Towards the developmental pathway of face perception abilities in the human brain

Simon van Rysewyk[1]
School of Philosophy, University of Tasmania

In: A. Freitas-Magalhães (Ed.), *'Emotional Expression: The Brain and the Face'* (V. II, Second Series), University of Fernando Pessoa Press, Oporto: pp. 111-131.

---

[1] PhD Candidate, School of Philosophy, University of Tasmania, Private Bag 41, Hobart, Tasmania 7001, Australia. email: spvan@postoffice.utas.edu.au Phone: +61 3 6226 7848. Fax: +61 3 6226 7847.

Abstract

This study examines data from developmental functional magnetic resonance (fMRI) studies to contribute to the unresolved issue whether the face-sensitive cortical regions in the ventral stream are specialized for faces as a stimulus category, and whether such specialization is determined by expertise or maturation. The developmental fMRI studies reviewed indicate that face-stimulated activity leads to increases in the extent of specialization and localization in the cortex during development. This challenges a maturational framework prediction that face perception in the child's brain is restricted to specialized neural modules that can be activated by faces in adults. Instead, it is argued that the evidence examined in this paper supports both the expertise hypothesis and interactive specialization as plausible frameworks to relate face perception abilities to brain development.

Keywords: development, face, face perception, fMRI, interactive specialization, prosopagnosia

Introduction

This study examines data from developmental functional magnetic resonance (fMRI) studies to contribute to the unanswered question whether the face-sensitive cortical regions in the ventral stream are specialized for faces as a stimulus category, and whether such specialization is determined by expertise or maturation. The aims of this study are as follows: first, to assess whether face perception in the child's brain is restricted to specialized neural 'modules' that can be activated by faces in adults; second, to assess whether the activity stimulated by faces lead to increases in the extent of specialization and localization in the cortex during development.

In the following sections, I briefly review the development and neuroanatomy of face perception. Detailed analysis of selected developmental neuroimaging studies of face perception in the human brain follow, focusing on the localization and specialization issues. Finally, neuroimaging studies on prosopagnosia are examined. I suggest that this condition can contribute valuable research on the developmental pathway of face-specialized cortical regions.

The neuroanatomy of face perception

It is thought that the visuospatial processing system in humans is organized into two anatomically and functionally dissociated subsystems, the ventral stream and the dorsal stream. The ventral stream projects from the primary visual cortex to ventral regions in the inferior temporal lobe, and is primarily associated with object processing. The dorsal stream projects from the primary visual cortex to superior and inferior regions of the parietal lobe and is associated with spatial processing of object movement. The dual dissociation for object and spatial processing has been reliably reproduced in several adult neuroimaging studies. For example, Haxby and colleagues (1994) investigated the functional dissociation of the processing streams for face perception and location perception in adults by measuring cerebral blood flow (rCBF) with H_2-^{15}O-positron emission tomography (PET). A face-identity task was correlated with selective rCBF increases within the fusiform gyrus in occipital and occipitotemporal cortex bilaterally (Brodmann areas 19 and 37) and in a right prefrontal region in the inferior frontal gyrus (Brodmann areas 45 and 47). By contrast, a location-identity task was correlated with selective rCBF increases in dorsal occipital (Brodmann area 19), superior parietal (Brodmann area 7), and intraparietal sulcus cortex bilaterally (Brodmann area 7) and in dorsal right premotor cortex (Brodmann area 6). These results suggest that, within a sensory modality, selective attention is not correlated with decreased activity in regions that process unattended visual information, but is correlated with increased activity in cortical regions that process the attended information. In addition, selective attention to one sensory modality is correlated with decreased activity in cortical areas involved in processing input from other sensory modalities. Therefore, cortical regions selectively modulated their activity depending on whether the focus of selective attention was face matching or location. These results support a double dissociation of visual functions correlated with extrastriate visual areas in the ventral and dorsal cortical processing streams.

While recent adult neuroimaging studies suggest that the ventral-dorsal dissociation may reflect further distinctions within the ventral stream, it is unclear whether face-sensitive cortical areas such as the fusiform face area (FFA) are dedicated to faces as a stimulus group. In an influential fMRI study conducted by Kanwisher and colleagues

