

Behavioral and Neural Representation of Emotional Facial Expressions Across the Lifespan

Leah H. Somerville

Sackler Institute for Developmental Psychobiology, Weill Medical College of Cornell University, New York, New York

Negar Fani and Erin B. McClure-Tone

Department of Psychology, Georgia State University, Atlanta, Georgia

Humans' experience of emotion and comprehension of affective cues varies substantially across the lifespan. Work in cognitive and affective neuroscience has begun to characterize behavioral and neural responses to emotional cues that systematically change with age. This review examines work to date characterizing the maturation of facial expression comprehension, and dynamic changes in amygdala recruitment from early childhood through late adulthood while viewing facial expressions of emotion. Recent neuroimaging work has tested amygdala and prefrontal engagement in experimental paradigms mimicking real aspects of social interactions, which we highlight briefly, along with considerations for future research.

The ability to communicate our own emotions and to understand the emotions of others is critical to the human experience. An observed emotional response provides a wealth of information relating to another individual's needs, communicating whether they are joyous or suffering, in need of assistance, or should be avoided. We are also able to garner important information regarding our own relative state of safety or threat from the emotional reactions of others. If we see another individual who is afraid, we can extrapolate that perhaps we too ought to be vigilant toward a potential threat.

One primary means of emotional communication is the display of emotional expressions on the face. Facial expressions are widely recognized as one of the most basic and universal methods of communicating one's internal affective state (Ekman & Oster, 1979). It is not surprising then, that facial expressions of emotion have been used ubiquitously as experimental stimuli in psychological and neuroscientific research aimed at elucidating the behavioral and neural substrates of emotion processing. They are fairly well-controlled in terms of visual characteristics, and many sets have been normalized for physical and emotional properties. Additionally, they

This work was supported by NIDA grant DA007274 (LHS) and Georgia State University Brains and Behavior Fellowship (NF).

Correspondence should be addressed to Leah H. Somerville, Ph.D., Sackler Institute for Developmental Psychobiology, Weill Cornell Medical College of Cornell University, 1300 York Avenue, Box 140, New York, NY 10065. E-mail: lhs2003@med.cornell.edu

are generally tolerated as emotional stimuli, making them suitable for experimental use with individuals of all ages. As such, an impressive literature has amassed using facial expressions as probes to interrogate psychological and neurological emotion processing systems.

These research efforts have provided important evidence regarding general emotion processing, its neural substrates, and its developmental timecourse. The present review examines important shifts in the experience and expression of emotion across the lifespan, and its supported neural correlates, from infancy through late adulthood. We focus primarily on studies using facial expressions of emotion due to the wealth of research employing these stimuli across age groups that has amassed to date. Table 1 outlines developmental neuroimaging experiments to date (literature review conducted in summer of 2008) that have utilized facial expressions of emotion to characterize the neural correlates of emotional processing; many of these studies are also highlighted in the main text. The experiments listed have either tested a single age group outside of the typical young adult demographic or compared neural responsivity across more than one age group. It should be noted that Table 1 includes sample demographics such as age and gender, a brief description of the stimuli and task(s) employed, and the primary findings with special emphasis on age differences in amygdala responsivity. Due to space limitations, we were unable to include work on autism in the present review, despite its inherent relevance to this topic. In addition, we are not able to discuss developmental work involving other psychiatric populations, although we do include a partial listing of these experiments in Table 1.

Finally, we recognize that more complex emotional processes, often involving social interactions or contexts, are of critical interest across development as well, and are an interesting topic for current and future research. Therefore, we highlight the results of some recent experiments that use more ecologically valid and socially relevant paradigms to examine the development of social and emotional processes in the brain.

THE DEVELOPMENT OF FACIAL EXPRESSION PROCESSING

Although facial expressions are argued to be among the most “basic” forms of emotional communication, it would be incorrect to assume that emotional expressions are decoded and comprehended perfectly from birth. A body of research has accumulated to characterize the acquisition of different expression recognition abilities across development. This section will briefly address the development of each of these stages of facial emotion recognition, and we refer readers to more comprehensive accounts of these issues that have been published elsewhere (Herba & Phillips, 2004; Nelson, 1987; Walker-Andrews, 1997).

Evidence suggests that around three months of age, infants’ ability to focus sight begins to approach maturity (Banks, 1980). Prior to this developmental landmark, infants likely rely on high-contrast features that may permit the detection of face-like shapes (Campos & Sternberg, 1981) but may not support the discrimination of distinct emotional expressions (for a review, see Nelson, 1987). Slightly later, infants show reliable changes in their behavior in response to viewing different emotional expressions. A creative experiment by Montague and colleagues (Montague & Walker-Andrews, 2001) measured looking time and imitation in infants during a “peek-a-boo” game. Each time the experimenter uncovered her face, she configured it into a happy, sad, fearful, or angry expression. Reliable differences in looking time as a function of expression provided evidence that infants as young as four months of age can discriminate between expressions, consistent with other reports (Field, Woodson, Greenberg, & Cohen, 1982;

TABLE 1
Summary of Studies of Emotion Processing Across Development

<i>Study</i>	<i>Participant Group(s)</i>	<i>Age M (SD)</i>	<i>Age Range (years)</i>	<i>N (% female)</i>	<i>Emotional Expressions Studied</i>	<i>Task</i>	<i>Amygdala Activation</i>	<i>Other Findings</i>
Hare et al. (2005)	Child Adol Adult	9.1 ± 1.6 16.0 ± 1.5 23.9 ± 3.0	7–32	60 (50)	F, H	emotional Go/No-Go	Adol > adults Adol > children	Adol: <PFC correlated with >AMG
Williams et al. (2006)	Adol YA MA OA	16.1 (NR) 24.8 (NR) 39.7 (NR) 59.3 (NR)	12–79	80 (50)	F, H, N	sex discrimination	F vs N: response > in YA relative to other groups, lowest in OA H vs N: response > in Adol, YA relative to MA, OA	H vs. N: mPFC ↓ with age
Thomas et al. (2001a)	Child Adult	11 ± 2.4 24 ± 6.6	8.6–30.6	18 (NR)	F, N	passive viewing	Child: N>F Adults: F>N	
Guyer et al. (2008)	Adol Adult	14.2 ± 2.4 31.1 ± 4.7	9–40	61 (46)	F, H, A, N	passive viewing	F: adol > adults	F: adol > adults in fusiform gyrus Adults: greater amygdala-hippocampus functional connectivity than adol
Pine et al. (2001)	Adol Adult	13.9 ± 1.4 28.5 ± 4.3	12–38	20 (50)	H, F (masked)	passive viewing	Null	Adol: H>F in posterior association cortex
Monk et al. (2003)	Adol Adult	13.1 ± 2.6 30.8 ± 3.1	9–36	34 (47)	F, H, A, N	rate fear/nose width, passive viewing	F vs N: Adol > Adults during passive view	F vs. N during nose width ratings: Adol > Adults in ACC F fear rate vs. F nose rate: Adults > Adol in OFC
McClure et al. (2004)	Adol	13.1 ± 2.6	9–36	34 (47)	F, H, A, N	“how hostile?”	A vs F: Adult females > males and adolescents	A vs. F: Adult females > males in OFC
Nelson et al. (2003)	Adult Adol Adult	30.8 ± 3.1 13.1 ± 2.6 30.8 ± 3.1	9–36	34 (NR)	F, H, A, N	rate hostile/fear/nose width	Null	Adol & Adults: left VLPFC activity predicted subsequent memory for faces

