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FUNCTIONAL DEVELOPMENT OF THE BRAIN'S FACE-PROCESSING SYSTEM

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Abstract

In the first 20 years of life, the human brain undergoes tremendous growth in size, weight, and synaptic connectedness. Over the same time period, a person achieves remarkable transformations in perception, thought, and behavior. One important area of development is face processing ability, or the ability to quickly and accurately extract extensive information about a person's identity, emotional state, attractiveness, intention, and numerous other types of information that are crucial to everyday social interaction and communication. Associating particular brain changes with specific behavioral and intellectual developments has historically been a serious challenge for researchers. Fortunately, modern neuroimaging is dramatically advancing our ability to make associations between morphological and behavioral developments. In this article, we demonstrate how neuroimaging has revolutionized our understanding of the development of face processing ability to show that this essential perceptual and cognitive skill matures consistently yet slowly over the first two decades of life. In this manner, face processing is a model system of many areas of complex cognitive development.

Keywords

Functional magnetic resonance imaging (FMRI); face processing; cognitive development; functional brain development; electroencephalography (EEG); event-related potentials (ERPs); fusiform face area (FFA); occipital face area (OFA); core face processing network; extended face processing network

INTRODUCTION

The first two decades of life is a dynamic period for human brain development. A full-term baby (39 to 40 gestational weeks) is born with its full complement of approximately 85 to 100 billion neurons[1], yet its brain is only one-quarter of the size that it will be as an adult. By 6 years of age, brain volume has reached 95% of adult size with peak volume reached between 10.5 years for girls and 14.5 years for boys[2, 3]. Peak brain weight is achieved in middle to late adolescence [4]. This period of brain growth is characterized by exuberance in the connections of the brain that include the evolution of axonal and dendritic branches, the formation of synapses and dendritic spines throughout cortical and subcortical areas, and the myelination of axons (see Jernigan and Stiles, *Construction of the human forebrain, WIREs*

Dev Biol, also in the collection *How We Develop)*. During this same time, the pruning process results in the elimination of ineffective neurons and synaptic connections[5]. The outcome of this structural brain growth and pruning is the establishment and refinement of patterns of brain connectivity[6].

Coincident with these changes in brain structure is the equally remarkable evolution in functional abilities. Prominent examples include the rapid development of motor and sensory abilities in the first year of life, followed soon thereafter by remarkable gains in language and communication functions, perceptual discrimination expertise, logical reasoning, executive control, and social behavior. One of the greatest challenges for developmental scientists is documenting the neural basis for these rapidly developing functional abilities during typical child and adolescent development: This is the realm of functional brain development. Meeting this challenge in humans increasingly relies on measures of brain activity captured with advanced functional neuroimaging technologies.

The body of work on functional brain development is very large, encompassing many behavioral domains and functional abilities. Thus, a summary of the full literature is far too large for this review. Instead, this essay will focus on a single domain, face processing, to illustrate the kinds of changes that we observe in brain-behavior relationships as children gradually acquire processing proficiency and conceptual expertise. Face processing is a critically important perceptual ability; it is the cornerstone of human social interaction. Expertise in processing faces is acquired over a protracted period. Development of this skill begins early in infancy but extends well into adolescence. Indeed, Cohen Kadosh[7] considers face processing an exquisite target for developmental neuroimaging studies that can document experience-dependent changes in regional activation related to increasing expertise as well as illustrate important changes in brain network connectivity related to expanding capabilities in complex cognitive and social functioning. A selection of these observations is considered below..

Measuring functional brain activity in human children and adolescents requires methods that are non-invasive *and* pose minimal risk for altering tissue development. Researchers today have a number of techniques at their disposal that meet these requirements. These techniques differ in their sensitivity to different aspects of brain function. Figure 1 provides a summary of the most commonly used techniques in developmental functional neuroimaging in terms of their spatial and temporal resolutions. Electroencephalography methods (EEG) and evoked-related potentials (ERP) measure electrical signaling in the brain, magnetoencephalography (MEG) records magnetic signals, and functional magnetic resonance imaging (FMRI) assesses blood flow and oxygen level dynamics. The different techniques vary in their sensitivity to temporal and spatial properties of brain activity. Electrophysiological (EEG and ERP) provide excellent temporal resolution, allowing for the detection of brain events at the millisecond time-scale, but the spatial localization of these signals is not as precise as other methods. By contrast, the temporal resolution of FMRI is measured in seconds, but the spatial localization of FMRI signals is measured in millimeters.

DEVELOPING AN EXPERTISE FOR PROCESSING FACES

Basic brain architecture

The fact that the human brain treats the visual processing of faces as a special stimulus was first identified from the study of patients exhibiting deficits in face recognition. These deficits were associated with brain damage in the region of the inferior occipital-temporal junction, particularly injuries to the right hemisphere[8, 9]. Since that time, functional neuroimaging studies have significantly refined our understanding of human face processing in adults[10–13]. Activity within two broad brain networks captures the complexity of visual face processing. Figure 2 shows the brain regions and networks associated with adult face processing.

The “core” face system processes the invariant aspects of faces, such as facial features and identity [12]. This system includes a region in the lateral middle fusiform gyrus (commonly referred to as the fusiform face area, FFA[11], the occipital face area (OFA) in the lateral inferior occipital gyrus[14, 15], and the posterior superior temporal sulcus (pSTS)[12]. One important feature of the adult FFA and OFA is that these regions are activated automatically when viewing faces[16–20]. In contrast, activation of the pSTS is most closely associated with monitoring dynamic face changes such as movements in eye gaze and the mouth[21, 22].

Recruitment of regions in the “extended” face system tends to be relatively task-specific[12, 23]. For example, the amygdala, insula, and other limbic regions are most active when tasks require the analysis of emotion[24, 25]. The retrieval of semantic knowledge for faces (remembering the last movie Benedict Cumberbatch starred in when you see his face) may engage the inferior frontal gyrus, whereas episodic memory retrieval (e.g., remembering a person I met at a party last summer) may recruit the precuneus, posterior cingulate cortex, and medial temporal lobe[25]. Analysis of intentions (e.g., whether someone is threatening or welcoming you) can activate the region of the temporal-parietal junction, whereas processing attitudes and mental states (e.g., is someone trustworthy) recruits the anterior cingulate cortex[26]. The anterior temporal pole may be active in tasks requiring individuation of faces and biographical information retrieval [27]. In summary, the differential activation of extended face network brain regions stems from the fact that many face tasks require processing of a wide array of information beyond the general appearance of the face.