(1997), an area in the fusiform gyrus was located in 12 of 15 subjects tested that was significantly more active when the subjects viewed faces than when they viewed assorted common objects. The study authors interpreted this result as demonstrating the existence of a region in the fusiform gyrus that is not only responsive to face stimuli, but is selectively activated by faces compared with various control stimuli. Similarly, Ishai and colleagues (1999) found three distinct regions of the ventral temporal cortex that responded selectively to faces, chairs and houses. Faces activated most of the fusiform gyrus within the inferior temporal region, chairs activated the more lateral ones, and houses activated more medio-temporal regions. But, in contrast to the maturational framework of Kanwisher et al. (1997) (Box 1), Ishai et al. (1999) found that each stimulus group elicited significant responses in the regions that responded maximally to other stimuli, and each group was correlated with distinctive patterns of response across ventral temporal cortex. Supportive of this finding, an fMRI study conducted by Haxby and colleagues (2001) found that while faces, cats, man-made objects and nonsense pictures evoked distinctive patterns of response across ventral temporal cortex, when the regions that responded maximally to a stimulus group were excluded, the stimulus group being viewed could be identified based on the pattern of activation. For example, even within cortical regions that responded maximally to only one category, patterns of response that discriminated among all categories were found. Although each stimulus group instigated distinctive patterns of cortical response in the ventral stream, they were widely distributed and overlapping, indicating a continuous featurotopic representation, rather than a stimulus group-based representation.

----- Insert Box 1 about here -----

Other adult neuroimaging studies suggest that distinctive stimulus group patterns of activation in the ventral stream may be modulated by perceptual expertise (Box 2).

----- Insert Box 2 about here -----

Gauthier and colleagues (1999) used fMRI to measure changes correlated with increasing expertise in regions selected for face perception, the middle and anterior fusiform gyri. Acquisition of expertise with novel objects (greebles) resulted in increased activation in the right hemisphere FFA for matching of upright greebles as compared to matching inverted greebles. In addition, the same regions were reliably activated in experts than in beginners during passive viewing of greebles. This suggests that the FFA is normally activated by faces in adults, not because it is a face-specific processing area, but because activation reflects expertise with categories of extremely well-known stimuli. Hence, it appears that expertise may be one factor that results in specialization in face-sensitive cortical regions. While studies reporting increasing expertise with face stimuli and possible changes in processing strategies are quickly accumulating, and offer an exciting avenue for research, further experiments should study changes in the pattern of cortical activation during training in adults and development in infants.

Although adult neuroimaging work has generated good understanding of the neural correlates of face perception in the mature adult brain, it is still unclear whether the face-sensitive cortical regions in the ventral stream are specialized for faces as a stimulus category, and whether such specialization is determined by expertise or maturation. The current study suggests that analysis of developmental neuroimaging studies can contribute to this issue. Before this, a summary is offered of what is known about the development of face perception and the brain.

The development of face perception

Available studies indicate that the development of face perception begins very early in life and is not complete until late adolescence. Within the first days of life, neonates preferentially orient to face-like stimuli (Farroni et al., 2005) and can discriminate among emotional facial expressions (Pascalis & de Schonen, 1994). It is thought that these functions are mediated by subcortical and cortical brain regions (Simion et al., 1998). At one-month, neonates can discriminate between individual faces (De Hann et al., 2001); at three-months, they show evidence of forming average prototypical representations of faces (De Hann et al., 2001). Right hemispheric mediated functions like processing the global aspects of face and objects have been observed in infants aged four months (Deruelle & de Schonen, 1995). Cohen and Cashon (2001) found that 7-month old infants show adult-like configural processing preference for upright faces, and process inverted faces as independent features. In the upright condition, infants looked longer at the composite face than at the familiar face, but in the inverted condition infants did not.

Although it is clear that face perception abilities undergo significant changes across the first years of life, studies of school-age children show that developmental change in face perception abilities continues throughout childhood. In a seminal study, Carey and Diamond (1977) investigated whether the ability of children aged 10 to represent orientation-specific configural properties of faces reveals maturation in the right cerebral hemisphere. They showed 6-, 8- and 10-year-old children upright and inverted photographs of unfamiliar people. Immediately after seeing the photographs, they were invited to identify the previously seen ‘old’ face from a never-before-seen ‘new’ face. The authors predicted that children depend more on featural (piecemeal) strategies to perceive faces, whereas older children and adults depend more on configural (holistic) strategies. The study found that, like the adults, the 8 and 10 year old children recognized the ‘old’ faces better when they were shown in their upright position than when they were shown in the inverted position. The 6-year old children, by contrast, recognized the upright and inverted faces equally well. The authors concluded that until the age of 6, children employ a featural representational strategy for perceiving upright and inverted faces. After the age of 10, children become sensitive to configural information and begin to perceive faces more holistically (‘encoding switch hypothesis’). A study by Tanaka and colleagues (1998) investigated memory for a face part in children when the part was presented in isolation and in the whole face. In contrast to the study by Carey and Diamond (1977), results indicate that by age 6, children are perceiving faces holistically as revealed by their improved recognition of face parts presented in the entire face rather than in isolation. Moreover, reliance on configural processing appears stable in children until age 10.