Fischer et al. (2005)	YA OA	24.7 ± 2.8 74.1 ± 3.8	20–80	46 (49)	A, N	passive viewing	A vs N: YA>OA	A vs. N: OA>YA in right insula
Iidaka et al. (2002)	YA OA	25.1 ± 5.0 65.2 ± 2.6	19–72	24 (50)	F, H, A, N, D, S, shapes	gender matching/ shape matching	Negative faces: YA>OA Within YA: Significant activity to all face conditions Within OA: Null to all face conditions	Positive faces: YA>OA in parahippocampal gyrus, lingual gyrus and angular gyrus
Gunning-Dixon et al. (2003)	YA OA	25.8 ± 3.1 72.3 ± 7.6	19–79	16 (50)	F, H, A D, S, N	emotion (+ or –) or age (</> 30) discrimination	Emotion vs. age discrimination: YA showed response, OA did not	Emotion discrimination compared to baseline & age discrimination: OA>YA in PFC
Keightley et al. (2007)	YA OA	27.2 ± 2.4 69.6 ± 9.2	NR	21 (52)	F, H, A, S, Su, D, N	emotion identification	H: YA>OA Within OA: Null to all face conditions	OA vs. YA: H, D > VMPFC, lingual gyrus and premotor cortex; F,A, S, N > dorsal ACC, frontal and temporal gyri, insula
Tessitore et al. (2005)	YA	25 ± 2.9	20–80	27 (48)	F, A	face and shape matching	F and A: right AMG response > for YA vs OA	OA>YA: mPFC and VLPFC
Grosbras et al. (2007)	OA Child	67 ± 6.2 10 ± 4.4	9.4–10.8	46 (48)	A, N (+ A, N hand move- ments)	passive view	Null	YA>OA: fusiform gyri > recruitment of lateral PFC in subjects ↑ resistant to peer influence while viewing angry faces and movements
Lobaugh et al. (2006)	Child	10.3 ± .6	10–12	10 (40)	F, H, A, S, Su, D, N	sex discrimination	D > other expressions	Typical adult cortical neural responses (but no direct comparison with adult data)
Kilgore et al. (2001)	Child-Adol	13.5 ± 2.1	9–17	19 (53)	F	passive viewing	Males: null Females: < Left AMG response correlated with >age	Males: >age correlated with <left DLPFC response >left DLPFC – left AMG difference in activation correlated with >age

(Continued)

TABLE 1
(Continued)

Study	Participant Group(s)	Age M (SD)	Age Range (years)	N (% female)	Emotional Expressions Studied	Task	Amygdala Activation	Other Findings
Yurgelun-Todd & Killgore (2006)	Child-Adol	11.6 ± 2.1	8–15	16 (44)	F, H	passive viewing	Null	Age correlated positively with > MFG/SFG, Females: > age correlated with > bilateral PFC Males: > age correlated with > right PFC
Killgore & Yurgelun-Todd (2005)	Child-Adol	11.6 ± 2.1	8–15	16 (44)	F, H	passive viewing	F > baseline	
Thomas et al. (2001b)**	Anxious MDD Control Adol	12.8 ± 2.1 12.3 ± 2.7 12.1 ± 2.6 13.9 (NR)	8–16	29 (52)	F, N	passive viewing	Correlated positively with social anxiety F > N in anxious vs. controls & MDD F < fixation in MDD F > baseline	
Baird et al. (1999)	GAD Control	11.7 ± 2 12.19 ± 2.1	9–17	35 (51)	F, H, A, N	rate hostile/fear/nose width oddball	F rate fear: GAD pts > controls S > N	> VMPPFC activation to sad distracters, not found in adults in previous study (Wang et al., 2005)
McClure et al. (2007a)**	Child-Adol	11.9 ± 1.9	10–15	10 (50)	S, N (faces in scenes) + faces	gender judgment	S > H	H > S engaged more dorsal ACC regions while S > H engaged ventral/anterior ACC
Wang et al. (2006)	Child-Adol	12.3 ± 3.0	9–17	10 (80)	S, H (masked by N)	rate hostile/fear/nose width/passive viewing	Rate fear: BI > NI across expression	
Killgore & Yurgelun-Todd (2008)	Behaviorally inhibited (BI)	12.8 ± 1.7	NR	10 (80)	F, H, A, N	rate hostile/fear/nose width/passive viewing	F: NI > BI when passive viewing across expression	
Pérez-Edgar et al. (2007)	Not inhibited (NI)	12.5 ± 1.8	NR	17 (53)				

Monk et al. (2008)**	GAD Control	13.1 ± 2.1 14.3 ± 1.7	NR	29 (44)	H, A, N	masked presentation	A vs N: GAD > controls	GAD & control: A vs. N showed positive coupling between the right amygdala cluster and the right VLPFC; GAD vs. control: weaker negative functional connectivity
Rich et al. (2006)**	BD Control	14.2 ± 3.1 14.5 ± 2.5	9 – 17	22 (54) 21 (48)	N	rate hostile/fear/nose width	F rate fear: BD > controls, exaggerated in BD individuals who rated own fear as higher	BD subjects rated pictures as more hostile and themselves as more fearful of the pictures
Marsh et al. (2008)**	Conduct disorder ADHD Control	14.5 ± 1.5 13.8 ± 2.5 14.2 ± 1.6	10 – 17	12 (42) 12 (32) 12 (50)	F, A, N	gender judgment	F: conduct disorder < ADHD and healthy controls	AMG-VMPPFC functional connectivity < in conduct disorder than ADHD and healthy controls, correlates negatively with callous-unemotional symptom severity
Yang et al. (2007)	Adol	16.2 ± 1.2	13 – 17	18 (83)	F, H, A	emotion matching task	F, H, A > shapes	
Deeley et al. (2008)	Adult	24 ± 9.6	8 – 50	40 (0)	F, N, D	gender judgment	Null	↓ activity in lateral and medial PFC with ↑ age

Studies, identified in a literature search conducted in the summer of 2008, are listed in the order of (a) breadth of sampled ages and (b) task.

NR = Not reported; Adol = Adolescent, YA = Young Adult, OA = Older Adult, MA = Mid-age Adult, BD = Bipolar Disorder, GAD = Generalized Anxiety Disorder, MDD = Major Depressive Disorder, ADHD = attention deficit hyperactivity disorder; A = Angry, F = Fearful, N = Neutral, S = Sad, H = Happy, Su = Surprised, D = Disgust; AMG = Amygdala, PFC = Prefrontal Cortex, mPFC = medial prefrontal cortex, VLPFC = ventrolateral prefrontal cortex, MFG = Middle Frontal Gyrus, SFG = Superior Frontal Gyrus, VMPPFC = ventromedial prefrontal cortex, OFC = orbitofrontal cortex.

** Study included at least one sample group with psychopathology.

Haviland & Lelwica, 1987). Slightly later, 7-month-old infants show longer looking times in response to fearful expressions (de Haan, Belsky, Reid, Volein, & Johnson, 2004), and around 10 months, infants are able to reliably differentiate between expressions within a canonical valence category (e.g., differentiation between expressions of happy and pleasant surprise within the class of “positive expressions”) (Ludemann, 1991). Thus, the available evidence suggests that a gradual refinement occurs in detection of and discrimination among facial expressions in the first year of life and beyond. However, under more difficult task conditions such as rapid presentation (Tottenham, Leon, & Casey, 2006) and presentation of subtle morphed expressions (Thomas, De Bellis, Graham, & LaBar, 2007), even adolescents show performance deficits relative to adults, suggesting that more fine-grained aspects of facial expression recognition continue to develop until adulthood.

Although expression detection and discrimination represent important developmental milestones, it remains unclear whether these effects are mediated by perceptual discrimination or a higher-order understanding of what different expressions mean. This issue is difficult to untangle, given the inherent problems in measuring higher order understanding using the instruments available to test the youngest infants, who are preverbal and limited in their capacity for intentional motor activity (McClure, 2000). The available evidence suggests that slightly later in development, infants not only understand expression meanings, but they also use this understanding to make behavioral choices. In a visual cliff paradigm, one year olds were much less likely to crawl over an apparent drop-off if their mothers posed fearful faces than if they posed happy faces (Sorce, Emde, Campos, & Klinnert, 1985). Similar social referencing effects have been observed in other contexts around this age as well (Feinman & Lewis, 1983; Gunnar & Stone, 1984; Hornik & Gunnar, 1988). So, around one year, there is clear evidence that infants look to the facial expressions of surrounding individuals, particularly parents, to guide their own behavior.

While expression differentiation abilities appear to be fairly mature by at least one year of age, the ability to accurately label and match different depictions of the same emotional expression slowly emerges throughout childhood (for a more comprehensive review, see Gross & Ballif, 1991). Performance on matching emotional expressions shows steady improvement over development, with prominent improvements in accuracy observed between 9 and 10 years, and then again between 13 and 14 years, after which performance approximates that of adults (Kolb, Wilson, & Taylor, 1992). Further, the developmental timecourse of this ability is not uniform across emotional expressions. While preschoolers can consistently label certain emotions correctly, such as happy, as happy or joyful (Camras & Allison, 1985), children remain susceptible to errors in labeling other emotions, such as sad, surprised, disgusted, and afraid for years to come (Herba, Landau, Russell, Ecker, & Phillips, 2006).

