomes restricted to a narrower set of circumstances (e.g., a region originally activated by a wide variety of visual objects, may come to confine its response to upright human faces; see Figure 1). The onset of new behavioral competencies during infancy and childhood will therefore be associated with changes in activity (adjustments in tuning functions) over several regions and not just by the onset of activity in one or more additional region(s).

IS assumes that cognitive functions are the emergent product of interactions between different brain regions and between the whole brain and its external environment. According to this view, brain regions do not develop in isolation but are heavily constrained by their connections and interactions with other regions, a phenomenon recently termed *embrainment* (Mareschal et al., 2007). In this respect, IS follows recent trends in adult functional neuroimaging in which the emphasis has shifted away from the attempt to localize particular functions to certain cortical regions and toward understanding the response properties of regions as determined by their patterns of functional connectivity to other regions (Fairhall & Ishai, 2007; Friston, 1994; Friston & Price, 2001; Summerfield et al., 2006). Applying these ideas in a developmental context, the IS approach emphasizes the importance of interregional connectivity, as opposed to the maturation of intraregional connections.

As well as the mapping between brain structure and function at one age, a critical question for developmental imaging is how this mapping changes during development. The IS approach suggests that when a new computation or skill is acquired, there is a reorganization of interactions between different brain structures and regions. This reorganization process could change previously existing mappings between cortical regions and their functions. Thus, the same behavior

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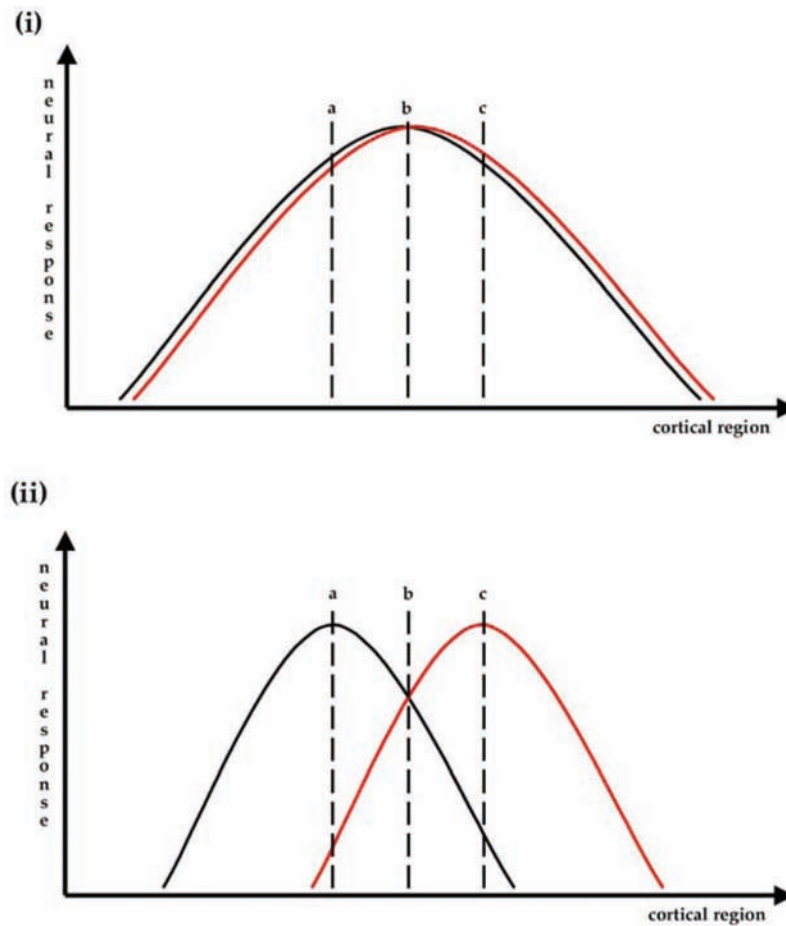


Figure 1. An illustrative schematic that represents the developmental changes associated with the processes of specialization and localization. In the initial state (i), Cortical Regions a, b, and c respond equally strongly to faces (red line) and objects (black line). After development (ii), Region a becomes specialized for objects (compared to faces) and Region c becomes specialized for faces (compared to objects). With regard to the degree of localization, in the initial state all three regions are activated by both stimuli. After development, faces no longer activate Region a, and therefore the cortical activation generated by this stimulus is more focal than in the initial state. The same applies to objects. Region b represents an intermediate zone of tissue that may respond less selectively.