Neurodevelopmental studies may contribute to the issue whether face perception undergoes quantitative or qualitative change with age. Taylor and colleagues (1999) studied ERPs with 48 children aged between 4 and 14 years, and 12 adults to assess if the early face-specific ERP component (N170) observed in adults would contribute neurodevelopmental correlates of face perception in children. Of the five categories presented, only faces recorded an N170 at posterior temporal sites across age groups, and steadily increasing latencies in younger children were recorded at the T6' electrode site. In adults, N170 was largest at T6'. Age-related increases in N170 amplitude were found at T6' (in adults, the N170 was largest at T6'). The authors suggest that the underlying neural correlates of face perception therefore mature in a gradual and quantitative manner throughout childhood. Neurodevelopmental ERP studies may also explain maturational differences in featural and configural perception of faces throughout childhood. In an ERP study by Taylor and colleagues (2001) on 128 4-15 year olds and adults, N170 was observed in the youngest children in response to upright faces, with similar activation patterns seen in adults. In contrast, shorter and larger latencies were recorded to eyes than to faces in children. Development of N170 to upright faces continued until adulthood, indicating a slower maturation of configural face perception as compared to featural perception of isolated eyes. This result may mean that holistic processing is a more complex strategy than piecemeal processing, and that it attains adult levels later in childhood.

The evidence presented in this brief review clearly demonstrates that the development of face perception begins in neonates and continues to undergo change well into late adolescence. Knowledge of the developmental issues of face-perception abilities in the brain, such as how closely, in what ways, and when children’s perception of faces approximates that of adults will further refine understanding of the development of the neurophysiological correlates and bases of face perception. The present study examines several fMRI papers on face perception abilities in children (Aylward et al., 2005; Gathers et al., 2004; Golarai et al., 2007; Passarotti et al., 2003; Scherf et al., 2007; Thomas et al., 2001) based on the assumption of interactive specialization that neuroimaging studies on functional brain development be understood in terms of both the extent of localization and specialization for a stimulus presentation or task context. Hence, the central questions of this study are:

1. Do children show reliable cortical activity for faces?
2. Is the activation for faces in children reliably localized to face-sensitive cortical areas typically found in adults?
3. Is the activation for faces in children reliably specialized to face-sensitive cortical areas typically found in adults?
4. Does prosopagnosia reveal neural activity for faces in face-selective cortical regions, and is this activation reliably localized and specialized for faces?

Reliable cortical activity for faces in children

Concerning activation for faces in general, all studies cited above revealed that specific regions of the cortex exhibit reliable activation to faces. For example, Passarotti and colleagues (2003) found reliable bilateral activation of specific regions in posterior parietal cortex in 10-12 year olds; Scherf et al. (2007) reported consistent response in a dorsal and medial area of the fusiform gyrus in children aged 5-8 years; Thomas et al. (2001) detected reliable activity in the left amygdala (AM) and substantia innominata for fearful faces relative to fixation in male children aged 2.5 years.

Cortical localization for faces in children and adults

Four studies found evidence for changes in the degree of cortical tissue activated between children and adults (Gathers et al., 2004; Golarai et al., 2007; Passarotti et al., 2003; Scherf et al., 2007). Scherf and colleagues (2004) reported that children showed less face-specific activation in the FFA, the occipital face area (OFA), and the superior temporal sulcus (STS) compared to adults. Tukey post-hoc comparisons showed that across all of the three adult-defined face-related regions, children activated smaller volumes than both adolescents and adults, and that there were no differences between the adolescents and adults. Moreover, children activated smaller portions of the right and left fusiform gyri, and the left OFA than the older age groups. The study conducted by Golarai and colleagues (2007) is consistent with these results. In the first experiment, the FFA was defined in each subject as an adjoining cluster of voxels peaking in the fusiform gyrus that was activated more in response to faces than to objects. The study found that the FFA was detected more consistently in adults and adolescents than in children, and that the right FFA increased in size with age. These results may indicate age-dependent difference in cortical selectivity for faces reflecting lower response amplitudes.

Cortical specialization for faces in children and adults

Several studies support question (3) of this study that face perception becomes more specialized with increasing age (Aylward et al., 2005; Gathers et al., 2004; Thomas et al., 2001). Alyward and colleagues (2005) investigated whether activation of the fusiform gyrus is greater during face perception in children aged 12-14 years than in children aged 8-10 years. The functional anatomy of faces versus houses was compared from fMRI scans. The study revealed increased bilateral activation for faces in the older children in comparison to the younger children. Activation in the fusiform gyrus was strongly associated with age and with a behavioural measure of configural face perception. Gathers and colleagues (2004) sought to identify neural correlates for face and object perception in children (aged 5-8 and 9-11 years) and adults within the ventral processing stream. Despite similar face-preferential activation patterns in the ventral stream across the different ages, the adults and children aged 9-11 years exhibited face-preferential loci near the fusiform face area (FFA) in comparison to objects, whereas children aged 5-8 years exhibited this activation in the posterior ventral stream. In addition, the extent of category-selectivity in other brain regions increased with age. Finally, Thomas and colleagues (2001) examined the specificity of the AM response to fearful and neutral facial expressions in adults and children aged 11 years. The AM plays a fundamental role in the human response to emotional stimuli, especially fear-inducing stimuli. Adults exhibited increased left AM response to fearful faces compared to neutral faces in contrast to children who showed less specificity in AM activity to fearful compared to neutral faces. Collectively, these studies support a central hypothesis of interactive specialization (Box 3) that face perception becomes more specialized with increasing age (Johnson, 2001, 2005).