One could argue that the capacity to label or match expressions is irrelevant to social behavior unless it facilitates the ability to infer the appropriate emotional response to a given situation. This has also been examined across development, and the results parallel those from studies of emotion matching and labeling. Kolb and colleagues (1992) presented 6- to 15-year-old children with a series of line-drawn cartoons. In each depicted scene, the facial expression of one character was left blank in the image (for example, a boy with a blank face holds a cat just hit by a car). The task was to choose the most appropriate facial expression to represent the emotion the blank-faced individual was likely to be feeling (in the example, the correct answer was sadness). As expected, performance on this task steadily improved with age, but not uniformly across

expression. Participants were fastest to achieve matching accuracy for angry and happy scenarios, with adult-level performance evident at the youngest age tested (6 years). In contrast, sad, fearful, disgusted, and surprised scenario-expression matching improved steadily with increasing age, only approaching adult performance during adolescence.

Finally, it should be noted that across all age groups, females appear to possess a subtle advantage in processing emotional expressions relative to males. In a meta-analysis focused on studies of youth, McClure (2000) observed a small yet reliable enhancement in performance on the tasks described above in females relative to males. This group difference was present across development, but was largest in infancy and early childhood. Taken together with Hall's (1984) meta-analytic findings of a consistent female advantage for expression processing in adults, these findings suggest that sex differences wax and wane at different points in the lifespan, with a small, but significant, tendency for females to perform better on relevant tasks.

Responses to emotional cues appear to undergo another fundamental shift in late adulthood. Psychological aging research has shown late adulthood to be characterized by an overall improvement of emotional experience. Empirically, it has been demonstrated that older adults experience less negative affect (Carstensen, Pasupathi, Mayr, & Nesselroade, 2000; Charles, Reynolds, & Gatz, 2001; Phillips, Henry, Hosie, & Milne 2006), show fewer outward displays of emotion (Magai, Cosedine, Krivoshekova, Kudadjic-Gyamfi, & McPherson, 2006; Phillips et al., 2006), and show a decreased magnitude of emotional memory enhancement for negative material (Charles, Mather, & Carstensen, 2003), despite the fact that threat detection processes (Mather & Knight, 2006) and physiological responses to negative images (Denberg, Buchanan, Tranel, & Adolphs, 2003) appear to be intact. In addition to less negative affect, older adults seem to also experience a heightened level of positive affect (Carstensen et al., 2000) and subjective quality of life (Phillips et al., 2006). This shift in emotional experience has been interpreted within the theoretical framework of socioemotional selectivity theory, developed by Carstensen and colleagues (Carstensen, 1995; Carstensen, Fung, & Charles, 2003). This theory posits that in late adulthood, individuals begin to think of their remaining time in life as limited, inducing a shift in focus away from future-oriented stressors and other sources of negative affect, and toward emotionally meaningful sources of positive affect.

Concurrent with shifts toward positive emotional experiences late in life is a change in the ability to recognize different categories of emotional facial expressions. It is plausible, and perhaps expected, that older adults (defined here as over 65 years of age) would show facial expression recognition deficits due to nonspecific decrements in cognitive and perceptual processing (Burke & Mackay, 1997). However, it is also possible that older adults demonstrate expression- or valence-specific deficits, consistent with changes in affective processing late in life (Calder et al., 2003). A recent meta-analysis (Ruffman, Henry, Livingstone, & Phillips, 2008) concluded that older adults show specific deficits in the ability to correctly recognize sad, angry and fearful expressions. This is not consistent with a general performance deficit, as the recognition of surprised, happy, and disgusted expressions does not appear to decline with advanced age. Interestingly, the expressions showing a drop in recognition with advancing age are all negative in valence, which may be consistent with older adults' renewed focus on positive affect. These findings provide further evidence for the dynamic nature facial expression recognition across the lifespan, with additional changes observed very late in life.

In summary, the development of facial expression recognition and comprehension is characterized by a gradual improvement in the ability to differentiate between emotions, to place verbal

labels on emotional expressions, and to determine the most appropriate emotional response to a given situation from early childhood to adulthood (Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006). However, the comprehension and identification of different emotions does not necessarily develop uniformly. Children appear quickest to master accurate recognition of happy expressions and slower to identify other expressions such as fear, sadness, anger, and disgust. Accurate discrimination among facial cues of different negative emotions does not reach adult-level performance until the teenage years. Emotional categories of sadness, anger, and fear—among the latest to attain accurate identification—are also those that show the earliest decrement in processing in the late adult years.

NEURAL UNDERPINNINGS OF EMOTION PROCESSING ACROSS THE LIFESPAN

Presumably, functional maturation of brain regions subserving face and emotion processing parallels the maturation of cognitive and emotional responses to facial expressions and other emotional cues. In this section, we focus on evidence regarding the development of brain regions mediating emotion processing. Due to space limitations, we focus primarily on the engagement of the amygdala, a brain region within the medial temporal lobes shown across several domains to be critical to emotion processing and social behavior (Aggleton, 2000). Individuals with damage to the amygdala demonstrate a deficiency in recognizing negative facial expressions, particularly fear (Adolphs, Tranel, Damasio, & Damasio, 1994), largely explained by their propensity not to scan the eye region of faces during free viewing conditions (Adolphs et al., 2005). Across functional neuroimaging methodologies including positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and magnetoencephalography (MEG) healthy adults generate a reliable response in the amygdala to facial expressions of emotion (Morris et al., 1998; Cornwell et al., 2008; Somerville, Kim, Johnstone, Alexander, & Whalen, 2004; Whalen et al., 1998), which will serve as a reference point with which to compare amygdala recruitment in older and younger age groups. According to a recent meta-analysis of 385 neuroimaging studies of predictors of amygdala activity in adults, the amygdala is reliably activated by both positive and negative categories of emotional material including but not limited to facial expressions of emotion (Costafreda, Brammer, David, & Fu, 2007). For a review of the facial expression processing literature in adults, we refer the reader to these excellent theoretical reviews (Adolphs, 2002; Davis & Whalen, 2001). Here we will examine fMRI research aimed at assessing the influence of age on amygdala engagement by emotional expressions, as this is the predominant technology used to assess subcortical brain responses in pediatric populations.

AMYGDALA ENGAGEMENT BY FACIAL EXPRESSIONS ACROSS THE LIFESPAN

While some brain regions, including the prefrontal cortex, show clear and substantial anatomical changes from early childhood to adulthood (Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008), structural properties of subcortical regions, including the amygdala, appear to vary across the lifespan but are less well characterized. One experiment used morphometric analyses

to measure volumetric changes in medial temporal lobe structures, including the amygdala, in subjects from age 4 to 18 and documented a modest but significant linear increase in left amygdala volume with age, but only in males (Giedd et al., 1996). This is in line with a recent report demonstrating a linear increase in left and right amygdala volume in a group of healthy 8–18-year-old male participants (Schumann et al., 2004). While this work provides interesting preliminary evidence of structural amygdala change, larger-scale anatomical tracing studies to precisely characterize these changes over development are only now underway (Giedd, 2008). In older adult samples, studies examining the effects of late-life aging on amygdala volume have documented a gradual linear decrease in gray matter volume from early to late adulthood (Allen, Bruss, Brown, & Damasio, 2005; Walhovd et al., 2005) suggesting a proliferation and subsequent loss of gray matter volume in the amygdala, potentially peaking in volume during late adolescence or early adulthood.