could potentially be supported by different neural substrates at different ages during development (see Grossmann, Striano, & Friederici, 2007). Stating that structure–function relations are dynamic during development is all very well, but it lacks the specificity required to make testable predictions. The IS perspective motivates the view that neuroimaging studies of development should be analyzed and interpreted with regard to two issues: (a) the degree of localization—How focal or diffuse is the activity that results from a stimulus presentation or task context? and (b) the degree of specialization—How finely or coarsely tuned is the activation that results from a given stimulus or task context? According to the IS view, the degree of localization and the degree of specialization for a given stimulus or task context are two sides of the same coin; as cortical tissue becomes more specialized (finely tuned), it will become activated by a narrow range of stimuli or tasks, and a natural consequence of this will be less extensive areas of cortex activated in response to any given stimulus or task as regions become more specialized.

In the next sections, we focus on two of the most basic aspects of social cognition—the detection and perception of faces, and the

detection of biological motion. We then examine evidence relating to functional imaging of a more complex aspect of social brain function: mentalizing. Mentalizing is commonly associated with the medial prefrontal cortex and thus provides an intriguing comparison case to the studies of more posterior regions (Amodio & Frith, 2006). Having traced the paths of emerging function within different regions of the social brain, we then speculate on the factors that may contribute to these regions becoming orchestrated into a network.

Perceiving Faces

Faces play an important role in social interaction. People rely on specific configurations of facial features for recognizing a friend or family member, or they study multiple cues associated with a person's facial expression to make inferences about her internal state. Additionally, perceived eye gaze can direct one's own attention to an object that is the subject of someone else's attention, thus creating a joint attention context (Tomasello, 1995). Consid-

ering the importance of faces to social interaction, it is not surprising newborn infants will preferentially orient toward facelike stimuli (Farroni et al., 2005; Johnson, Dziurawiec, Ellis, & Morton, 1991). However, it is evident that massive changes in face-processing abilities occur the first decade or more of life (see Johnson, 2005, for a review). Thanks to a parallel line of work on adult neuroimaging, researchers now have an understanding of how and where faces are represented in the mature adult brain (Allison et al., 1994; Haxby, Hoffman, & Gobbini, 2000; Haxby et al., 1994). However, while researchers' understanding of the neural substrate is good, continuing debate focuses on the unresolved question whether face-sensitive cortical areas are unique for faces as a stimulus group (*domain specificity*; Kanwisher, McDermott, & Chun, 1997) or whether such specialization is due to extensive perceptual training (*expertise approach*; Gauthier & Nelson, 2001).

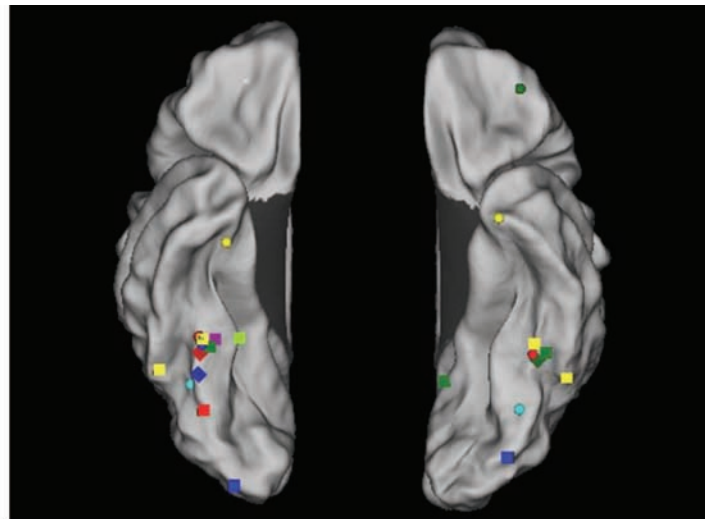
Developmental neuroimaging work can potentially contribute to this debate by providing evidence about the developmental trajectory of face-processing abilities in the human brain. The IS view predicts increases in both the degree of specialization and localization of face-evoked activity in cortex during development. This stands in contrast to a maturational perspective prediction that face

processing in the child's brain should be limited to a subset of the areas that can be activated by faces in adults.