----- Insert Box 3 about here -----

Two developmental fMRI studies on localization and specialization

The studies by Schef et al. (2007) and Golarai et al. (2007) are of importance to the specialization and localization question. Schef et al. (2007) investigated the developmental organization of category-selective regions in ventral visual cortex. The authors compared the developmental trajectories for face-, object-, and place-selective activation in the ventral visual cortex in children (5-8 years), adolescents (11-14 years), and adults. Participants passively viewed short movie vignettes containing scenes of faces, miscellaneous common objects, buildings, and navigation through open fields. The study found that the children and adolescents exhibited bilateral parahippocampal place area (PPA) activation in response to scenes of buildings and navigation that was comparable to adults in location, extent, magnitude of activation, and magnitude of specificity. This may indicate that adult-like functional specificity for both the object and place activation in the ventral temporal lobe is in place in early childhood. In addition, 80% of the children exhibited adult-like magnitudes of face selective activation in some region of the fusiform gyrus and lateral occipital region, but this selectivity was not uniform across individuals nor was it located in the same region as that of adults and adolescents. Concerning age group differences, the study found extensive differences between the children and adolescents in the development of face-selective cortex, including the FFA, OFA, and STS. The only face-selective region activated by the children was located in a ventral and posterior region of the right fusiform. This result stands in contrast to specific preferential activation patterns for other object categories (occipital object areas and the PPA). According to the authors of the study, this difference is due to reduced face-selectivity activation within the adult FFA, OFA, and STS, and also smaller volumes and inconsistency in the locus of face-selective activation in individual children. Therefore, it appears that greater consistency in the development of face-selectivity activation in the right hemisphere and left hemisphere does not become adult-like until the onset of adolescence and adulthood, respectively.

Golarai et al. (2007) investigated the development of functional object, face and place regions in high-level visual cortex in relation to recognition memory. Object (lateral occipital complex, LOC), face (FFA and STS), and place (PPA) selective cortices were examined using fMRI in children (7–11 years), adolescents (12–16 years) and adults. Participants were tested with static object categories (faces, objects, places, scrambled abstract sculptures and textures). The study found significantly larger right FFA and left PPA volumes of selective activation in adults than in children. By contrast, LOC and STS volumes of selective activation and object recognition memory were constant across ages. The authors conclude that the ventral stream develops slowly and varies temporally across functional regions, is determined by brain region rather than stimulus category, and is positively associated with recognition memory. It appears that face-related cortex is immature in children and different visual categories follow different developmental trajectories of functional specialization within the ventral processing stream. As the ability to recognize different categories of visual stimuli matures, so does the functional specificity of the brain activation, with faces being the last visual stimuli to exhibit adult-like recognition abilities and specialization in the ventral visual cortex.

The developmental changes reported in these studies are consistent with the idea of specialization in the brain as emerging from interactions between experience-dependent learning and the maturing brain, in contrast to endogenous maturation models of brain development. Again, they are compatible with interactive specialization as a plausible framework to relate face perception to brain development.

Cortical activity for faces in prosopagnosia

Studying individuals who lack specific cognitive abilities is a powerful framework for understanding the relation between brain development and cognitive functions. Hence, research on developmental prosopagnosia (DP) may corroborate and further refine current understanding of the development of face-specialized cortical regions. DP is characterized by severely impaired face perception abilities, especially facial identity recognition skills (Duchaine & Nakayama, 2006). In contrast to individuals with acquired prosopagnosia (AP), who selectively lose the ability to recognise faces due to brain damage, DPs never develop typical adult face-processing abilities. Impairments in face identity recognition in DPs can be as selective and as severe as those observed in APs, despite the absence of brain and sensory processing deficits, or known acquired injury (Duchaine & Nakayama, 2006). It appears to be extremely rare in children, and only a few cases have been reported (e.g., Ariel and Sadeh, 1996).