In addition to structural changes, we can examine functional changes within the amygdala. For example, it is of interest to ascertain whether the engagement of the amygdala while viewing emotional facial expressions is variant or stable across development. From childhood through adolescence, altered amygdala responsivity may result from functional maturity of the amygdala *per se*. Alternatively or concomitantly, differential strength of functional inputs that modulate amygdala activity (namely from the prefrontal cortex) may influence developmental changes (Casey, Giedd, & Thomas, 2000; Casey, Jones, & Hare, 2008). Further, the amygdala response may vary in linear or nonlinear ways throughout development due to such influences as alterations in social and emotional functioning (Sebastian, Burnett, & Blakemore, 2008; Spear, 2000), hormonal changes during puberty (Romeo, Diedrich, & Sisk, 2000; Buchanan, Eccles, & Becker, 1992; Nelson, Leibenluft, McClure, & Pine, 2005; Spear, 2000), and/or biased emotional processing related to mood or affect changes across development (Ernst, Pine, & Hardin, 2006; Casey et al., 2008; Steinberg, 2005). For these reasons, it is plausible to expect the amygdala response to vary from childhood to adulthood. Further, older adults' change in focus from negative to positive affect may be accompanied by an altered response in brain regions involved in processing emotional significance, including the amygdala. In the next sections, we explore the evidence to date assessing these possibilities.

Amygdala Response in Childhood and Pre-Adolescence

Although there is marked interest in changes in amygdala responsivity across the lifespan—including very young children—experiments testing individuals younger than the age of 10 are largely unavailable. One experiment measured neural activation in children as young as 7 years old (mean age in child group: 9.1 years) while they performed an emotional Go/No-Go task using fearful and happy facial expressions (Hare, Tottenham, Davidson, Glover, & Casey, 2005). In this study, children showed an attenuated amygdala response relative to adolescents, and a comparable response to that observed in adults. This initial evidence suggests that children younger than 10 years of age show reliable activation of the amygdala to facial expressions of emotion, but without additional findings, there are insufficient data to adequately compare response magnitudes relative to older individuals.

The research base on amygdala activation in pre-adolescents, defined here as individuals 10 to 12 years of age, is slightly larger and has yielded interesting results. Using a variety of emotional

expressions, Lobaugh and colleagues examined amygdala responses in 10- to 12-year-olds and observed a significantly enhanced response to disgusted faces relative to several other emotional expressions (Lobaugh, Gibson, & Taylor, 2006). Another study found an enhanced amygdala response to sad relative to neutral faces in 10- to 15-year-olds (Wang, LaBar, & McCarthy, 2006). These studies provide initial evidence that the pre-adolescent amygdala codes emotional properties of facial expressions in similar ways to those documented in the adult literature (Britton, Taylor, Sudheimer, & Liberzon, 2006). However, neither of these studies compared this age group with adults, so it is not clear whether the magnitude of activity is consistent with that observed in older samples.

In contrast, other studies have found distinctive neural responses to neutral face stimuli in this age group. A sample of 11 year olds, for instance, showed a greater amygdala response to neutral than fearful faces, while the opposite pattern was found in adults (Thomas et al., 2001a). This is consistent with the idea that children may have inherent difficulty decoding adult neutral faces (Gross & Ballif, 1991; Herba & Phillips, 2004), possibly due to a heightened ambiguity of neutral faces for individuals at this stage of development (Whalen, 1998; Tottenham et al., 2009). Taken together, these data suggest that facial expressions of emotion generate reliable activation patterns in the amygdala, although the response magnitude to particular expressions remains less definitive due to a lack of large-scale samples specifically of pre-adolescents, who tend to be included in adolescent or child samples rather than treated as a unique age group.

Adolescents

Adolescence can be defined as the phase of gradual transition between childhood and adulthood. Commencement of physical puberty is a common temporal marker of the onset of adolescence, whereas the boundary between the end of adolescence and the beginning of adulthood lacks a clear physical or psychological milestone (Ernst et al., 2006; Spear, 2000). For the purposes of the present review, samples with a mean age between 13 and 17 years are considered and discussed as adolescent samples (see Table 1) although this is likely an oversimplification, as the specific ages associated with the transition into and out of adolescence are subject to substantial variability across individuals. Aside from physical changes associated with this time of life, adolescence is additionally characterized by the maturation of a wide variety of cognitive processes, notably cognitive and attentional control (Casey et al., 2000; Hare & Casey, 2005). In addition, adolescence is a period of intense emotional experiences, driven by alterations in self-referential processing, enhanced salience of interpersonal relationships, and increased risk for experiencing negative affect (for reviews on the topic, see Kloep, 1999; Sebastian et al., 2008; Steinberg, 2005).

It has been proposed that adolescence is characterized by heightened psychosocial stress relative to childhood and adulthood (Spear, 2000). This may be related to other emotional experiences that seem to peak in adolescence, including a marked increase in experience of negative affect and depressed mood (Petersen et al., 1993; Rutter, Graham, Chadwick, & Yule, 1976), volatility in mood (Arnett, 1999), and anxiety (Buchanan et al., 1992). These nonlinear changes in emotional experience may be accompanied by enhancements in neural recruitment during emotional processing, a tenet that has been examined empirically. Here we examine evidence for and against this possibility derived from neuroimaging experiments focused on the amygdala response to emotional facial expressions.

Findings from several neuroimaging studies suggest a nonlinear amplification of amygdala response to emotional facial expressions during adolescence relative to other ages. Guyer and colleagues (2008) recently demonstrated, with robust sample sizes, that adolescents showed an exaggerated amygdala response to passively viewed fearful facial expressions (versus neutral faces) relative to adults. This is consistent with other reports of significantly greater amygdala response magnitudes in adolescents than adults during passive viewing of several different emotional facial expressions (Monk et al., 2003), as well as within the context of an emotional Go/No-Go task (Hare et al., 2008). Taken as a group, these findings suggest that adolescents show greater activation than adults to a variety of facial emotional cues presented in different contexts.

However, not all studies have replicated this effect. Some experiments using similar paradigms have found no association between amygdala recruitment and age during facial expression processing (Deeley et al., 2007; Nelson et al., 2003; Pine et al., 2001). One possible source for these discrepancies lies in differences in sample characteristics, as Deeley and colleagues only tested males (see Table 1). In addition, one study found that 12- to 19-year-old participants showed an enhanced amygdala response to happy relative to neutral faces, but no difference in activity to fearful relative to neutral faces (Williams et al., 2006), which is analogous to one study's findings in preadolescents (Thomas et al., 2001b). Thus, although the most comprehensive experiments with the largest samples suggest an exaggeration in amygdala response during adolescence, the specificity of these effects remains ambiguous, with widely different use of expressions and experimental contexts rendering cross-study comparisons difficult.

Older Adults

As discussed previously, a final shift in emotional experience, characterized by enhanced positive and attenuated negative emotional experiences, appears to occur in late adulthood (Carstensen et al., 2000), coupled with decreased accuracy at recognizing sad, fearful, and angry expressions. An open question is whether the amygdala response to emotional material reflects this psychological shift. A number of experiments have addressed this question, and available findings suggest that patterns of amygdala activation parallel older adults' emotional experiences. Several reports, for example, document an attenuated amygdala response to negatively valenced emotional material in older relative to younger adults. In an influential study on the topic, Mather and colleagues found that unlike younger adults, older adults did not show amygdala activation to negative scenes from the International Affective Picture System (Lang, Bradley, & Cuthbert, 1997) relative to resting baseline, while they showed an enhanced amygdala response to positive images relative to young adults (Mather et al., 2004).

This bias toward attenuated amygdala responses to negative cues with age has been demonstrated in other contexts as well. In experiments presenting a variety of emotional facial expressions to participants, older adults showed a diminished amygdala response relative to younger adults while performing emotion discrimination (Gunning-Dixon et al., 2003) and emotional expression matching tasks (Iidaka et al., 2002). While both of these studies used both positive and negative facial expressions, they did not report amygdala responses separately for each expression used. Other work complements the conclusions of these studies, separately reporting that older adults show diminished amygdala activity to negatively valenced (Fischer et al., 2005; Tessitore et al., 2005) and positively valenced facial expressions (Keightley, Chiew,

Winocur, & Grady, 2007) Thus, the available evidence suggests that older adults may be characterized by a pattern of under-recruitment of the amygdala to both positive and negative emotional cues relative to young adults.

Finally, perhaps the most informative study on this topic to date completed fMRI scans on 80 participants ranging in age from 12 to 79 while they viewed happy, neutral, and fearful expressions. Among adults, results suggest that neural responses to both happy and fearful expressions relative to neutral was greatest in young adulthood (20 to 39 years old); in contrast, older adults (aged 50 to 79 years) showed no differences among their amygdala responses to happy, neutral, or fearful expressions (Williams et al., 2006). Thus, the largest experiment of its kind also lends support to the conclusion that the amygdala response to emotional stimuli attenuates with advancing age.