Recently, several researchers have used functional magnetic resonance imaging (fMRI) to investigate face processing in children (Aylward et al., 2005; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Golarai et al., 2007; Passarotti et al., 2003; Scherf, Behrmann, Humphreys, & Luna, 2007; Thomas et al., 2001; see also Figure 2). Several of these studies have yielded support for the dynamic changes predicted by the IS hypothesis.

As far as face processing in general is concerned, all studies to date were able to show that certain regions of the cortex show reliable activation to faces from at least midchildhood. With regard to the localization issue, researchers in four studies found evidence for dynamic changes in the extent of cortical tissue activated between children and adults (Gathers et al., 2004; Golarai et al., 2007; Passarotti et al., 2003; Scherf et al., 2007), and two of those studies reported the activation of additional areas that are not typically found in the mature adult brain, such as the left and right inferior frontal gyrus (Gathers et al., 2004; Passarotti et al., 2003).

Several studies provided evidence relevant for the specialization question (Aylward et al., 2005; Gathers et al., 2004; Golarai et al., 2007; Scherf et al., 2007; Thomas et al., 2001). For example,



Cluster*	Age groups (Years)	Stimuli categories presented	References
■	8-10, 12-14	Faces, houses	Aylward et al., 2005
■	5-8, 9-11	Faces, objects	Gathers et al., 2004
■	Adults		
■	10-12	Emotional faces	Lobaugh et al., 2006
■	10-12, Adults	Faces	Passarotti et al., 2003
■	8-11, 13-17 Adults	Faces (upright or inverted)	Passarotti et al., 2007
■	5-8, 11-14	Faces, objects, buildings,	Scherf et al., 2007
■	Adults	navigation	
■	Adults	Faces, objects	Kanwisher et al., 1997

* Shape coding: adults=●, older children group=◆, younger children group=■

Figure 2. Ventral view of the occipito-temporal stream (the right hemisphere is presented on the left side and vice versa). Face-processing-related activation clusters are depicted in colored shapes (see the table below the ventral view).

Thomas and colleagues (2001) found less specificity in amygdala response to fearful and neutral faces in 11-year-old children. Another fMRI study (Gathers et al., 2004) with two groups of children (5–8 and 9–11 years) and adults showed that in spite of similar activation profiles in the fusiform gyrus for the different age groups, only the 9- to 11-year-olds showed the commonly reported face preferential, specialized responses in comparison to objects. Finally, Aylward and colleagues (2005) compared the functional anatomy for faces versus houses in two different age groups (children aged 8–10 years and 10–12 years) and found increased bilateral selective activation for faces in the older children in comparison to the younger children, a finding that correlated with the behavioral results. Hence, these studies support the notion that face processing becomes more specialized with increasing age.

Of the studies mentioned above, two are of particular relevance as they specifically address both the localization and the specialization issues. Scherf et al. (2007) used naturalistic movies of faces, objects, buildings, and navigation scenes in a passive viewing task with children (5–8 years), adolescents (11–14 years), and adults. They found that the children exhibited similar patterns of activation of the face-processing areas commonly reported in adults (such as the fusiform face area [FFA]). However, this activation was not selective for the category of face stimuli; the regions were equally strongly activated by objects and landscapes. Moreover, this lack of fine tuning of classical face-processing areas stood in contrast to distinct preferential activation patterns for other object categories (occipital object areas and the parahippocampal place area). In a similar study, Golarai et al. (2007) tested children (7–11 years), adolescents (12–16 years), and adults with static object categories (faces, objects, places, and scrambled abstract patterns). They found substantially larger right FFA and left parahippocampal volumes of selective activation in adults than in children. While this increase in functionally defined areas with development may initially appear to contradict predictions of the IS view, it is important to note that the contrasts employed defined the increase as an expansion of the area of category-specific activation of FFA. The developmental changes observed in these recent studies thus provide strong support for IS as a framework within which to interpret functional brain development (Cohen Kadosh & Johnson, 2007).