Case studies of AP support the idea that human facial recognition is subserved by selective cortical regions dedicated to face perception. McMullen and colleagues (2000) presented a case study of an adult with apperceptive object agnosia and an alexia for words as a result of a stroke involving the left posterior cortex. The patient nonetheless demonstrated relatively spared visual perception for faces. According to the authors of the study, this suggests that early visual processes such as perceptual identification and figure-ground segmentation can function during the recognition of face stimuli, but not during object recognition. It appears that the brain can determine perceived visual information correlates to a face or an object long before it has been identified as such. Moreover, since face-processing deficits result from bilateral or right occipital lesions, and object-processing deficits result from bilateral or left occipital lesions, the patient’s lesion in the left posterior cortex explains his impaired object perception and relatively intact face perception. Paired with AP, this study is consistent with the dual dissociation between face and object, and implies that object and face-perception streams separate from early visual cortical processing centres. It is also compatible with the idea that the two hemispheres are specialized to process faces and objects in parallel, and that a part-based module in the left hemisphere processes objects, and a holistic module in the right hemisphere processes faces and some objects (Farah, 1990).

As the subject in the McMullen study occupies the extreme end of the putative whole and part-based perception continuum (Farah, 1990), he presents the greatest dissociation between face and object perception in an apperceptive object agnosic. Other studies argue, however, that no unambiguous dissociation between face and object perception exists due in part to reports of prosopagnosia accompanied by object agnosia (Damasio et al., 1982). In a case study of a child with DP, Ariel and Sadeh (1996) found that the condition does not appear to be highly selective and cannot be easily dissociated from adult apperceptive agnosia. Consistent with Passarotti et al. (2003), the authors speculated that children may employ a more distributed network of brain regions than adults in face perception. Moreover, a lack of appropriate response time measurements in accuracy-based studies gives reason for further scepticism about the dual dissociation hypothesis. For, it may be the case that prosopagnosics attained normal accuracy on non-face object tests by exchanging speed for accuracy, thereby concealing actual deficits (Duchaine & Nakamura, 2005). If it were the case that prosopagnosia and agnosia arise from deficits to the same neural mechanisms, then there would be no reason to distinguish between the two conditions. To assess dual dissociation between faces and objects in DP, Duchaine and Nakamura (2005) tested seven DPs to measure their accuracy and reaction times with multiple tests of face recognition and compared this with a larger battery of object recognition tests. All subjects performed poorly with the face memory tests, and four subjects revealed a very strong dissociation between the face and object tests. Comparison of the response time measurements for all tests demonstrated that the accuracy dissociations cannot be explained by differences in response times. Hence, measurement of reaction times excluded speed-accuracy trade-offs. This study establishes that face and non-face recognition can dissociate over a wide range of testing conditions, and that some cases of DP are accompanied by developmental agnosia, and other cases reveal prosopagnosia with normal object perception. Hence, the unequivocal dissociation between face and object perception remains to be demonstrated. While adult DPs generally activate face-sensitive cortical regions (Duchaine & Nakayama, 2006), the extent of selectivity of this activation remains in doubt compared to the response of typically developing children, as reported above in the fMRI studies.

Support for this scepticism comes from recent fMRI studies which investigated whether individuals with congenital prosopagnosia (CP) reveal an atypical FFA (Hasson et al., 2003; Avidan et al., 2005). CPs show severe impairment in face recognition from birth or early childhood, despite the absence of any cortical lesion or brain disease. The Hasson et al. study assessed FFA activity for face and non-face stimuli in an adult with CP and 12 experimental controls. The face-sensitive activation patterns of the CP subject in the FFA was similar to that recorded in the controls on locality and hemispheric laterality parameters. In the second experiment, selective activation during a modified Rubin-face illusion compared to the Rubin-vase perceptual states revealed that holistic processing; that is, grouping face components into a global facial configuration, contributed to his face-related activation. Subtle differences in the lateral occipital cortex were also observed in the selectivity between faces and objects. Similarly, the Avidan et al. (2005) study found no difference in the BOLD activation in ventral occipital-temporal regions between the CPs and the 10 controls. The CPs exhibited normal face and object activations in the FFA, and normal activations in the lateral occipital area across different types of stimuli and different experimental paradigms. In addition, strong bilateral face-related activation was seen in the precentral sulcus, inferior frontal sulcus and anterior lateral sulcus in the CPs, but not in the controls. These findings may indicate that CP is not the outcome of decreased activation or lack of selectivity in face-related regions in the ventral stream. Importantly, fMRI measured face-related activity in the ventral processing stream is necessary but appears insufficient for normal face identification. Adult DPs, like the children examined earlier who showed neural activity for faces in cortical areas normally found in adults (e.g., Passarotti et al., 2003), generally activate the same areas as typically developing children, but, as we have seen, this activation is less reliably localized and less reliably specialized for faces.