Summary: Facial Emotion Processing Across the Lifespan

Taken together, the available evidence suggests that the amygdala is responsive to facial expressions of emotion from youth through old age. However, the magnitude of response that different emotions elicit appears to vary throughout the lifespan. Although there is not enough evidence to definitively characterize amygdala response profiles prior to approximately 10 years of age, existing data suggest a peak in response during the adolescent to young adult years, with a gradual decrease in response with greater age. It should be noted, however, that not all work to date is consistent with this pattern; more research examining the role of age in modulating amygdala responses to emotional cues, particularly faces, is needed to clarify how amygdala responses to emotional cues vary across the lifespan.

Interactions Between the Amygdala and Prefrontal Cortex During Facial Affect Processing

Although the present report has focused on the amygdala response to facial expressions of emotion, it would be incomplete to consider these response patterns in isolation from functional patterns of activity in other regions of the brain. One brain region implicated in interacting with the amygdala to govern emotional responding is the prefrontal cortex (PFC), which is thought to play an important role in exerting cognitive control over emotional responses in adults (Ochsner & Gross, 2005) and developing populations (Casey et al., 2000). A study by Monk and colleagues (2003) compared neural activity of adolescent and adult participants while they either passively viewed fearful and neutral facial expressions or attended to their own emotional states while viewing the same stimuli. This task, unlike many face processing tasks used in fMRI studies, calls for the use of controlled processes in the presence of emotional cues. When fearful faces were presented, adults recruited the ventrolateral prefrontal cortex, localized to the inferior frontal gyrus to a greater extent than adolescents, during trials requiring attention to one's own emotional response rather than passive viewing. From these findings, the authors suggest that lateral prefrontal control mechanisms remain immature during the adolescent years. In addition, a recent experiment by Hare and colleagues (2008) employed a Go/No-Go paradigm with emotional faces that required participants to monitor and inhibit behavioral responses to different emotional categories. Functional connectivity analyses yielded evidence of an inverse

functional relationship between the amygdala and prefrontal cortex, such that greater recruitment of the PFC predicted attenuation in the amygdala signal, as well as faster task performance. Developmentally, adolescents showed an under-recruitment of the PFC, inversely predicting greater amygdala activity and poorer behavioral performance relative to adults. Taken together, these studies suggest that the functional “balance” between amygdala–PFC circuitry may be critical to engaging in control over emotional responses, with under-recruitment of PFC regions in adolescents having potential consequences for the regulation of adolescent emotional behavior (see Somerville, Jones, & Casey, 2010).

FUTURE DIRECTIONS

While studies to date have provided important insights into the developmental trajectory of both behavioral and neural aspects of emotion processing across the lifespan, limitations to the literature make it difficult to develop a cohesive and empirically driven model. We highlight a few of these limitations in hopes of motivating future work to develop creative and thoughtful solutions to these issues.

Inherent to developmental research is enhanced difficulty related to recruiting and testing individuals outside of the typical “healthy young adult” population. Some of these difficulties are straightforward procedural complications that include more challenging subject recruitment, reduced tolerance of emotional stimuli and experimental set-ups, and heightened concern for data quality due to increased movement, greater susceptibility to distraction, and so forth. In addition to these challenges are some more nuanced difficulties that we will highlight briefly.

First, the most useful studies for informing a developmental model of emotion processing directly compare neural recruitment during emotion processing across participants of different ages. Although this may seem self-evident, such studies are rare. Indeed, as Table 1 indicates, a large number of experiments report findings in only one age group, for example 12–16-year-olds. Although the neural correlates of emotion processing in this age group are interesting in and of themselves, observation of a single age group does little to further the understanding of how emotion processing develops and changes across the lifespan. In future work, within-study comparisons of participants in multiple age groups would facilitate inferences about developmental trajectories of amygdala function, as would treating age as a continuous rather than a categorical variable (Somerville et al., 2010). Longitudinal studies tracking the same individuals across different stages of development would be particularly fruitful for enabling robust cross-age comparisons.

Clear conclusions about the nature of amygdala responding in young children will require research that both targets much younger samples than have most studies to date and uses a variety of tasks thought to engage the amygdala, facilitating direct cross-study comparisons. Functional neuroimaging research using emotional faces as stimuli is underway in children as young as 5 years (Anderson, personal communication); proliferation of such studies would flesh out the currently sparse literature on amygdala function in early childhood.

A second barrier to understanding developmental changes in emotion processing is variability across paradigms. For example, in research examining neural responses to facial expressions, there is substantial variability in the expressions presented, the stimuli used, and the tasks that participants perform. As such, it can be difficult to attribute between-study differences in

neural responses to age effects, when stimuli and task paradigms were dissimilar. This issue could be circumvented if researchers placed greater constraints on the paradigms that are used, focusing perhaps on tasks and stimuli that have been well validated in the behavioral literature. Additionally, formal replication of studies, using the same stimuli and task across multiple samples, would not only provide evidence that effects are reliable, but would also permit more focused examination of group differences.

Finally, the vast majority of experiments found in the literature examining emotional processing of faces use either standardized facial expression images such as the classic Ekman Pictures of Facial Affect (Ekman & Friesen, 1976) or other validated image sets developed in an individual laboratory. Most of these stimulus sets depict exclusively young and middle-aged adults, which means that some age groups (e.g., adults) view same-aged individuals, while others (e.g., children and older adults) view stimuli depicting individuals who differ substantially in age from themselves and whose emotional expressions may thus convey different messages to them. It is unclear if, or how, this aspect of the literature influences our conclusions regarding the behavioral and neural development of emotion processing. However, when Easter and colleagues (Easter et al., 2005) asked adolescents (mean age 13 years) to label the expressions depicted by adult and adolescent stimuli, performance was significantly enhanced for peer-aged stimuli. This finding could stem from a number of factors. One possibility is that adolescents may be more attuned to peer emotions and may thus more easily decode expressions encoded by peers. Alternatively, facial expressions that youths produce may be easier to decode than those of adults, regardless of the age of the decoder. Regardless, however, of underlying mechanisms, this finding offers some evidence that exclusive use of adult stimuli may be consequential for emotion research comparing performance across development.

NEW DIRECTIONS IN EXAMINING EMOTIONAL AND SOCIAL PROCESSING ACROSS DEVELOPMENT

Facial expressions of emotion are just one of many potential experimental stimuli that can be used to examine the neural substrates of social and emotional processing across development. Interestingly, the past few years have seen a surge of neuroimaging studies employing innovative paradigms that attempt to elucidate more complex aspects of social and emotional processing across development (Sebastian et al., 2008; Casey et al., 2008). Here we highlight a few of these recent efforts, with an emphasis on those that examine social cue processing, which assumes enhanced importance during adolescence (Nelson et al., 2005; Spear, 2000).

First, recent behavioral research has adapted paradigms from the economics literature, (e.g., Prisoners Dilemma, Ultimatum Game) to examine social interaction patterns (McClure et al., 2007b; Rilling, Sanfey, Aaronson, Nystrom, & Cohen, 2004; Rilling, King-Casas, & Sanfey, 2008). Although most studies using such tasks have focused on adults (for a review, see Rilling et al., 2008), one recent study administered the Prisoner's Dilemma task to adolescents in an effort to simulate reciprocal, potentially conflict-laden, social interactions involving cooperative and competitive monetary exchange offers (McClure et al., 2007b). Comparison of patterns of performance on the task between healthy adolescents and peers with mood and anxiety disorders revealed that anxious and depressed adolescents were less likely to disrupt cooperative patterns of interaction, even when it meant winning less money in the short

term. This finding provides interesting clues about individual differences in motivation related to social interactions during the adolescent years.