Overall, adult expertise for processing faces depends on activity within a complex network of brain regions. A central challenge for developmental scientists is documenting how this expertise develops through experience. If face expertise develops over an extended period, at what age does this ability reach adult levels, and is the development of the core and extended systems different? Functional imaging of the developing brain is beginning to answer these questions.

Behavioral observations of face processing across development

Within hours of birth, newborns show a preference for faces and can discriminate faces from other objects and abstract stimuli[28–33]. This preference for faces is driven by early visual preferences for bounded stimuli with more features on the top than on the bottom, and the presence of darker features on a lighter background[34–37]. There is a significant debate regarding whether such preferences for face-like characteristics stem from an innate predisposition that ensures that newborns orient to potential caregivers and social partners. However, the following overview of the developmental literature clearly shows that expert face processing abilities unfold over an extended time.

By 3–5 months of age, infants can identify faces using the specific features of faces (featural information) and the arrangement of those features on the face [38–40] , and by 6–10 months of age, infants categorize faces by gender, race, and attractiveness [41–43]. Expertise in face processing continues to develop over many years [44] , with the use of featural and configural cues developing well into the late childhood and the adolescent years [45–47]}. In addition, extraneous features such as clothing and hats easily distract children younger than 10 years of age when identifying individual faces [48–51]}. Thus, the behavioral data clearly show that the development of face processing expertise improves through childhood and into adolescence. Our next question concerns the relations between these behavioral changes and brain activity.

Electrophysiological measures of face processing

Electroencephalography records the summated synchronous electrical activity of neurons in the brain. While recording EEG activity, researchers can present stimuli to a subject over many trials and average the EEG response in a manner that is time-locked to the delivery of the stimuli; the resulting average is the event-related potential (ERP). Using this method, researchers discovered a specific electrical signature or marker of brain activity related to face processing. Specifically, researchers found a negative voltage deflection recorded at posterior scalp electrodes occurring approximately 170 ms after presentation of a face [52–54]. Figure 3B shows this “N170” waveform produced over posterior scalp sites in children and adults. Children show evidence of the N170 waveform, but it differs significantly from adults. Specifically, the N170 in children is delayed and smaller in amplitude, shifting in time and increasing in amplitude across development and reaching the adult form some time during the middle to late teen years[55–57]. Thus, age-related changes in this electrophysiological marker for face stimuli parallel the behavioral improvements in face processing expertise discussed above.

It has also been speculated that a developmental precursor to the more mature N170 is evident as two distinct components, rather than a single component, in infants. That is, during the first year of life, a negative and a positive voltage deflection at posterior scalp electrodes approximately 290 ms and 400 ms, respectively, become increasingly responsive to the typical viewpoint of a face in an upright orientation. By 12 months of age, the N290 is larger in amplitude and the P400 is longer in latency for inverted than for upright faces, reflective of older infants’ accumulated experience with faces typically viewed in upright orientations [58].

ERP studies in face perception have also found more widespread visually evoked responses over larger regions of the cortical surface in younger infants and children than in older infants and children, respectively[55, 59]. While such findings hint at broad spatial changes in brain function with development, EEG is not sufficiently sensitive to functional changes in closely spaced brain regions. Establishing functional brain changes with finer spatial resolution requires other functional imaging techniques such as FMRI.

FMRI measures of face processing

FMRI measures the blood oxygen-level dependent (BOLD) signal[60]. The BOLD signal is the result of a complex physiological interaction affecting the local ratio of red blood cells (hemoglobin) that contain oxygen versus those that have given up oxygen [61]. More simply, as a brain region responds to a stimulus, it signals the brain's vascular system to increase local blood flow, which peaks approximately 4–8 seconds after the stimulus, and thereby increases the locally available oxygen. The increased hemoglobin that contains oxygen, relative to hemoglobin that lacks oxygen, alters the local magnetic properties of the region and produces the increased BOLD signal, which is detected by the MRI scanner[62]. The complexity of the BOLD signal, and specifically its potential sensitivity changes across development, is a growing issue in developmental neuroscience. We briefly discuss this below.

The majority of developmental FMRI studies on face processing have focused primarily on activity within the core face network. The preponderance of evidence indicates that activity in the FFA can be observed in 5- to 7-year-old children[63–65]. However, the FFA shows an extended developmental trajectory that extends beyond late adolescence as measured by the volume of the fusiform gyrus[66, 67], the intensity of BOLD activation[63, 66, 68–70], and the spatial location of the FFA within the fusiform gyru[67]. Examples of FFA developmental changes are shown in Figure 4. A similarly prolonged developmental trajectory has been described for the other core face network areas of the OFA and superior temporal gyrus/ sulcus which may not be adult-like until mid-adolescence.

In addition to examining activation within isolated brain regions, researchers have become increasingly interested in *networks* of brain regions that work together to accomplish a given task. Functional connectivity analysis is a class of analytical techniques that seeks to establish how distributed regions of brain activity are organized into networks. Analysis of the core face network as a whole through the examination of functional connectivity, or the interaction between face preferential brain regions, also indicates that the developmental path to adult-like expertise in face processing extends into adolescence. Cohen Kadosh and colleagues[71] evaluated directional functional connectivity within the core face network. They scanned younger (7–8 years) and older (10–12 years) children and adults during tasks involving face identification, emotion detection, and gaze detection and found that the inferior occipital gyrus (i.e., occipital face area) exerted a separate influence on the FFA and STS in all three groups, suggesting that the OFA provides crucial information to support the perceptual processing in the other core regions. Furthermore, this finding suggested that an integrated core face network is functional in children as early as 7 years of age. However, the magnitude of effects differed among the children and adults. Specifically, children at both ages exhibited weaker connectivity between the inferior occipital gyrus (IOG) and the fusiform gyrus (FG), and no significant connectivity between the IOG and STS (see Figure 5A). Findings in even younger children between 3 to 6 years of age have also alluded to the presence of *additional* connectivity between the OFA and the contralateral FFA –

connections that are likely eliminated alongside a reorganization of brain function during development[72].

In addition to age differences in connectivity, the effects of task demand have been found to differentiate between children and adults[71]. Different tasks selectively modulated network patterns in adults: A face identity task has been found to increase the IOG's influence on the FFA, whereas an expression task increases the IOG's influence on the STS. In contrast, children have not shown such selective task effects. Thus, although the rudimentary structure of face processing networks is observable in young school-age children, the neural systems involved are not yet fully developed.