Another area of face-processing research that could potentially contribute to researchers' understanding of the developmental trajectory of face-specialized cortical areas is the work on developmental prosopagnosia. *Developmental prosopagnosia* refers to individuals who never develop typical adult face-processing abilities (Duchaine & Nakayama 2006) and in particular facial identity recognition skills. This condition can occur in the absence of any obvious sensory or intellectual deficit (Avidan, Hasson, Malach, & Behrmann, 2005; Behrmann & Avidan, 2005; Yovel & Duchaine, 2006). Moreover, while there are cases of developmental prosopagnosia that arise from brain trauma early in life, there is increasing evidence for cases in which typical adultlike face-processing skills fail to develop in the absence of any known acquired injury (Duchaine & Nakayama 2006). Some of these cases have family members also affected, and it is tempting to speculate on a genetic cause. However, since nothing is currently known about the early rearing and social interaction environment of these families, the specificity or directness of this genetic effect remains unknown.

Functional MRI studies have generally shown that developmental prosopagnosics activate face-sensitive regions of cortex (for a review, see Duchaine & Nakayama 2006). However, the degree of selectivity of this response remains in doubt, and a plausible interpretation of these results is that while adult developmental prosopagnosics show activation in face-sensitive regions, they may also show the lack of specificity in this response reported earlier for typically developing children. Moreover, a recent fMRI study (Avidan et al., 2005) showed that in four developmental prosopagnosics, face perception recruited additional brain areas (e.g., the inferior frontal gyrus) that were not commonly found in typical adults. Interestingly, however, inferior frontal gyrus activation has been observed in children in several of developmental neuroimaging studies reported above (Gathers et al. 2004; Passarotti et al. 2003; Passarotti, Smith, DeLano, & Huang, 2007; Scherf et al., 2007). Thus, both components of the IS account (localization and specialization) may accommodate data from developmental prosopagnosia. If this account of developmental prosopagnosia is correct, then with sufficient training on faces the selectivity of the response of cortical areas, and their interconnectivity, should change toward the typical pattern. This was tested in a recent training study with a developmental prosopagnosic patient that showed that as behavioral performance improved the selectivity of cortical processing of faces (as measured by the N170 component) increased (DeGutis, Bentin, Robertson, & D'Esposito, 2007). Further, these authors also observed increased functional connectivity between face-selective regions as measured by fMRI, particularly the right occipital face area and the right fusiform face area.

In sum, the functional anatomy and behavioral abilities exhibited by developmental prosopagnosics are reminiscent of the findings obtained in developmental neuroimaging studies (see above), in which children exhibit neural activity for faces in the brain areas typically found in adults, but this activation while less reliably localized is also still far from being face specialized. Further studies on both adults and children suffering from developmental prosopagnosia will be needed to shed light on this issue.

Perceiving Dynamic Social Stimuli

Another cortical area known to respond to social stimuli and also implicated in social perception is the superior temporal sulcus (STS; Allison, Puce, & McCarthy, 2000). In adults, the response properties of portions of the STS are highly specific. For example, while STS responds to moving biological stimuli, it does not respond as well to nonbiological similar moving stimuli or to static pictures of biological stimuli (Puce, Allison, Bentin, Gore, & McCarthy, 1998). Does this specialization emerge during postnatal development in accord with predictions from the IS view?

Neuroimaging studies with children (Mosconi, Macka, McCarthy, & Pelphrey, 2005) have shown that STS can be activated by dynamic social stimuli from midchildhood. A recent optical imaging study with 5-month-old infants also found patterns of activation consistent with STS activity when they viewed dynamic social stimuli (an actress moving her hands, eyes, and mouth) as compared to dynamic nonsocial stimuli (moving machinery; Lloyd-Fox et al., in press). However, the precise degree of specialization of this response during infancy remains to be determined.

Carter and Peltch (2006) used fMRI to test the specificity of response of the STS and other regions in 7- and 10-year-old children while they viewed a variety of biological motion and related stimuli (such as walking robots). They observed that, consistent with predictions from the IS view, the STS became increasingly specific in its response properties to biological motion with increasing age. Thus, while research on the STS is not as advanced as that on the FFA, the evidence currently available suggests that similar processes of emerging functional specialization may occur.