Future research that advances this line of questioning should be helpful in characterizing changes in social interaction style, as well as their neural underpinnings, across development. Indeed, neuroimaging paradigms mimicking real social interactions have been developed in recent years and tested on adult populations (Eisenberger, Lieberman, & Williams, 2003; Somerville, Heatherton, & Kelley, 2006). One recently developed paradigm simulated mutual social evaluation in adolescents within the context of choosing peers to interact with in an internet chatroom (Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009). Participants aged 9 to 17 years responded to pictures of peer-aged individuals based on how interested they were in chatting online with them, which permitted categorization of the pictures into subsets of low and high interest individuals for each participant. During fMRI scanning, participants viewed pictures of each rated peer and predicted whether these individuals would also like to chat with them. Imaging results demonstrated that several affective and reward-sensitive brain regions, including the insula, nucleus accumbens, and hypothalamus, but interestingly, not the amygdala, were recruited differentially as a function of social interest, participant sex, and age. While this experiment provides important initial clues into the brain processes subserving peer interactions in adolescents, further work in this direction will continue to advance the understanding functional changes in the brain underlying social development in adolescence.

As discussed previously, adolescents are particularly susceptible to the influence of peers when making behavioral decisions. An innovative recent experiment sought to identify brain regions that, when engaged, could facilitate resistance to peer influence (Grosbras et al., 2007). During fMRI scanning, pre-adolescent participants viewed video clips depicting neutral faces and common movements, as well as angry faces and aggressive movements. Participants also completed a scale designed to measure the extent to which they resist peer pressure during their everyday lives. Functional connectivity analyses showed that when participants viewed angry faces and movements, those who described themselves as less influenced by peers showed more coordinated recruitment of areas of the prefrontal cortex thought to be important in decision making. This experiment suggests that the maturity of these frontal regions may serve to buffer youths from undue influence from peers, particularly in emotionally laden contexts. The authors suggest that in the future, these findings and others may inform the development of tools for reducing susceptibility to negative peer influences in vulnerable youth.

The studies described and cited above constitute just a few examples of a recent surge of work aimed at characterizing the neural responses that accompany important developmental changes related to social behavior. In the coming years, research examining changes in brain structure and function with age has the potential to more clearly link psychological and neural patterns of change across development.

SUMMARY AND CONCLUSION

Recent research has markedly advanced our understanding of the neurobiological mechanisms of emotional facial expression processing and how these responses change across the lifespan. As work in this area continues, it has the potential not only to enhance knowledge about the functional maturation of the human brain, but also to inform mechanistic explanations for changes in

social cognition and behavior that occur across the lifespan. We hope that the present brief survey of these issues will assist in the interpretation of the literature as a whole, illuminate its strengths and weaknesses, and identify future research directions that will help elucidate the development trajectory of emotional and social processes in the brain.

ACKNOWLEDGMENTS

We thank Erika Ruberry for assistance with manuscript preparation and three anonymous reviewers for their helpful comments.

REFERENCES

- Adolphs, R. (2002). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews, 1*(1), 21–62.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature, 433*(7021), 68–72.
- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature, 372*(6507), 669–672.
- Aggleton, J. P. (2000). *The amygdala. A functional analysis*. New York, NY: Oxford University Press.
- Allen, J. S., Bruss, J., Brown, C. K., & Damasio, H. (2005). Normal neuroanatomical variation due to age: The major lobes and a parcellation of the temporal region. *Neurobiology of Aging, 26*, 1245–1260.
- Arnett, J. (1999). Adolescent storm and stress, reconsidered. *American Psychologist, 54*, 317–326.
- Baird, A. A., Gruber, S. A., Fein, D. A., Maas, L. C., Steingard, R. J., Renshaw, P. F., et al. (1999). Functional magnetic resonance imaging of facial affect recognition in children and adolescents. *Journal of the American Academy of Child and Adolescent Psychiatry, 38*(2), 195–199.
- Banks, M. S. (1980). The development of visual accommodation during early infancy. *Child Development, 51*, 646–666.
- Britton, J. C., Taylor, S. F., Sudheimer, K. D., & Liberzon, I. (2006). Facial expressions and complex IAPS pictures: common and differential networks. *Neuroimage, 31*(2), 906–919.
- Buchanan, C. M., Eccles, J. S., & Becker, J. B. (1992). Are adolescents the victims of raging hormones: Evidence for activation effects of hormones on moods and behavior at adolescence. *Psychological Bulletin, 111*, 62–107.
- Burke, D. M., & Mackay, D. G. (1997). Memory, language, and ageing. *Philosophical transactions of the Royal Society of London B, 3*(52), 1845–1856.
- Calder, A. J., Keane, J., Manly, T., Sprengelmeyer, R., Scott, S., Nimmo-Smith, I., & Young, A. W. (2003). Facial expression recognition across the adult life span. *Neuropsychologia, 41*, 195–202.
- Campos, J. J., & Sternberg, C. R. (1981). Perception, appraisal, and emotion: The onset of social referencing. In M. E. Lamb & L. R. Sherrod (Eds.), *Infant social cognition: Empirical and theoretical considerations* (pp. 273–314). Hillsdale, NJ: Erlbaum.
- Camras, L. A., & Allison, K. (1985). Children's understanding of emotional facial expressions and verbal labels. *Journal of Nonverbal Behavior, 9*(2), 84–94.
- Carstensen, L. L. (1995). Evidence for a life-span theory of socioemotional selectivity. *Current Directions in Psychological Science, 4*, 151–156.
- Carstensen, L. L., Fung, H. H., & Charles, S. T. (2003). Socioemotional selectivity theory and the regulation of emotion in the second half of life. *Motivation and Emotion, 27*, 103–123.
- Carstensen, L. L., Pasupathi, M., Mayr, U., & Nesselroade, J. R. (2000). Emotional experience in everyday life across the adult lifespan. *Journal of Personality and Social Psychology, 79*, 644–655.
- Casey, B. J., Giedd, J. N., & Thomas, K. M. (2000). Structural and functional brain development and its relation to cognitive development. *Biological Psychology, 54*, 241–247.
- Casey, B. J., Jones, R. M., & Hare, T. A. (2008). The adolescent brain. *Annals of the New York Academy of Sciences, 1124*, 111–126.