Our understanding of the developmental trajectories in the extended face network regions is still limited. Recently, Haist and colleagues[67] reported findings from a developmental FMRI study using regression analysis across a continuous sample of subjects spanning 7-year-olds to adults. They found wide-ranging hyperactivation of multiple regions of the extended face network in children that included the anterior temporal pole, amygdala, insula, inferior frontal gyrus, and lateral parietal cortex (see Figure 5B). These regions showed that younger participants produce greater activation than adults. These findings were interpreted as suggesting that the development of expertise in processing faces is characterized by improved ability to inhibit non-relevant information and thereby selectively recruit and engage only those areas of the extended network necessary for completing the specified task. Recall above that we described the various aspects of the extended face network in adults as activated in a task-specific fashion. For example, the amygdala is typically recruited in tasks requiring processing of emotion of faces and the anterior temporal pole recruited when identifying specific individuals. The findings from children suggest that this selective task-specific recruitment of extended face processing regions is acquired over an extended developmental period.

Studies focusing specifically on face processing in adolescence confirm the protracted nature of maturation in this domain. For example, Golarai and colleagues[69] found that the volume of the FFA in adolescents between 12 and 16 years had not reached the size of adults and that the changes in size positively correlated with age and with face recognition abilities. Scherf and colleagues[73] have proposed that an important mechanism driving face processing changes in adolescents is the presence of pubertal hormones critical for altering social and affective demands related to face processing. Such changes may drive alterations in functional network activity critical in developing social information processing systems.

There is no question that functional neuroimaging, and particularly FMRI using the BOLD signal, has revolutionized our appreciation of the dynamic nature of the development of face processing expertise from childhood until maturation in adulthood. Much is still to be learned. For example, work using a form of neuroimaging sensitive to biochemical and neurotransmitter concentrations called magnetic resonance spectroscopy (MRS, specifically ^{1}H-MRS) has shown that the balance of concentrations of excitatory and inhibitory neurotransmitters in lateral frontal cortex are related to face processing abilities, specifically face discrimination and recognition[74]. Namely, a greater concentration of glutamate, an excitatory neurotransmitter, relative to GABA, an inhibitory neurotransmitter, was positively correlated to face processing proficiency independent of gray matter density, suggesting that excitatory activity was linked to a greater capability for neuroplastic changes. Thus, our understanding of the complexity of brain-related changes related to face processing development will require multiple avenues of neuroimaging sensitive to the full range of changes supporting such development.

In addition, it is becoming increasingly clear that our current foundational neuroimaging measure, BOLD FMRI, may require refinement to address arising issues regarding potential changes in the sensitivity of the BOLD signal across development. The fundamental concept to keep in mind is that the BOLD signal is *indirectly* related to neural activation. Harris and colleagues[75] have noted myriad developmental factors that might affect the validity of contrasts using BOLD magnitude in developmental studies. They cited such factors as vascular and neuronal developmental trajectories, neurotransmitter responsiveness, and astrocyte developmental differences as potentially affecting baseline and stimulus modulated responsivity. Two[76, 77] recent studies appear to confirm the importance of this issue in demonstrating a negative relationship between cortical neural activities measured by estimates of oxygen metabolism and age, yet an insensitivity of the BOLD signal to this feature. That is, brain metabolism changes across age, indicating a negative correlation between neural activation and age, but the BOLD signal is relatively blind to these important changes[78, 79]. Thus, our current knowledge of face processing differences as measured by the BOLD signal will require continuous refinement as these findings become integrated with developmental changes in neurotransmitter levels and brain metabolism.

CONCLUSION

Modern functional brain imaging technologies are fundamentally changing our understanding of brain development and its links to changes in sensory, motor, perceptual, and cognitive abilities. In many cases, we now realize that structural brain changes that occur from birth through adulthood are accompanied by slowly developing brain function with an equally long trajectory. With regard to face processing, functional neuroimaging data clearly indicate that abilities begin early in development and have an extended developmental trajectory. Adult-like levels of face expertise are not obtained until middle-adolescence at the earliest. These effects cut across both the core and extended face networks. The findings inform our ideas about functional brain development across many domains; specifically, they suggest that experience shapes the connections that the brain makes between and within regions, and that connectivity changes are associated with increasingly refined brain activity that produces increasingly sophisticated perception, thought, and behavior.

It is important to note that our current methods only scratch the surface in informing our understanding of the specific brain activity supporting functional development. Brain development not only involves changes in brain size and connectivity, but also dynamic changes in the balance of excitatory and inhibitory influences on neural activity, the density of neurons and synapses, the blood circulatory system, the effects of neurotransmitters, as well as the development and function of glial cells[75, 77]. Each of these factors may fundamentally affect the precision of our functional brain measurements such that we are not appropriately comparing brain activity in children and adolescents with adults—that is, we may be less able to detect some aspects of brain activity in children, or we may be overestimating brain activity in adults. In other words, comparing children to adults with our current measures may sometimes be like comparing apples to oranges. To address these concerns, our functional imaging measures must continue to advance, increasing our ability to define the specific physiological changes that produce the functional brain signals that we measure. Thus, although we have learned a great deal about functional brain development through our use of neuroimaging technologies, there is much more work to be done before we achieve a deeper appreciation of the links between brain structure and function across early development.