Mentalizing

Since areas of the prefrontal cortex are some of the last to show neuroanatomical change in postnatal life, the region has frequently been associated with the onset of behavioral abilities that emerge at, or beyond, the first year of life (Baird et al., 2002). In contrast, the IS view predicts activation of PFC early in life, even if its response properties are less well tuned than in adults (Grossmann, Johnson, Farroni, & Csibra, 2007; Grossmann et al., 2008). Among the specific brain areas involved in the adult social brain, functional activity in prefrontal cortex (PFC), particularly medial prefrontal cortex (MPFC), is of special importance for human social interaction (Amodio & Frith, 2006; Frith & Frith, 1999, 2006) and has been shown to top-down modulate activity in other social brain regions such as amygdala and midfusiform gyrus (Summerfield et al., 2006). Indeed, patients with damage to PFC can be severely impaired in their social and moral behavior despite normal basic cognitive abilities (Anderson, Bechara, Damasio, Tranel, & Damasio, 1999). From a developmental perspective, it is interesting to note that although patients with early onset PFC lesions (acquired during infancy, before 16 months of age) resemble adult-onset patients in some ways in their social impairments, behavioral deficits in early onset patients tend to be more severe. More specifically, early onset patients are characterized by their failure to retrieve complex social knowledge at a factual level, and they show signs of antisocial behavior (e.g., stealing, violence against properties and persons) that are not found in the adult-onset patients (Anderson et al., 1999; Bird, Castelli, Malik, Frith, & Husain, 2004). These characteristic differences observed in patients with PFC damage point to the important developmental role the PFC plays during the acquisition and formation of social processing.

The notion that PFC is a cortical structure that can be activated relatively early in postnatal development is in general agreement with a body of evidence indicating that some aspects of functioning of the social brain network emerge surprisingly early in development (for a review, see Grossmann & Johnson, 2007). More specifically, in recent electroencephalography and near-infrared spectroscopy studies with young infants, it has been shown that prefrontal cortical areas responded differentially to face stimuli depending on whether the face was looking at the infant or to the side (Grossmann et al., 2007; Grossmann et al., 2008). These findings are of particular interest because fMRI studies show that medial prefrontal brain structures implicated in mentalizing are activated by the detection of mutual gaze in adults (Kampe, Frith, & Frith, 2003).

Similarly to the case of face processing presented in the previous section, in recent years a number of researchers have begun to

study the neural basis of children's understanding of mental states by using fMRI (see Figure 3). There is now a group of fMRI studies with children of various ages using different tasks showing that MPFC is consistently activated when children engage in mentalizing (Blakemore, den Ouden, Choudhury, & Frith, 2007; Kobayashi, Glover, & Temple, 2007; Ohnishi et al., 2004; Pfeifer, Lieberman, & Dapretto, 2007; Wang, Lee, Sigman, & Dapretto, 2006).

In all of these studies, children recruited MPFC more extensively (see Figure 3) than adults when engaged in mentalizing tasks, even when researchers controlled task performance and possible baseline differences. For example, Wang et al. (2006) employed an irony task to investigate the comprehension of communicative intentions from cartoons in adults and children (9–14 years) and found that children recruited MPFC and left inferior frontal gyrus to a greater extent than adults, whereas adults recruited the fusiform gyrus, extrastriate areas, and the amygdala more strongly than children. Furthermore, in a correlation analysis the authors showed that, within the group of children, there was a positive correlation between age and fusiform gyrus activity and a negative correlation of age with extent of MPFC activity. Similarly, Blakemore et al. (2007) reported that adolescent participants (12–18 years) when thinking about intentions showed more extensive activity in MPFC than adults, whereas adults activated parts of the right STS more than adolescents. Finally, two other developmental mentalizing studies available revealed very similar patterns of findings. Pfeifer and colleagues (2007) examined brain activity during self-knowledge retrieval and found that children (10 years) engaged MPFC to a much greater extent than adults. In this study, adults activated the lateral temporal complex significantly more than children. Moreover, Kobayashi et al. (2007) presented adults and children (8–11 years) with classical theory-of-mind tasks and also reported that the children showed greater activity in MPFC than adults but that adults exhibited great activity in the right amygdala than children. Taken together, these studies (Blakemore et al., 2007; Pfeifer et al., 2007; Wang et al., 2006) consistently indicate that with age the extent of MPFC activation during mentalizing tasks becomes more focal, whereas activity in (task-dependent) posterior (temporal) cortical areas sometimes increases.