- Charles, S. T., Mather, M., & Carstensen, L. L. (2003). Aging and emotional memory: The forgettable nature of negative images for older adults. *Journal of Experimental Psychology: General*, *132*, 310–324.
- Charles, S. T., Reynolds, C. A., & Gatz, M. (2001). Age-related differences and change in positive and negative affect over 23 years. *Journal of Personality and Social Psychology*, *80*(1), 136–151.
- Cornwell, B. R., Carver, F. W., Coppola, R., Johnson, L., Alvarez, R., & Grillon, C. (2008). Evoked amygdala responses to negative faces revealed by adaptive MEG beamformers. *Brain Research*, *1244*, 103–112.
- Costafreda, S. G., Brammer, M. J., David, A. S., & Fu, C. H. Y. (2008). Predictors of amygdala activation during the processing of emotional stimuli: A meta-analysis of 385 PET and fMRI studies. *Brain Research Reviews*, *58*(1), 57–70.
- Davis, M., & Whalen, P. J. (2001). The amygdala: Vigilance and emotion. *Molecular Psychiatry*, *6*, 13–34.
- Deeley, Q., Daly, E. M., Azuma, R., Surguladze, S., Giampietro, V., Brammer, M. J., et al. (2007). Changes in male brain responses to emotional faces from adolescence to middle age. *Neuroimage*, *40*, 389–397.
- de Haan, M., Belsky, J., Reid, V., Volein, A., & Johnson, M. H. (2004). Maternal personality and infants' neural and visual responsivity to facial expressions of emotion. *Journal of Child Psychology and Psychiatry*, *45*(7), 1209–1218.
- Denberg, N. L., Buchanan, T. W., Tranel, D., & Adolphs, R. (2003). Evidence for preserved emotional memory in normal older persons. *Emotion*, *3*(3), 239–253.
- Easter, J., McClure, E. B., Monk, C. S., Dhanani, M., Hodgdon, H., Leibenluft, E., et al. (2005). Emotion recognition deficits in pediatric anxiety disorders: implications for amygdala research. *Journal of Child and Adolescent Psychopharmacology*, *15*(4), 563–570.
- Eisenberger, N. I., Lieberman, M. D., & Williams, K. D. (2003). Does rejection hurt? An fMRI study of social exclusion. *Science*, *302*(5643), 290–292.
- Ekman, P., & Friesen, W. V. (1976). *Pictures of Facial Affect [slides]*. Palo Alto, CA: Consulting Psychologists Press.
- Ekman, P., & Oster, H. (1979). Facial expressions of emotion. *Annual Reviews in Psychology*, *30*, 527–554.
- Ernst, M., Pine, D. S., & Hardin, M. (2006). Triadic model of the neurobiology of motivated behavior in adolescence. *Psychological Medicine*, *36*(3), 299–312.
- Feinman, S., & Lewis, M. (1983). Social referencing at ten months: A second-order effect on infants' responses to strangers. *Child Development*, *54*, 878–887.
- Field, T. M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expression by neonates. *Science*, *218*(4568), 179–181.
- Fischer, H., Sandblom, J., Gavazzeni, J., Fransson, P., Wright, C. I., & Bäckman, L. (2005). Age-differential patterns of brain activation during perception of angry faces. *Neuroscience Letters*, *386*(2), 99–104.
- Giedd, J. N. (2008). The teen brain: Insights from neuroimaging. *Journal of Adolescent Health*, *42*, 335–343.
- Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, *2*, 861–863.
- Giedd, J. N., Vaituzis, A. C., Hamburger, S. D., Lange, N., Rajapakse, J. C., Kaysen, D., et al. (1996). Quantitative MRI of the temporal lobe, amygdala, and hippocampus in normal human development: Ages 4–18 years. *The Journal of Comparative Neurology*, *366*, 223–230.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences, USA*, *101*(21), 8174–8179.
- Grosbras, M.-H., Jansen, M., Leonard, G., McIntosh, A., Osswald, K., Poulsen, C., et al. (2007). Neural mechanisms of resistance to peer influence in early adolescence. *The Journal of Neuroscience*, *27*(30), 8040–8045.
- Gross, A. L., & Ballif, B. (1991). Children's understanding of emotion from facial expressions and situations: A review. *Developmental Review*, *11*, 368–398.
- Gunnar, M. R., & Stone, C. (1984). The effects of positive maternal affect on infant responses to pleasant, ambiguous, and fear-provoking toys. *Child Development*, *55*, 1231–1236.
- Gunning-Dixon, F. M., Gur, R. C., Perkins, A. C., Schroeder, L., Turner, T., Turetsky, B. I., et al. (2003). Age-related differences in brain activation during emotional face processing. *Neurobiology*, *24*, 285–295.
- Guyer, A. E., McClure-Tone, E. B., Shiffrin, N. D., Pine, D. S., & Nelson, E. E. (2009). Probing the neural correlates of anticipated peer evaluation in adolescence. *Child Development*, *80*(4), 1000–1015.
- Guyer, A. E., Monk, C. S., McClure-Tone, E. B., Nelson, E. E., Roberson-Nay, R., Adler, A., et al. (2008). A developmental examination of amygdala response to facial expressions. *Journal of Cognitive Neuroscience*, *20*(9), 1565–1582.

- Hall, J. A. (1984). *Nonverbal sex differences: Communication accuracy and expressive style*. Baltimore: Johns Hopkins University Press.
- Hare, T. A., & Casey, B. J. (2005). The neurobiology and development of cognitive and affective control. *Cognition, Brain and Behavior*, *9*(3), 273–286.
- Hare, T. A., Tottenham, N., Galvan, A., Voss, H. U., Glover, G. H., & Casey, B. J. (2008). Biological substrates of emotional reactivity and regulation in adolescence during an emotional go-nogo task. *Biological Psychiatry*, *63*(10), 927–934.
- Haviland, J. M., & Lelwica, M. (1987). The induced affect response: 10-week-old infants' responses to three emotion expressions. *Developmental Psychology*, *23*, 97–104.
- Herba, C., Landau, S., Russell, T., Ecker, C., & Phillips, M. L. (2006). The development of emotion-processing in children: Effects of age, emotion, and intensity. *Journal of Child Psychology and Psychiatry*, *47*(11), 1098–1106.
- Herba, C., & Phillips, M. (2004). Annotation: Development of facial expression recognition from childhood to adolescence: Behavioral and neurological perspectives. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *45*(7), 1185–1198.
- Hornik, R., & Gunnar, M. R. (1988). A descriptive analysis of infant social referencing. *Child Development*, *59*, 626–634.
- Iidaka, T., Okada, T., Murata, T., Omori, M., Kosaka, H., Sadato, N., et al. (2002). Age-related differences in the medial temporal lobe responses to emotional faces as revealed by fMRI. *Hippocampus*, *12*, 352–362.
- Keightley, M. L., Chiew, K. S., Winocur, G., & Grady, C. L. (2007). Age-related differences in brain activity underlying identification of emotional expressions in faces. *Social, Cognitive, and Affective Neuroscience*, *2*, 292–302.
- Killgore, W. D., & Yurgelun-Todd, D. A. (2005). Social anxiety predicts amygdala activation in adolescents viewing fearful faces. *Neuroreport*, *16*(15), 1671–1675.
- Killgore, W. D., & Yurgelun-Todd, D. A. (2008). Unconscious processing of facial affect in children and adolescents. *Social Neuroscience*, *2*(1), 28–47.
- Kloep, M. (1999). Love is all you need? Focusing on adolescents' life concerns from an ecological point of view. *Journal of Adolescence*, *22*, 49–63.
- Kolb, B., Wilson, B., & Taylor, L. (1992). Developmental changes in the recognition and comprehension of facial expression: Implications for frontal lobe function. *Brain and Cognition*, *20*, 74–84.
- Lang, P. L., Bradley, M. M., & Cuthbert, B. N. (1997). International Affective Picture System [Pictures]. Gainesville, FL: NIMH Center for the Study of Emotion and Attention.
- Lewis, M. D., Lamm, C., Segalowitz, S. J., Stieben, J., & Zelazo, P. D. (2006). Neurophysiological correlates of emotion regulation in children and adolescents. *Journal of Cognitive Neuroscience*, *18*(3), 430–443.
- Lobaugh, N. J., Gibson, E., & Taylor, M. J. (2006). Children recruit distinct neural systems for implicit emotional face processing. *Neuroreport*, *17*(2), 215–219.
- Ludemann, P. M. (1991). Generalized discrimination of positive facial expressions by seven- and ten-month-old infants. *Child Development*, *62*, 55–67.
- Magai, C., Cosedine, N. S., Krivoshekova, Y. S., Kudadjic-Gyamfi, E., & McPherson, R. (2006). Emotion experience and expression across the adult life span: Insights from a multimodal assessment study. *Psychology and Aging*, *21*(2), 303–317.
- Marsh, A. A., Finger, E. C., Mitchell, D. G. V., Reid, M. E., Sims, C., Kosson, D. S., et al. (2008). Reduced amygdala response to fearful expressions in children and adolescents with callous-unemotional traits and disruptive behavior disorders. *American Journal of Psychiatry*, *165*(6), 712–720.
- Mather, M., Canli, T., English, T., Whitfield, S., Wais, P., Ochsner, K. M., et al. (2004). Amygdala responses to emotionally valenced stimuli in older and younger adults. *Psychological Science*, *15*(4), 259–263.
- Mather, M., & Knight, M. (2006). Angry faces get noticed quickly: Threat detection is not impaired among older adults. *Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *61*, P54–P57.
- McClure, E. B. (2000). A meta-analytic review of sex differences in facial expression processing and their development in infants, children, and adolescents. *Psychological Bulletin*, *126*(3), 424–453.
- McClure, E. B., Monk, C. S., Nelson, E. E., Parrish, J. M., Adler, A., Blair, R. J., et al. (2007a). Abnormal attention modulation of fear circuit function in pediatric generalized anxiety disorder. *Archives of General Psychiatry*, *64*(1), 97–106.