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References

1. Azevedo FA, Carvalho LR, Grinberg LT, Farfel JM, Ferretti RE, Leite RE, Jacob Filho W, Lent R, Herculano-Houzel S. Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain. J Comp Neurol. 2009; 513:532–541. [PubMed: 19226510]
2. Giedd JN, Raznahan A, Alexander-Bloch A, Schmitt E, Gogtay N, Rapoport JL. Child psychiatry branch of the National Institute of Mental Health longitudinal structural magnetic resonance imaging study of human brain development. Neuropsychopharmacology. 2015; 40:43–49. [PubMed: 25195638]
3. Lenroot RK, Gogtay N, Greenstein DK, Wells EM, Wallace GL, Clasen LS, Blumenthal JD, Lerch J, Zijdenbos AP, Evans AC, et al. Sexual dimorphism of brain developmental trajectories during childhood and adolescence. Neuroimage. 2007; 36:1065–1073. [PubMed: 17513132]
4. Dekaban AS. Changes in brain weights during the span of human life: relation of brain weights to body heights and body weights. Ann Neurol. 1978; 4:345–356. [PubMed: 727739]
5. Riccomagno MM, Kolodkin AL. Sculpting neural circuits by axon and dendrite pruning. Annu Rev Cell Dev Biol. 2015; 31:779–805. [PubMed: 26436703]
6. Innocenti GM, Price DJ. Exuberance in the development of cortical networks. Nat Rev Neurosci. 2005; 6:955–965. [PubMed: 16288299]
7. Cohen Kadosh K. What can emerging cortical face networks tell us about mature brain organisation? Dev Cogn Neurosci. 2011; 1:246–255. [PubMed: 22436510]
8. Bodamer J. Die Proso-Agnosie. Archiv für Psychiatrie und Nervenkrankheiten. 1947; 179:6–53.
9. Meadows JC. The anatomical basis of prosopagnosia. J Neurol Neurosurg Psychiatry. 1974; 37:489–501. [PubMed: 4209556]
10. Tsao DY, Livingstone MS. Mechanisms of face perception. Annual Review of Neuroscience. 2008; 31:411–437.
11. Kanwisher N, Yovel G. The fusiform face area: a cortical region specialized for the perception of faces. Philos Trans R Soc Lond B Biol Sci. 2006; 361:2109–2128. [PubMed: 17118927]
12. Haxby JV, Hoffman EA, Gobbini MI. The distributed human neural system for face perception. Trends Cogn Sci. 2000; 4:223–233. [PubMed: 10827445]
13. Behrmann M, Avidan G. Congenital prosopagnosia: face-blind from birth. Trends Cogn Sci. 2005; 9:180–187. [PubMed: 15808500]
14. Gauthier I, Tarr MJ, Moylan J, Anderson AW, Skudlarski P, Gore JC. Does visual subordinate-level categorisation engage the functionally defined fusiform face area? Cogn Neuropsychol. 2000; 17:143–164. [PubMed: 20945177]

15. Rossion B, Caldara R, Seghier M, Schuller AM, Lazeyras F, Mayer E. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. Brain. 2003; 126:2381–2395. [PubMed: 12876150]
16. Yovel G, Kanwisher N. The neural basis of the behavioral face-inversion effect. Current Biology. 2005; 15:2256–2262. [PubMed: 16360687]
17. Morris JP, Pelphrey KA, McCarthy G. Face processing without awareness in the right fusiform gyrus. Neuropsychologia. 2007; 45:3087–3091. [PubMed: 17643452]
18. Haist F, Lee K, Stiles J. Individuating faces and common objects produces equal responses in putative face-processing areas in the ventral occipitotemporal cortex. Front Hum Neurosci. 2010; 4:181. [PubMed: 21206532]
19. Grill-Spector K, Knouf N, Kanwisher N. The fusiform face area subserves face perception, not generic within-category identification. Nat Neurosci. 2004; 7:555–562. [PubMed: 15077112]
20. Gauthier I, Curby KM, Skudlarski P, Epstein RA. Individual differences in FFA activity suggest independent processing at different spatial scales. Cogn Affect Behav Neurosci. 2005; 5:222–234. [PubMed: 16180628]
21. Ishai A, Schmidt CF, Boesiger P. Face perception is mediated by a distributed cortical network. Brain Res Bull. 2005; 67:87–93. [PubMed: 16140166]
22. Rolls ET. The representation of information about faces in the temporal and frontal lobes. Neuropsychologia. 2007; 45:124–143. [PubMed: 16797609]
23. Ishai A. Let's face it: it's a cortical network. Neuroimage. 2008; 40:415–419. [PubMed: 18063389]
24. Ishai A, Pessoa L, Bikle PC, Ungerleider LG. Repetition suppression of faces is modulated by emotion. Proc Natl Acad Sci U S A. 2004; 101:9827–9832. [PubMed: 15210952]
25. Gobbini MI, Haxby JV. Neural systems for recognition of familiar faces. Neuropsychologia. 2007; 45:32–41. [PubMed: 16797608]
26. Redcay E, Dodell-Feder D, Pearrow MJ, Mavros PL, Kleiner M, Gabrieli JD, Saxe R. Live face-to-face interaction during fMRI: a new tool for social cognitive neuroscience. Neuroimage. 2010; 50:1639–1647. [PubMed: 20096792]
27. Nestor A, Plaut DC, Behrmann M. Unraveling the distributed neural code of facial identity through spatiotemporal pattern analysis. Proceedings of the National Academy of Sciences of the United States of America. 2011; 108:9998–10003. [PubMed: 21628569]
28. Mondloch CJ, TLL, Budreau DR, Maurer D, Dannemiller JL, Stephens BR, KAK-G. Face perception during early infancy. Psychological Science. 1999; 10:419–422.
29. Maurer D, Young RE. Newborn's following of natural and distorted arrangements of facial features. Infant Behavior and Development. 1983; 6:127–131.
30. Macchi Cassia V, Simion F, Umilta C. Face preference at birth: The role of an orienting mechanism. Developmental Science. 2001; 4:101–108.
31. Goren CC, Sarty M, Wu PY. Visual following and pattern discrimination of face-like stimuli by newborn infants. Pediatrics. 1975; 56:544–549. [PubMed: 1165958]
32. Fantz RL. Pattern Vision in Newborn Infants. Science. 1963; 140:296–297. [PubMed: 17788054]
33. Johnson MH, Dziurawiec S, Ellis H, Morton J. Newborns' preferential tracking of face-like stimuli and its subsequent decline. Cognition. 1991; 40:1–19. [PubMed: 1786670]
34. Turati C, Simion F, Milani I, Umilta C. Newborns' preference for faces: What is crucial? Developmental Psychology. 2002; 38:875–882. [PubMed: 12428700]
35. Simion F, Valenza E, Cassia VM, Turati C, Umilta C. Newborns' preference for up-down asymmetrical configurations. Developmental Science. 2002; 5:427–434.
36. Farroni T, Johnson MH, Menon E, Zulian L, Faraguna D, Csibra G. Newborns' preference for face-relevant stimuli: effects of contrast polarity. Proc Natl Acad Sci U S A. 2005; 102:17245–17250. [PubMed: 16284255]
37. Cassia VM, Turati C, Simion F. Can a nonspecific bias toward top-heavy patterns explain newborns' face preference? Psychological Science. 2004; 15:379–383. [PubMed: 15147490]
38. Bhatt RS, Bertin E, Hayden A, Reed A. Face processing in infancy: developmental changes in the use of different kinds of relational information. Child Dev. 2005; 76:169–181. [PubMed: 15693765]

39. Hayden A, Bhatt RS, Reed A, Corbly CR, Joseph JE. The development of expert face processing: are infants sensitive to normal differences in second-order relational information? J Exp Child Psychol. 2007; 97:85–98. [PubMed: 17339043]

40. Quinn PC, Tanaka JW. Infants' Processing of Featural and Configural Information in the Upper and Lower Halves of the Face. Infancy. 2009; 14:474–487.