Future research may wish to ponder evidence of activation in DPs of areas not commonly recruited in typical adults in face perception, such as the inferior frontal sulcus (Hasson et al., 2003; Avidan et al., 2005). This may be important because activation of this region was observed in children in some of the developmental neuroimaging papers described above (e.g., Gathers et al., 2004; Passarotti et al., 2003; Scherf et al., 2007). Based on an interactive specialization framework, it could be hypothesized that face perception abilities during infancy and childhood might be the result of emerging patterns of activations between different regions. Moreover, some of the changes between regions might also be characteristic of perceptual and motor expertise in adults. Consistent with these assumptions, expertise for faces could increase the selectivity and interconnectivity of cortical activation in adult and children DPs toward the neurotypical pattern. DeGutis and colleagues (2007) measured neural changes correlated with expertise-based configural face perception in an adult with DP. Following the 14-month training task, the patient significantly improved at face recognition. The fMRI results revealed that, except for a relatively lower absolute signal in the FFA during the first scan, differences in absolute activity between trained and untrained states were not observed in face-sensitive left FFA, right FFA and right OFA. Hence, the selectivity of the response of face-sensitive cortical areas did not change with training or with the patient's face recognition improvements. However, the study found increased functional connectivity and activity between the right OFA and the right FFA post-training. Moreover, the N170 modulation revealed a significant amplitude decrease for objects compared to faces following training, thus increasing face selectivity. In contrast to a maturational perspective, this study indicates that training on faces in DPs improves the activity and interconnectivity of face-selective cortical areas toward the typical pattern. Further studies on children and adult DPs are needed to test this important finding.

Conclusion

Based on developmental neuroimaging studies, the central finding of this study is that children show activity for faces in the neural regions typically found in adults, but this activation is less reliably localized and less reliably specialized for faces. Studies of the anatomical and behavioural abilities of individuals with prosopagnosia reviewed in this paper support this central conclusion. In addition, the developmental pathway of face perception in the brain does not merely reflect the sequential maturation of specific cortical areas, but might be the result of interregional connectivity also characteristic of perceptual expertise in adults. It is suggested that further studies investigate the influence of training on faces on the selectivity and interconnectivity of cortical regions, in both typical and atypical developing children and adults.

References

1. Ariel, R., & Sadeh, M. (1996). Congenital visual agnosia and prosopagnosia in a child – a case report. *Cortex, 32(2),* 224–234.
2. Avidan, G., Hasson, U., Malach, R., & Behrmann, M. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: II. Functional neuroimaging. *Journal of Cognitive Neuroscience, 17,* 1150–1167.
3. Aylward, E. H., Park, J. E., Field, K. M., Parsons, A. C., Richards, T. L., & Cramer, S. C. (2005). Brain activation during face perception: Evidence of a developmental change. *Journal of Cognitive Neuroscience, 17,* 308–319.
4. Baron-Cohen, S. (1997). *Mindblindness: an essay on autism and theory of mind* Cambridge, MH: The MIT Press.
5. Carey, B.J., & Diamond, R. (1977). From piecemeal to configurational representations of faces. *Science, 195(4275),* 312-314.
6. Cohen, L.B., & Cashon, C.H. (2001). Do 7-month old infants process independent features or facial configurations? *Infant and Child Development, 10(1–2),* 83-92.
7. Damasio, A.R., Damasio, H., & Van Hoesen, G.W (1982). Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology, 32*, 331–341.
8. DeGutis, J. M., Bentin, S., Robertson, L. C., & D’Esposito, M. (2007). Functional plasticity in ventral temporal cortex following cognitive rehabilitation of a congenital prosopagnosic. *Journal of Cognitive Neuroscience,19,* 1790–1802.

9. De Hann, M., Johnson, M.H., Maurer, D., & Perret, D.I. (2001). Recognition of individual faces and average face prototypes by 1- month and 3-month old infants. *Cognitive Development, 16*, 659–678.
10. Deruelle, C., & de Schonen, S. (1995). Pattern processing in infancy: hemispheric differences in the processing of shape and location of visual components. *Infant Behavior and Development, 18(2),* 123–132.
11. Diamond, A., & Goldman-Rakic, P. S. (1989). Comparison of human infants and infant rhesus monkeys on Piaget's AB task: evidence for dependence on dorsolateral prefrontal cortex. *Experimental Brain Research, 74,* 24–40.
12. Dickson, K. L., Fogel, A., & Messinger, D. (1998). The development of emotion from a social process view. In: M.F. Mascolo & S. Griffin (Eds.), *What develops in emotional development? Emotions, personality, and psychotherapy* (pp. 253–71). New York: Plenum Press.
13. Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience, 17,* 249–261.
14. Duchaine, B., & Nakayama, K. (2006). Developmental prosopagnosia: A window to content-specific face processing. *Current Opinion in Neurobiology, 16,* 166–173.
15. Ekman, P. (1980). *The face of man: Expressions of universal emotions in a New Guinea village.* New York: Garland STPM Press.
16. Ekman, P. (1992). Are there basic emotions? *Psychological Review, 99(3),* 550–553.
17. Farah, M.J. (1990). *Visual agnosia: disorders of object recognition and what they tell us about normal vision.* Cambridge, MA: MIT Press.

18. Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborn’s preference for face-relevant stimuli: Effects of contrast polarity. *Proceedings of the National Academy of Sciences, USA, 102,* 17245–17250.
19. Filipek, P. A., Richelme, C., Kennedy, D.N., & Rademacher, J. (1992). Morphometric analysis of the brain in developmental language disorders and autism. *Annals of Neurology, 32,* 475.
20. Gathers, A. D., Bhatt, R., Corbly, C. R., Farley, A. B., & Joseph, J. E. (2004). Developmental shifts in cortical loci for face and object recognition. *Neuro Report, 15,* 1549–1553.
21. Gauthier, I., Tarr, M.J., Moylan, P., Skudlarski, P., & Gore, J.C. (1999). Activation of the middle fusiform ‘face area’ increases with expertise in recognizing novel objects. *Nature Neuroscience 12,* 495-504.
22. Golarai, G., Gharemani, D. G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J. L., & Gabrieli, J. D. E. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nature Neuroscience, 10,* 512–522.
23. Hasson, U., Avidan, G., Deouell, L., Bentin, S., & Malach, R. (2003). Face-selective activation in a congenital prosopagnosic subject. *Journal of Cognitive Neuroscience, 15,* 419–431.
24. Haxby, J.V., Horwitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P., & Grady, C.L. (1994). The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. *Journal of Neuroscience, 11(2),* 6636–6353.

25. Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4,* 223–233.
26. Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., & Haxby, J.V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America, 96(16),* 9379–9384.
27. Johnson, M.H. (2001). Functional Brain Development in Humans. *Nature Reviews Neuroscience, 2,* 475–483.
28. Johnson, M. H. (2005). *Developmental cognitive neuroscience* (2nd ed.). Oxford, England: Blackwell.
29. Kanwisher, N., McDermott, J., & Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17(11),* 4302–4311.
30. Le Doux, J. (1996). *The emotional brain.* New York: Simon & Schuster.
31. Pascalis, O., & de Schonen, S. (1994). Recognition memory in 3- to 4-day old human neonates. *Neuro Report, 5,* 1721–1724.
32. Passarotti, A. M., Paul, B. M., Bussiere, J. R., Buxton, R. B., Wong, E. C., & Stiles, J. (2003). The development of face and location processing: An fMRI study. *Developmental Science, 6,* 100–117.
33. McMullen, P., Fisk, J., & Phillips, S. (2000). Apperceptive agnosia and face recognition. *Neurocase, 6,* 403–414.
34. Pierce, K., Müller, R.A., Ambrose, J., Allen, J., & Courchesne, E. (2001). Face processing occurs outside the fusiform ‘face area’ in autism: evidence from functional MRI. *Brain, 124(10),* 2059–2073.

35. Rumsey, J. M., & Ernst, M. (2000). Functional neuroimaging of autistic disorders. *Mental Retardation and Developmental. Disability. Research Reviews, 6,*171–179.
36. Sakai, K., Hikosaka, O., Miyauchi, S., Sasaki, Y., Fujimaki, N., & Benno, P. (1998). Transition of brain activation from frontal to parietal areas in visuo-motor sequence learning. *Journal of Neuroscience, 18,* 1827–1840.
37. Scherf, K. S., Behrmann, M., Humphreys, K., & Luna, B. (2007). Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. *Developmental Science, 10,* F15–F31.
38. Simion, F., Valenza, E., & Umiltà, C. (1998). Mechanisms underlying face preference at birth. In: F. Simion & G. Butterworth (Eds.), *The development of sensory, motor and cognitive capacities in early infancy: From perception to cognition* (pp. 87–101). Hove: Psychology Press/Erlbaum/Taylor & Francis.
39. Summerfield, C., Egner, T., Greene, M., Koechlin, E., Mangels, J., & Hirsch, J. (2006). Predictive codes for forthcoming perception in the frontal cortex. *Science, 314,* 1311–1314.
40. Tanaka, J.W., Kay, J.B., Grinnell, E., Stansfield, B., & Szechter, L. (1998). Face recognition in young children: when the whole is greater than the sum of its parts. *Visual Cognition, 5(4),* 479–496.
41. Taylor, M.J., McCarthy, G., Saliba, E., & Degiovanni, E. (1999). ERP evidence of developmental changes in processing of faces. *Clinical Neurophysiology, 110(5),* 910–915.
42. Taylor, M.J., Edmonds, G.E., McCarthy, G., & Allison, T. (2001). Eyes first! Eye processing develops before face processing in children. *Neuro Report, 12(8),* 1671–1676.

43. Thomas, K. M., Drevets, W. C., Whalen, P. J., Eccard, C. H., Dahl, R. E., & Ryan, N. D. (2001). *Biological Psychiatry, 49,* 309–316.