- McClure, E. B., Monk, C. S., Nelson, E. E., Zarahn, E., Leibenluft, E., Bilder, R. M., et al. (2004). A developmental examination of gender differences in brain engagement during evaluation of threat. *Biological Psychiatry*, *55*(11), 1047–1055.
- McClure, E. B., Parrish, J. M., Nelson, E. E., Easter, J., Thorne, J. F., Rilling, J. K., et al. (2007b). Responses to conflict and cooperation in adolescents with anxiety and mood disorders. *Journal of Abnormal Child Psychology*, *35*(4), 567–577.
- Monk, C. S., McClure, E. B., Nelson, E. E., Zarahn, E., Bilder, R. M., Leibenluft, E., et al. (2003). Adolescent immaturity in attention-related brain engagement to emotional facial expressions. *Neuroimage*, *20*, 420–428.
- Monk, C. S., Telzer, E. H., Mogg, K., Bradley, B. P., Mai, X., Louro, H. M., et al. (2008). Amygdala and ventrolateral prefrontal cortex activation to masked angry faces in children and adolescents with generalized anxiety disorder. *Archives of General Psychiatry*, *65*(5), 568–576.
- Montague, D. P. F., & Walker-Andrews, A. S. (2001). Peekaboo: A new look at infants' perception of emotional expressions. *Developmental Psychology*, *37*(6), 826–838.
- Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., et al. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121* (Pt 1), 47–57.
- Nelson, C. A. (1987). The recognition of facial expression in the first two years of life: Mechanisms of development. *Child Development*, *58*(4), 889–909.
- Nelson, E. E., Leibenluft, E., McClure, E. B., & Pine, D. S. (2005). The social re-orientation of adolescence: A neuroscience perspective on the process and its relation to psychopathology. *Psychological Medicine*, *35*(2), 163–174.
- Nelson, E. E., McClure, E. B., Monk, C. S., Zarahn, E., Leibenluft, E., Pine, D. S., et al. (2003). Developmental differences in neuronal engagement during implicit encoding of emotional faces: an event-related fMRI study. *Journal of Child Psychology and Psychiatry*, *44*(7), 1015–1024.
- Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences*, *9*(5), 242–249.
- Pérez-Edgar, K., Roberson-Nay, R., Hardin, M. G., Poeth, K., Guyer, A. E., Nelson, E. E., et al. (2007). Attention alters neural responses to evocative faces in behaviorally inhibited adolescents. *Neuroimage*, *35*(4), 1538–1546.
- Petersen, A. C., Compas, B. E., Brooks-Gunn, J., Stemmler, M., Ey, S., & Grant, K. E. (1993). Depression in adolescence. *American Psychologist*, *48*, 155–168.
- Phillips, L. H., Henry, J. D., Hsieh, J. A., & Milne, A. B. (2006). Age, anger regulation and well-being. *Aging & Mental Health*, *10*(3), 250–256.
- Pine, D. S., Grun, J., Zarahn, E., Fyer, A., Koda, V., Li, W., et al. (2001). Cortical brain regions engaged by masked emotional faces in adolescents and adults: An fMRI study. *Emotion*, *1*(2), 137–147.
- Rich, B. A., Vinton, D. T., Roberson-Nay, R., Hommer, R. E., Berghorst, L. H., McClure, E. B., et al. (2006). Limbic hyperactivation during processing of neutral facial expressions in children with bipolar disorder. *Proceedings of the National Academy of Sciences, USA*, *103*(23), 8900–8905.
- Rilling, J. K., King-Casas, B., & Sanfey, A. G. (2008). The neurobiology of social decision-making. *Current Opinion in Neurobiology*, *18*(2), 159–165.
- Rilling, J. K., Sanfey, A. G., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2004). Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. *Neuroreport*, *15*(16), 2539–2543.
- Romeo, R. D., Diedrich, S. L., & Sisk, C. L. (2000). Effects of gonadal steroids during pubertal development on androgen and estrogen receptor- α immunoreactivity in the hypothalamus and amygdala. *Journal of Neurobiology*, *44*(3), 361–368.
- Ruffman, T., Henry, J. D., Livingstone, V., & Phillips, L. H. (2008). A meta-analytic review of emotion recognition and aging: Implications for neuropsychological models of aging. *Neuroscience and Biobehavioral Reviews*, *32*(4), 863–881.
- Rutter, M., Graham, P., Chadwick, O. F. D., & Yule, W. (1976). Adolescent turmoil: Fact or fiction? *Journal of Child Psychology and Psychiatry*, *17*, 35–56.
- Schumann, C. M., Hamstra, J., Goodlin-Jones, B. L., Lottspeich, L. J., Kwon, H., Buonocore, M. H., et al. (2004). The amygdala is enlarged in children but not adolescents with autism; the hippocampus is enlarged at all ages. *Journal of Neuroscience*, *24*(28), 6392–6401.
- Sebastian, C., Burnett, S., & Blakemore, S.-J. (2008). Development of the self-concept during adolescence. *Trends in Cognitive Sciences*, *12*(11), 441–446.
- Shaw, P., Kabani, N., Lerch, J. P., Eckstrand, K., Lenroot, R., Gotay, N., et al. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *Journal of Neuroscience*, *28*(14), 3586–3594.

- Somerville, L. H., Heatherton, T. F., & Kelley, W. M. (2006). Anterior cingulate cortex responds differentially to expectancy violation and social rejection. *Nature Neuroscience*, *9*(8), 1007–1008.
- Somerville, L. H., Jones, R. M., & Casey, B. J. (2010). A time of change: Behavioral and neural correlates of adolescent sensitivity to appetitive and aversive environmental cues. *Brain and Cognition*, *72*(1), 124–133.
- Somerville, L. H., Kim, H., Johnstone, T., Alexander, A. L., & Whalen, P. J. (2004). Human amygdala responses during presentation of happy and neutral faces: Correlations with state anxiety. *Biological Psychiatry*, *55*(9), 897–903.
- Sorce, J. F., Emde, R. N., Campos, J., & Klinnert, M. D. (1985). Maternal emotional signaling: Its effect on the visual cliff behavior of 1-year-olds. *Developmental Psychology*, *21*, 195–200.
- Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Reviews*, *24*(4), 417–463.
- Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences*, *9*(2), 69–74.
- Tessitore, A., Hariri, A. R., Fera, F., Smith, W. G., Das, S., Weinberger, D., et al. (2005). Functional changes in the activity of brain regions underlying emotion processing in the elderly. *Psychiatry Research: Neuroimaging*, *139*, 9–18.
- Thomas, K. M., Drevets, W. C., Dahl, R. E., Ryan, N. D., Birmaher, B., Eccard, C. H., et al. (2001b). Amygdala response to fearful faces in anxious and depressed children. *Archives of General Psychiatry*, *58*, 1057–1063.
- Thomas, K. M., Drevets, W. C., Whalen, P. J., Eccard, C. H., Dahl, R. E., Ryan, N. D., et al. (2001a). Amygdala response to facial expressions in children and adults. *Biological Psychiatry*, *49*, 309–316.
- Thomas, L. A., DeBellis, M. D., Graham, R., & LaBar, K. S. (2007). Development of emotional facial recognition in late adulthood and adolescence. *Developmental Science*, *10*(5), 547–558.
- Tottenham, N., Leon, A. C., & Casey, B. J. (2006). The face behind the mask: A developmental study. *Developmental Science*, *9*(3), 288–294.
- Tottenham, N., Tanaka, J., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., et al. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research*, *168*(3), 242–249.
- Walhovd, K. B., Fjell, A. M., Reinvang, I., Lundervold, A., Dale, A. M., Eilertsen, D. E., et al. (2005). Effects of age on volumes of cortex, white matter and subcortical structures. *Neurobiology of Aging*, *26*, 1261–1270.
- Walker-Andrews, A. S. (1997). Infants' perception of expressive behaviors: Differentiation of multimodal information. *Psychological Bulletin*, *121*(3), 437–456.
- Wang, L., LaBar, K. S., & McCarthy, G. (2006). Mood alters amygdala activation to sad distractors during an attentional task. *Biological Psychiatry*, *60*(10), 1139–1146.
- Whalen, P. J. (1998). Fear, vigilance, and ambiguity: Initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science*, *7*(6), 177–188.
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, *18*(1), 411–418.
- Williams, L. M., Brown, K. J., Palmer, D., Liddell, B. J., Kemp, A. H., Olivieri, G., et al. (2006). The mellow years? Neural basis of improving emotional stability with age. *Journal of Neuroscience*, *26*(24), 6422–6430.
- Yang, T. T., Simmons, A. N., Matthews, S. C., Tapert, S. F., Bischoff-Grethe, A., Frank, G. K. W., et al. (2007). Increased amygdala activation is related to heart rate during emotion processing in adolescent subjects. *Neuroscience Letters*, *428*, 109–114.
- Yurgelun-Todd, D. A., & Killgore, W. D. (2006). Fear-related activity in the prefrontal cortex increases with age during adolescence: a preliminary fMRI study. *Neuroscience Letters*, *406*(3), 194–199.