41. Anzures G, Quinn PC, Pascalis O, Slater AM, Lee K. Categorization, categorical perception, and asymmetry in infants' representation of face race. Dev Sci. 2010; 13:553–564. [PubMed: 20590720]

42. Ramsey JL, Langlois JH, Hoss RA, Rubenstein AJ, Griffin AM. Origins of a stereotype: categorization of facial attractiveness by 6-month-old infants. Developmental Science. 2004; 7:201–211. [PubMed: 15320380]

43. Younger BA, Fearing DD. Parsing items into separate categories: Developmental change in infant categorization. Child Development. 1999; 70:291–303.

44. Lee, K.; Anzures, G.; Quinn, PC.; Pascalis, O.; Slater, AM. Development of face processing expertise. In: Calder, A.; Rhodes, G.; Johnson, MH.; Haxby, JV., editors. Handbook of face perception. Oxford, UK: Blackwell Publishing; 2011. p. 753-778.

45. Liu S, Anzures G, Ge L, Quinn PC, Pascalis O, Slater AM, Tanaka JW, Lee K. Development of Recognition of Face Parts from Unfamiliar Faces. Infant Child Dev. 2013; 22:165–179. [PubMed: 24009474]

46. Mondloch CJ, Geldart S, Maurer D, Le Grand R. Developmental changes in face processing skills. J Exp Child Psychol. 2003; 86:67–84. [PubMed: 12943617]

47. Mondloch CJ, Le Grand R, Maurer D. Configural face processing develops more slowly than featural face processing. Perception. 2002; 31:553–566. [PubMed: 12044096]

48. Carey S, Diamond R. From piecemeal to configurational representation of faces. Science. 1977; 195:312–314. [PubMed: 831281]

49. Diamond R, Carey S. Developmental changes in the representation of faces. J Exp Child Psychol. 1977; 23:1–22. [PubMed: 839154]

50. Freire A, Lee K. Face recognition in 4- to 7-year-olds: processing of configural, featural, and paraphernalia information. J Exp Child Psychol. 2001; 80:347–371. [PubMed: 11689035]

51. Freire A, Lee K, Williamson KS, Stuart SJ, Lindsay RC. Lineup identification by children: effects of clothing bias. Law Hum Behav. 2004; 28:339–354. [PubMed: 15264450]

52. Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological Studies of Face Perception in Humans. J Cogn Neurosci. 1996; 8:551–565. [PubMed: 20740065]

53. Eimer M. The face-specific N170 component reflects late stages in the structural encoding of faces. Neuroreport. 2000; 11:2319–2324. [PubMed: 10923693]

54. Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S, Crommelinck M. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. Neuroreport. 2000; 11:69–74. [PubMed: 10683832]

55. Taylor MJ, Batty M, Itier RJ. The faces of development: A review of early face processing over childhood. Journal of Cognitive Neuroscience. 2004; 16:1426–1442. [PubMed: 15509388]

56. Itier RJ, Taylor MJ. Face recognition memory and configural processing: a developmental ERP study using upright, inverted, and contrast-reversed faces. J Cogn Neurosci. 2004; 16:487–502. [PubMed: 15072683]

57. Taylor MJ, McCarthy G, Saliba E, Degiovanni E. ERP evidence of developmental changes in processing of faces. Clinical Neurophysiology. 1999; 110:910–915. [PubMed: 10400205]

58. Halit H, de Haan M, Johnson MH. Cortical specialisation for face processing: face-sensitive event-related potential components in 3- and 12-month-old infants. Neuroimage. 2003; 19:1180–1193. [PubMed: 12880843]

59. de Haan M, Johnson MH, Halit H. Development of face-sensitive event-related potentials during infancy: a review. Int J Psychophysiol. 2003; 51:45–58. [PubMed: 14629922]

60. Ogawa S, Lee TM, Kay AR, Tank DW. Brain magnetic resonance imaging with contrast dependent on blood oxygenation. Proc Natl Acad Sci U S A. 1990; 87:9868–9872. [PubMed: 2124706]