Overall, these developmental patterns concord with findings from nonsocial tasks indicating that (a) in accord with the IS view, a diffuse to focal transition in prefrontal cortex functional activity during development (Durstun et al., 2006; Amso & Casey, 2006) and (b) functional involvement of posterior (temporal) cortex may show more protracted development than that of frontal cortex (Brown et al., 2005). Furthermore, the pattern of more widespread frontal cortex activation at younger ages and an expansion of temporal cortex selective activation at older ages may be related to longitudinal findings on structural brain development indicating that peaks of gray matter increase are observed earlier in frontal cortex (prepuberty) than in temporal cortex (where they are observed after puberty; Giedd et al., 1999). It may therefore reflect a more general organization principle, applicable to all kinds of social and nonsocial aspects of functional brain development, resulting in differential functional specialization trajectories across the anterior and posterior brain areas.

With regard to the skill learning hypothesis, there is also an interesting parallel between these developmental fMRI findings on

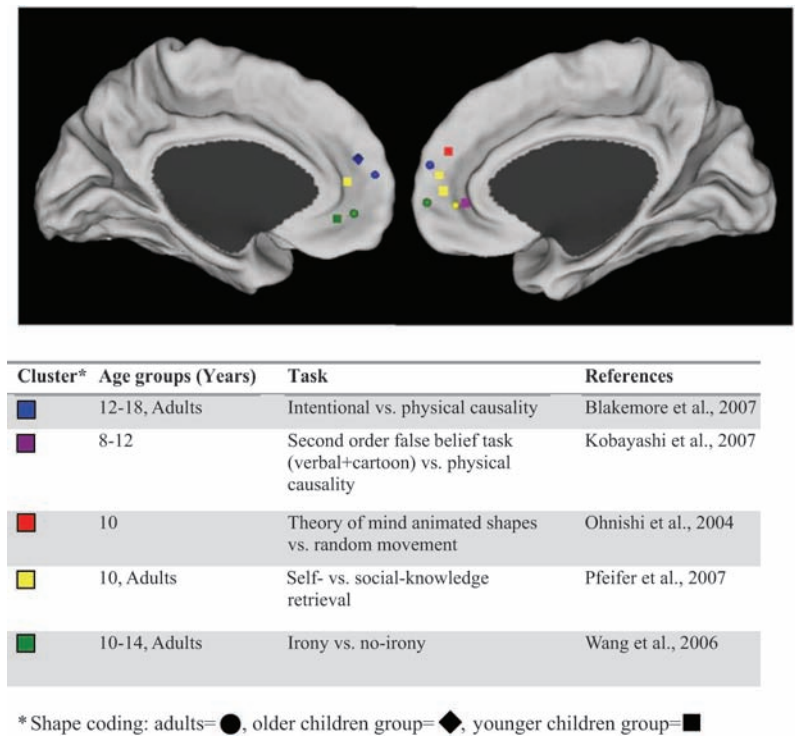


Figure 3. Medial view of left and right hemispheres of the brain (the left hemisphere is presented on the left side; frontal portions of both hemispheres are shown in the middle). Mentalizing-related activation clusters are depicted in colored shapes (see the table below the medial view).