Appendix I

Box 1 The maturational framework

A maturational framework attempts to relate the anatomical maturation of specific regions of the brain, typically areas of the cerebral cortex, to newly emerging cognitive, perceptual and motor competencies. The localization of particular psychological functions is an attribute of a specific brain region and its patterns of functional connectivity, rather than its patterns of functional connectivity to other regions, to the whole brain and its external environment. Developmentally, a maturational view assumes maturation of intraregional connections, rather than interregional connectivity.

- Although the object retrieval task reveals activity in several brain regions, it is claimed to be maturation of only one of these, the dorsolateral prefrontal cortex, (DLPC) that explains the onset of this competency (Diamond et al., 1989).
- Developmental disorders of genetic origin are characterised in terms of damaged ‘innate computational modules’ in the human brain. For example, autism is thought to be the result of impairment of the domain-specific cortical mechanism of metarepresentation, dedicated to the processing of social stimuli; an impairment in the so-called ‘theory of mind’ module (Baron-Cohen, 1997). Non-social deficits in autism are explained in terms of unrelated additional cognitive impairments with other brain regions thought to be biologically intact (Baron-Cohen, 1997).
- Maturation of the AM has been related to the emergence of the stereotypical facial expression of fear in humans (Le Doux, 1996). It is argued that the emergence of all the stereotypical facial expressions of basic emotions during infancy and childhood are associated with changes in activity in one or more additional brain regions or systems (Ekman, 1980, 1992).

Appendix II

Box 2 The expertise hypothesis

The expertise hypothesis assumes that the acquisition of new skills throughout the lifespan changes the patterns of activation of cortical areas. An expertise perspective hypothesizes that areas active in infants during the acquisition of new perceptual or motor abilities are the same as those involved in expertise training in adults.

- Sakai and colleagues (1998) found that as adults perform a visuomotor sequence learning task, decreasing activation of DLPC and medial frontal cortex was accompanied with increasing activation of more posterior areas of the frontal cortex (Sakai et al., 1998). The expertise model predicts that similar changes may occur in infants as a result of acquiring perceptual or motor expertise.
- One characteristic of autism is the failure to selectively attend to faces. An fMRI study conducted by Pierce and colleagues (2001) found that despite the absence of structural abnormality in the fusiform area, autistic adults process faces by activating more inferior occipital-temporal regions, rather than the predicted fusiform area. In contrast to a maturational framework, this result appears to support an expertise hypothesis prediction that fusiform activation is due to expertise with categories of stimuli rather than face-specific specialization.
- In one developmental clinical study, Dickson and colleagues (1998) found that specific types of infant smiles (simple, Duchenne, play, and duplay) become correlated with different kinds of pleasurable activities, and with different kinds of pleasure (e.g., the pleasure of anticipation or engagement, the excitement of an activity, the pleasure of enjoyable sensations). The infant experiences the pleasure of observing her caregiver's pleasure and of seeing the effects of her own facial expressions and behaviour on her caregiver. This suggests that infant facial

expressions are a consequence of acquiring perceptual and motor expertise from infant-caregiver interactions. However, the extent of changes in the neural correlates of behaviour in infants compared to those observed during more complex expertise training in adults requires further study.

Appendix III

Box 3 Interactive specialization

Interactive specialization (IS) views postnatal functional brain development, particularly within the cerebral cortex, as involving a process of organizing patterns of interregional connections (Johnson, 2001, 2005). In contrast to attempts by maturational researchers to localize particular psychological functions to specific cortical regions, IS underscores the response attributes of regions as determined by their patterns of functional connectivity to other regions, to the whole brain and its external environment (Summerfield et al., 2006). Developmentally, IS stresses interregional connectivity rather than maturation of intraregional connections.

- In the object retrieval paradigm, IS predicts that refinement in the connections between DLPC, parietal cortex and cerebellum explain the onset of this ability (Johnson, 2001). Consequently, brain regions and structures reorganize their interactions to acquire new skills or computations.
- Structural imaging studies on groups with autism and developmental language disorders reveal that abnormalities in white matter are at least as extensive as those in grey matter (Filipek et al., 1992), and that numerous subcortical and cortical regions are involved in these disorders (Rumsey & Ernst, 2000). These general findings may support the prediction of IS that initial brain abnormalities are subsequently worsened by atypical patterns of interaction and interregional connectivity.
- IS assumes that during infancy, patterns of cortical activation during behavioural tasks might differ from those observed in adults. Success in a new behavioural task is correlated with a reorganization of interactions between different brain structures and regions. Potentially, the same behaviour could be subserved by

different neural substrates at different stages during development. For example, the stereotypical facial expressions of basic emotions may be supported by different brain regions at different developmental levels.

Acknowledgements

This paper was written with the support of a Tasmania Graduate Research Scholarship.

Author Biography

Simon van Rysewyk is a PhD candidate in the School of Philosophy, University of Tasmania, in Australia. His thesis relates the emergence of empathy for pain in infants and children to postnatal functional brain development.