61. Buxton RB. The physics of functional magnetic resonance imaging (fMRI). Rep Prog Phys. 2013; 76:096601. [PubMed: 24006360]
62. Fox PT, Raichle ME. Focal physiological uncoupling of cerebral blood flow and oxidative metabolism during somatosensory stimulation in human subjects. Proc Natl Acad Sci U S A. 1986; 83:1140–1144. [PubMed: 3485282]
63. Scherf KS, Behrmann M, Humphreys K, Luna B. Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. Dev Sci. 2007; 10:F15–30. [PubMed: 17552930]
64. Pelphrey KA, Lopez J, Morris JP. Developmental continuity and change in responses to social and nonsocial categories in human extrastriate visual cortex. Front Hum Neurosci. 2009; 3:25. [PubMed: 19826492]
65. Cantlon JF, Pinel P, Dehaene S, Pelphrey KA. Cortical representations of symbols, objects, and faces are pruned back during early childhood. Cereb Cortex. 2011; 21:191–199. [PubMed: 20457691]
66. Golarai G, Ghahremani DG, Whitfield-Gabrieli S, Reiss A, Eberhardt JL, Gabrieli JD, Grill-Spector K. Differential development of high-level visual cortex correlates with category-specific recognition memory. Nat Neurosci. 2007; 10:512–522. [PubMed: 17351637]
67. Haist F, Adamo M, Han Wazny J, Lee K, Stiles J. The functional architecture for face-processing expertise: FMRI evidence of the developmental trajectory of the core and the extended face systems. Neuropsychologia. 2013; 51:2893–2908. [PubMed: 23948645]
68. Joseph JE, Gathers AD, Bhatt RS. Progressive and regressive developmental changes in neural substrates for face processing: testing specific predictions of the Interactive Specialization account. Dev Sci. 2011; 14:227–241. [PubMed: 21399706]
69. Golarai G, Liberman A, Yoon JM, Grill-Spector K. Differential development of the ventral visual cortex extends through adolescence. Front Hum Neurosci. 2010; 3:80. [PubMed: 20204140]
70. Peelen MV, Glaser B, Vuilleumier P, Eliez S. Differential development of selectivity for faces and bodies in the fusiform gyrus. Dev Sci. 2009; 12:F16–25. [PubMed: 19840035]
71. Cohen Kadosh K, Cohen Kadosh R, Dick F, Johnson MH. Developmental changes in effective connectivity in the emerging core face network. Cereb Cortex. 2011; 21:1389–1394. [PubMed: 21045001]
72. He W, Garrido MI, Sowman PF, Brock J, Johnson BW. Development of effective connectivity in the core network for face perception. Hum Brain Mapp. 2015; 36:2161–2173. [PubMed: 25704356]
73. Scherf KS, Behrmann M, Dahl RE. Facing changes and changing faces in adolescence: a new model for investigating adolescent-specific interactions between pubertal, brain and behavioral development. Dev Cogn Neurosci. 2012; 2:199–219. [PubMed: 22483070]
74. Cohen Kadosh K, Krause B, King AJ, Near J, Cohen Kadosh R. Linking GABA and glutamate levels to cognitive skill acquisition during development. Hum Brain Mapp. 2015; 36:4334–4345. [PubMed: 26350618]
75. Harris JJ, Reynell C, Attwell D. The physiology of developmental changes in BOLD functional imaging signals. Dev Cogn Neurosci. 2011; 1:199–216. [PubMed: 22436508]
76. Jog MA, Yan L, Kilroy E, Krasileva K, Jann K, LeClair H, Elashoff D, Wang DJ. Developmental trajectories of cerebral blood flow and oxidative metabolism at baseline and during working memory tasks. Neuroimage. 2016; 134:587–596. [PubMed: 27103136]
77. Schmithorst VJ, Vannest J, Lee G, Hernandez-Garcia L, Plante E, Rajagopal A, Holland SK. Consortium CA. Evidence that neurovascular coupling underlying the BOLD effect increases with age during childhood. Hum Brain Mapp. 2015; 36:1–15. [PubMed: 25137219]
78. Moses P, DiNino M, Hernandez L, Liu TT. Developmental changes in resting and functional cerebral blood flow and their relationship to the BOLD response. Hum Brain Mapp. 2014; 35:3188–3198. [PubMed: 24142547]
79. Moses P, Hernandez LM, Orient E. Age-related differences in cerebral blood flow underlie the BOLD fMRI signal in childhood. Front Psychol. 2014; 5:300. [PubMed: 24795666]
80. Churchland PS, Sejnowski TJ. Perspectives on cognitive neuroscience. Science. 1988; 242:741–745. [PubMed: 3055294]

FURTHER READINGS

81. Dalrymple KA, Corrow S, Yonas A, Duchaine B. Developmental prosopagnosia in childhood. Cognitive Neuropsychology. 2012; 29:393–418. DOI: 10.1080/02643294.2012.722547 [PubMed: 23140142]
82. de Haan M, Humphreys K, Johnson MH. Developing a brain specialized for face perception: a converging methods approach. Developmental Psychobiology. 2002; 40:200–212. [pii]. DOI: 10.1002/dev.10027 [PubMed: 11891633]
83. Vanderwert RE, Nelson CA. The use of near-infrared spectroscopy in the study of typical and atypical development. Neuroimage. 2014; 85:264–271. DOI: 10.1016/j.neuroimage.2013.10.009 [PubMed: 24128733]

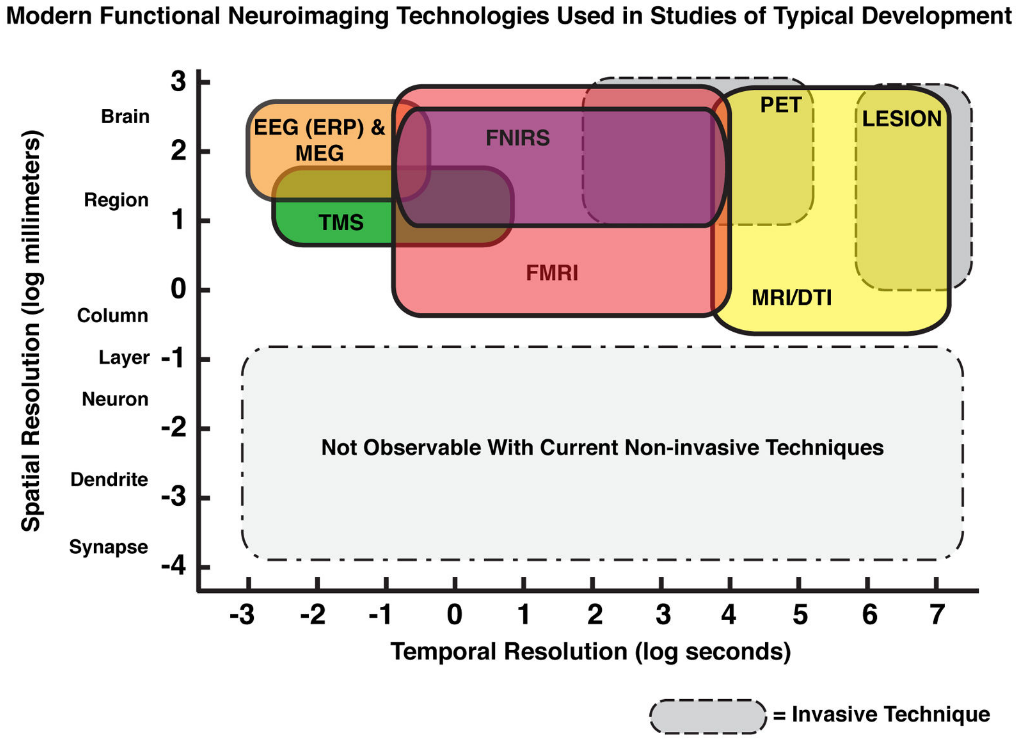

Figure 1.