mentalizing and studies on functional brain activation changes associated with practice and learning in adults (for a recent review, see Kelly & Garavan, 2005). For example, Sigman and colleagues (2005) found that in a visual shape discrimination task, extensive learning resulted in increased activity in posterior visual cortex and decreased activity in frontal and parietal cortex. These large-scale reorganizations of brain activity in the adult cortex as a result of learning have been interpreted as reduced executive control and increased automatization and may, at least in part, account for the patterns of activity observed in the developing social brain. However, skill learning alone cannot explain so-called “age of acquisition” effects, that is, the age at which learning occurs has an effect on how a skill is acquired and which cortical mechanisms are used. These effects have been widely observed in other domains of cognition (see Hernandez & Li, 2007), and as recent research suggests, they also seem to apply to mentalizing activity in MPFC. For example, Kobayashi, Glover, and Temple (2008), comparing early and late bilinguals (Japanese who also speak English) of similar proficiency in a mentalizing task, found that early bilinguals (children 8–12 years of age) showed an overlap in brain activity between the first and second language in MPFC during a mentalizing task, whereas late bilinguals (adults 18–40 years of age) activated more dorsal MPFC in the first language mentalizing condition and more ventral MPFC during the second language mentalizing condition.

While the more focal patterns of PFC activation seen in adults accords well with the increase in localization predicted by the IS view, a further question is whether the location of the peak of

activation in tasks is the same in children and adults. A preliminary analysis (S. J. Gilbert & Grossmann, 2007) revealed that the coordinates of activation peaks in children and adults taken from the following studies—Blakemore et al., 2007; Kobayashi et al., 2007; Pfeifer et al., 2007; Wang et al., 2006—did not differ significantly from each other. Moreover, the child activation peaks fell within a subsection of MPFC identified as preferentially activated by mentalizing in adults (this functionally specialized subsection was identified on the basis of a meta-analysis involving 108 neuroimaging studies: S. J. Gilbert et al., 2006; see also Figure 3). How the more widespread activation observed in children shrinks to the focal activation observed in adults remains to be studied in detail. One possibility is that parts of the MPFC that become specialized for other functions in adults are more broadly tuned in childhood and thus are also activated in mentalizing tasks. Thus, while adults may selectively activate subregions of MPFC, children may activate the whole area in response to different aspects of social cognition.

Emerging Networks

The evidence reviewed so far is generally consistent with the changes in localization and specialization predicted by the IS view. However, questions remain unanswered about how regions interact to produce differential specialization within a region and how networks involving different regions, each with their own different specializations, emerge. In other words, while researchers are beginning to understand functional brain development at the level

of individual cortical regions, they are still in the dark about how the larger scale of cortical function in terms of networks of regions develops (Johnson & Munakata, 2005). In this section, we advance some fragments of the answer to this intriguing issue for the emerging social brain network.

The first piece of the jigsaw comes from a recent study by Fair et al. (2007), who used functional connectivity analyses in fMRI to study resting state “control” networks in children and adults. They found that development entailed both segregation (i.e., decreased short range connectivity) and integration (i.e., increased long-range connectivity) of brain regions that contribute to a network. The decrease in short-range interregional functional connectivity is readily explicable in terms of the IS view. As neighboring regions of cortical tissue become increasingly specialized for different functions (e.g., objects vs. faces), they will less commonly be coactivated. This process may also involve synaptic pruning and has been simulated in neural network models of cortex in which nodes with similar response properties cluster together spatially distinct from nodes with other response properties (Oliver, Johnson, & Shrager, 1996). Thus, decreasing functional connectivity between neighboring areas of cortex is readily predicted by models implementing the IS view. More challenging from the current perspective is to account for the increase in long-range functional connections.

A maturational explanation of the increase in long-range functional connectivity would suggest that this increase is due to the establishment or to strengthening of the relevant fiber bundles. However, the increase in functional connectivity during development may occur after the relevant long-range fiber bundles are in place (see Fair et al., 2007, for discussion). While increased myelination is likely to be a contributory factor, (a) myelination itself can be a product of the activity–usage of a connection (Markham & Greenough, 2004) and (b) a general increase in myelin does not in itself account for the specificity of interregional activity into functional networks that support particular computations (but see Nagy, Westerberg, & Klingberg, 2004).