Description of commonly used non-invasive imaging techniques in terms of their spatial (in millimeters) and temporal (in seconds) resolution. Electroencephalographic (EEG) and the signal-averaged EEG measure of event-related potentials (ERP) measures, and the closely related magnetoencephalography (MEG) measures have very good temporal resolution, but limited spatial resolution. That means they can distinguish different brain events with millisecond accuracy, but are relatively limited in defining the precise location of the activity in the brain. Functional magnetic resonance imaging (FMRI) and a technique called functional near-infrared spectroscopy (FNIRS), a technique that uses near-infrared light to observe underlying brain activity, provide exceptional spatial resolution but are less precise in defining the timing of brain events. Thus, to understand functional brain development with good spatial and temporal resolution, multiple techniques must be used in combination. Although not directly measuring brain function, traditional magnetic resonance imaging (MRI) measures of brain development such as brain volume and cortical thickness, and diffusion tensor imaging (DTI) that can measure white matter changes, may be correlated with behavioral measures (e.g., IQ, face processing accuracy) to make structure-functional associations. Two highly invasive techniques, the study of permanent brain lesions acquired in development and positron emission tomography (PET), a functional brain imaging technique that requires the injection of radioactive substances to obtain it measures are shown to illustrate the functional imaging space they cover. Note that fine resolution imaging using non-invasive techniques is currently not possible for developmental populations. Adapted from Churchland and Sejnowski[80].

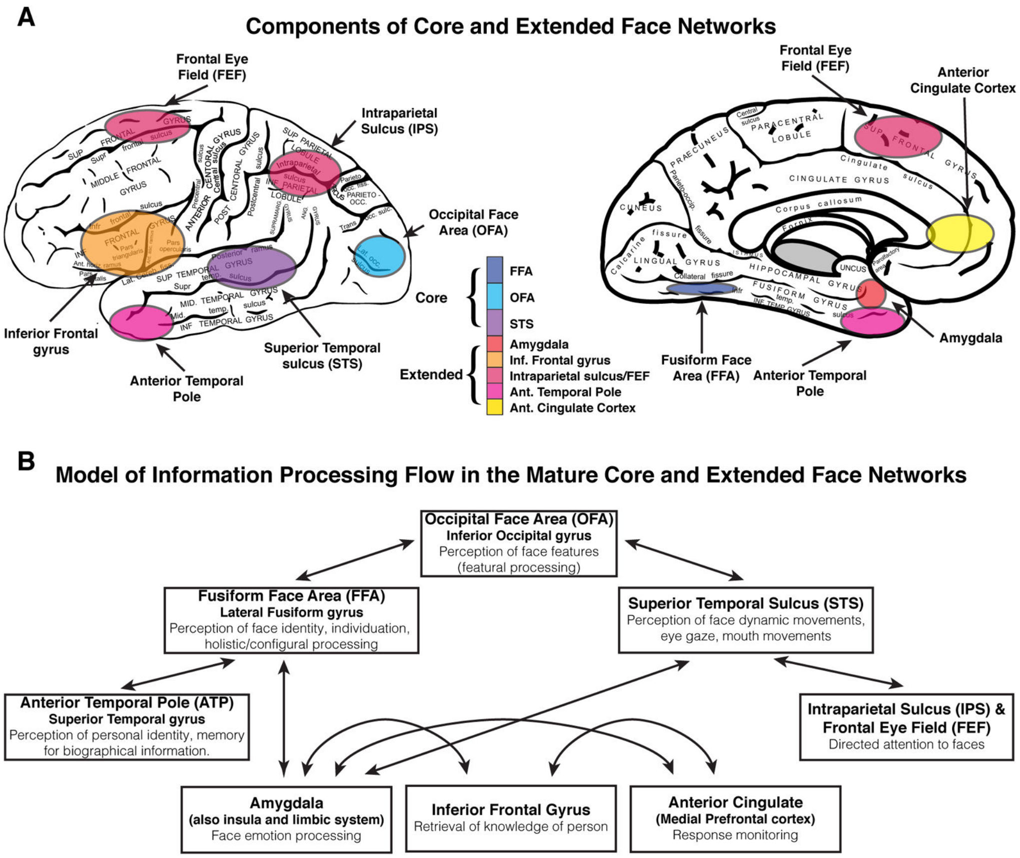

Figure 2.

Description of the core and extended face networks. *A*) Schematic of various regions associated with the core (cooler colors) and extended (warmer colors) face networks. Core face network regions, particularly the fusiform face area (FFA) and occipital face area (OFA), are activated automatically in response to viewing a face. Extended network regions tend to be activated on a task-specific basis. For example, the amygdala and limbic regions may be activated during tasks that require analysis of face emotion. *B*) Diagram of information flow between regions in the core and extended regions and brief descriptions of the role of the different regions in face processing. Adapted from Haxby et al.[12].

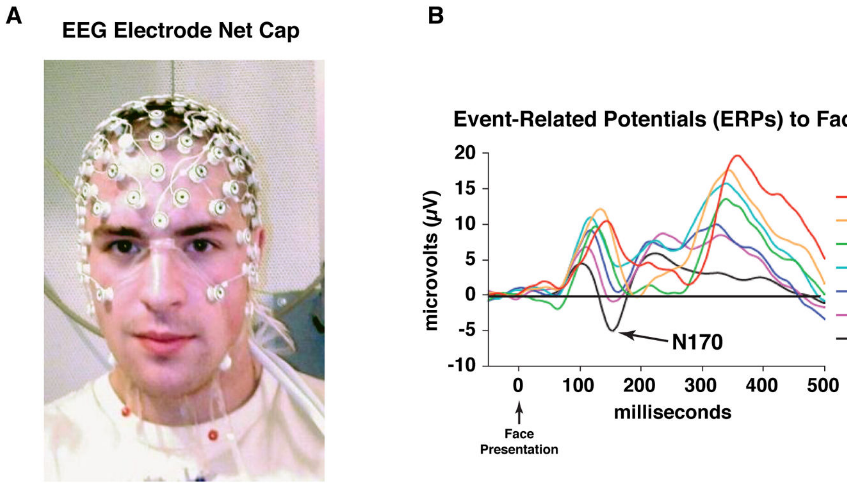

Figure 3.

EEG and ERP in face processing studies of development. *A*) Example of electrode placement in the scalp for typical EEG and ERP studies (source: https://commons.wikimedia.org/wiki/File:EEG_cap.jpg). *B*) Findings from developmental studies of a face-specific ERP component sensitive to processing faces, the N170, a negative voltage wave with a peak in adults at about 170 milliseconds after the presentation of a face. The N170 shows that face processing expertise develops gradually across development not reaching mature levels until early adulthood. From Taylor et al.[55].