Most of the long-range functional connections studied by Fair et al. (2007) involve links to parts of the prefrontal cortex. As mentioned earlier, this part of the cortex is generally considered to have a special role during development in childhood and skill acquisition in adults (C. D. Gilbert & Sigman, 2007; Thatcher, 1992). Johnson (2005) reviewed a number of studies consistent with the idea that PFC may play a role in orchestrating the collective functional organization of other cortical regions during development. While there are several neural network models of PFC functioning in adults (e.g., O’Reilly, 2006), few if any of these have addressed development. However, another class of model intended to simulate aspects of development may be relevant both to PFC and to the issue of how networks of specialized regions come to coordinate their activity to support cognition. Knowledge-based cascade correlation (Shultz, Rivest, Egri, Thivierge, & Dandurand, 2007) involves an algorithm and architecture that recruits previously learned functional networks when required during learning. Computationally, this dynamic neural network architecture has a number of advantages over other learning systems. Put simply, it can learn many tasks faster, or learn tasks that other networks cannot, because it can recruit the knowledge and computational ability of other self-contained networks as and when required. In a sense, it selects from a library of available computational systems to or-

chestrate the best combination for the learning problem at hand. While this class of model is not intended to be a detailed model of brain circuits (Shultz & Rivest, 2001; Shultz et al., 2007), it has been used to characterize frontal systems (Thivierge, Titone, & Shultz, 2005) and may capture important elements of the emerging interactions between PFC and other cortical regions at an abstract level. In addition, it offers initially attractive accounts of (a) why PFC is required for the acquisition of new skills, (b) why PFC is active from early in development but also shows prolonged developmental change, and (c) why early damage to PFC can have widespread effects over many domains.

Under this scenario of the emerging social brain network, MPFC may be activated from early on (Grossman et al., 2008) but at that point may play a little role in selectively activating other regions due to their own lack of functional specialization and a lack of myelination of the relevant long-range connections. Once relatively posterior regions such as STS and the FFA become more finely tuned to their different functions, the role of MPFC, or other frontal areas, becomes important in orchestrating the combinations of regions activated for a given social cognition task. These prefrontal areas will be required more when learning a task, or acquiring a new skill, then once it is acquired (with the appropriate combination of other posterior regions already selected). This may explain the observation that there is a general migration of activity during childhood from greater activity in MPFC than in STS and FFA to the reverse pattern in later development. Once PFC has learned the appropriate pattern of posterior regional activation to succeed in a task, cortical activity will tend to migrate to these posterior regions.

Top-down feedback from PFC may also have a direct role in shaping the functional response properties of posterior cortical areas. In cellular recording studies from both humans and animals, evidence has accrued that the selectivity of response of neurons in areas such as the fusiform cortex may increase in real time following the presentation of a stimulus. For example, Puce, Allison, and McCarthy (1999) measured local field potentials in regions of lateral fusiform cortex in human adults and found that responses of these neurons go from being face selective at around 200 ms after stimulus presentation to being modulated by top-down information such as face identity at later temporal windows. This suggests that top-down cortical feedback pathways, in addition to their importance in attention and object processing (Spratling & Johnson 2004, 2006), may increase the degree of specialization and localization in real time, as well as in developmental time. Thus, some of the changes in functional specialization and localization seen in face-sensitive regions may reflect the increasing influence of interregional coordination with other regions, including the PFC.

Conclusions

We presented the IS approach to understanding the mapping between brain structure and function in human postnatal development and examined this viewpoint in the context of fMRI evidence on the emerging social brain. Clusters of relevant studies have appeared for three regions of the social brain: FFA, STS, and MPFC. For all of these regions, dynamic developmental changes are observed between midchildhood and adulthood. Recent studies of FFA and STS support predictions from the IS view that the cortical tissue supporting social processing becomes increasingly selective in its response properties

during the later stages of development. Evidence from MPFC studies shows that the extent of activation decreases with development in late childhood resulting in the focal selective activation of specialized subregions of MPFC in adults. Alongside this change in MPFC responses is a corresponding increase in the extent of activation in more posterior regions such as FFA and STS. This suggests that a dynamic interplay between prefrontal and posterior regions is one of the sources of constraint on the specialization of some posterior structures. We speculate further on a class of learning systems that may explain the role of prefrontal areas in orchestrating the differential activation of regions into functional networks, including those that underlie social cognition. Clearly much work will be required to test these highly speculative proposals about how the social brain network and subnetworks emerge during development. This research will specifically require studies that simultaneously combine the study of structural and functional changes in the brain during development (Olesen, Nagy, Westerberg, & Klingberg, 2003).

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