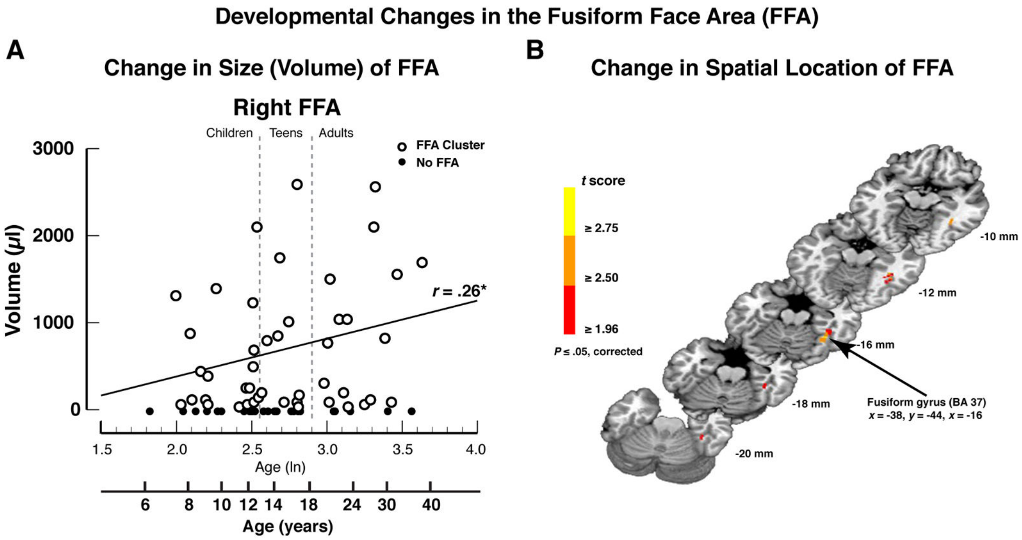

Figure 4.

FMRI evidence of development of the fusiform face area (FFA) across development. *A*) Changes in the size of the right hemisphere FFA, the dominant brain hemisphere for face processing, across development measured as the volume of the fusiform gyrus that was more active to face than objects. From age 6 years through adulthood, the FFA gradually increases in size. The correlation between age and FFA size is shown in the regression line. Open circles indicate participants (N=71) that showed a detectable FFA and closed circles show the participants that did not produce a reliable FFA. *B*) Developmental changes in the location of the FFA. Regions in warm colors indicated the region in the fusiform gyrus that became more consistently associated with face processing in adults relative to children. No regions were observed as consistently active in children but not adults. This suggests that the FFA location in children is more variable than in adults. From Haist et al.[67].

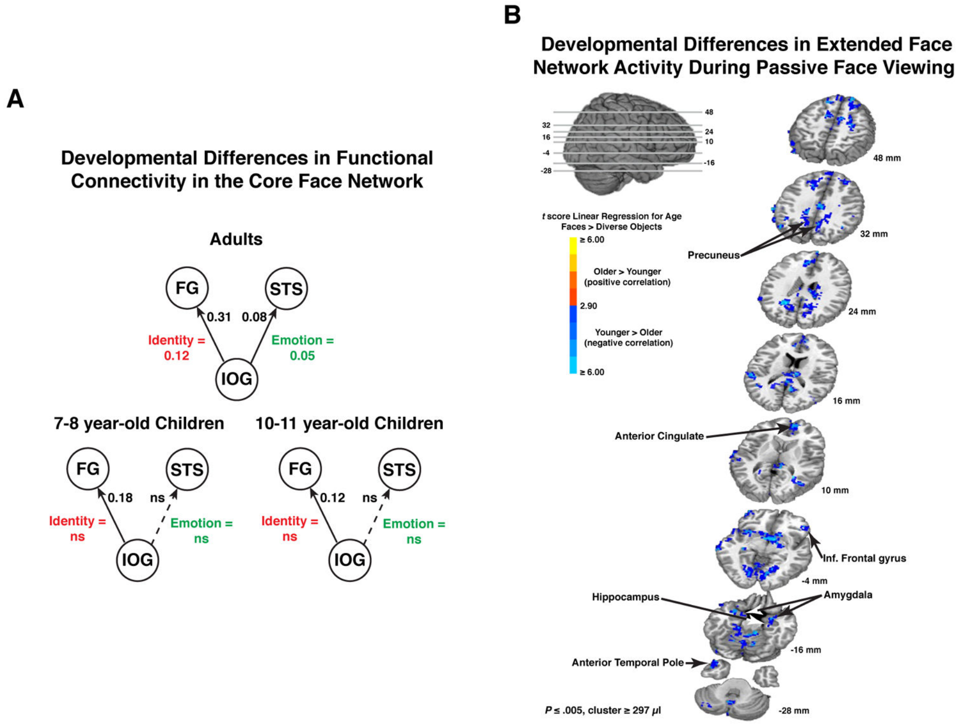

Figure 5.

Examples of FFA functional connectivity and activation of the extended face network across development. *A*) Findings from a study of functional connectivity within the core face network for children and adult. Here, functional connectivity is measured by a specialized statistical technique that examines how information flows from one region to another[71]. The abbreviations stand for: FG = fusiform gyrus in the region of the fusiform face area (FFA); IOG = inferior occipital gyrus in the region of the occipital face area (OFA); STG = superior temporal gyrus. The researchers tested participants in each group with tasks that asked them to identify an individual, to judge the emotion expression in a face, and to judge the direction of eye gaze. They calculated the strength of the connection between the core network regions as an estimate of how much each region depends on the information from other regions feeding into it. In this example, the FG region is highly dependent on information from the IOG in all three groups (solid lines). However, as signified by the values next to the lines, which is a measure of the strength of the connection between IOG and FG, both child groups displayed weaker connectivity compared to adults. In the emotion task, the connection between IOG and STG in children was not reliable (ns = not significant), whereas this connection was significant in adults (solid line). Overall, the findings suggest that certain aspects of the core network are integrated in childhood, but not with the strength seen in adults, and other aspects of the network are not integrated in childhood. Thus, functional connectivity in the extended network has a protracted developmental trajectory that extends beyond the 10–11 year old range that was tested. *B*) Findings from face specific processing regions across the whole brain when children, adolescents, and adults viewed face passively. Regions in blue indicate activity that was greater in children than adults. Children showed greater activation than adults in many extended face processing regions. Adults are expected to activate regions in the extended network to match task demands. In this passive viewing task, there were no explicit demands that should invoke such processing. The fact children activate these regions suggests children do not modulate extended face network activity as efficiently as adults, consistent with the proposal that such modulation is the result of face processing expertise that takes an extended period to develop. From Haist et al.[67].