Editorial

Adolescent social cognitive and affective neuroscience: past, present, and future

In this article, we review three areas of research within adolescent social cognitive and affective neuroscience: (i) emotion reactivity and regulation, (ii) mentalizing and (iii) peer relations, including social rejection or acceptance as well as peer influence. The review provides a context for current contributions to the special issue of *Social Cognitive and Affective Neuroscience on Adolescence*, and highlights three important themes that emerge from the special issue, which are relevant to future research. First, the age of participants studied (and labels for these age groups) is a critical design consideration. We suggest that it might be logical to reduce the reliance on convenience samples of undergraduates to represent adults in psychology and cognitive neuroscience studies, since there is substantial evidence that the brain is still developing within this age range. Second, developmental researchers are broadening their scope of inquiry by testing for non-linear effects, via increased use of longitudinal strategies or much wider age ranges and larger samples. Third, there is increasing appreciation for the interrelatedness of the three areas of focus in this special issue (emotion reactivity and regulation, mentalizing, and peer relations), as well as with other areas of interest in adolescent development.

Adolescence is a time of transition from childhood to being an independent adult; it is a period of life characterized by change and by moving away from one's family and towards one's peers. It is flexibly defined as the period of life that starts in early puberty and finishes when an individual attains a stable, independent role in society (Dahl, 2004). Puberty itself is a multi-faceted construct with many genetic and environmental determinants, as well as robust gender differences, making it extremely difficult to specify a precise onset of adolescence simply via chronological age. Meanwhile, the end of adolescence is marked by social achievements, not biological ones, and is even more fluid. In the West, the duration of adolescence is constantly being extended as it is more and more common for individuals to continue their education, and live at the family home, into their twenties or even later.

While teenagers have been studied for many decades by anthropologists, sociologists and social psychologists, until recently, very little was known about the brain in adolescence. In the last decade, neuroscience has given us new insights into the behavior of teenagers. The number of empirical studies assessing brain function associated with social cognitive and affective processes in neurotypical adolescents has grown exponentially, now at three to four times the rate of publication from five years ago. In this introduction, we provide a context for the contributions to

the special issue of *Social Cognitive and Affective Neuroscience* on Adolescence by briefly reviewing past research, with a focus on these recent years of rapid progress. The past and present findings, taken together, are then used to fuel suggestions for future progress in characterizing typical adolescent functional brain development. We note that in parallel, progress is also being made towards understanding changes in brain function during adolescence that are associated with various mental health and developmental disorders (for reviews, see Monk, 2008; Paus *et al.* 2008; Shaw *et al.*, 2010). Here, we focus on neurotypical adolescent development because this reflects the majority of contributions to the special issue, and understanding typical brain development lays the foundations for a better understanding of atypical development. This review is organized into several broad content areas focusing on the neural systems supporting adolescent emotion processing, mentalizing and peer relations, domains of significant transformation during adolescence.

fMRI studies of emotion processing during adolescence

One of the areas of longest standing interest in adolescent social cognitive and affective neuroscience research is emotion processing. The vast majority of these studies have focused on changes in emotion reactivity during adolescence, predominantly the neural responses to facial expressions of emotion. Indeed, the first social developmental neuroscience studies to include adolescents looked at their responses to expressions such as fear, anger, happiness and sadness (Baird *et al.*, 1999; Killgore *et al.*, 2001; Pine *et al.*, 2001; Monk *et al.*, 2003; Nelson *et al.*, 2003;

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Yang *et al.*, 2003; McClure *et al.*, 2004). A prime region of interest in those early years was the amygdala, due to its known involvement in adult processing of emotional facial expressions. In these early studies, if any analysis associated with age was carried out, findings tended to suggest no differences in amygdala responses between adolescents and adults (Pine *et al.*, 2001; McClure *et al.*, 2004; Nelson *et al.*, 2003), although one study found the amygdala was more responsive in adolescents than adults (Monk *et al.*, 2003). In recent years, however, studies have more consistently found the amygdala to be more reactive to facial expressions of emotion during adolescence than either childhood or adulthood (Killgore and Yurgelun-Todd, 2007; Guyer *et al.*, 2008; Hare *et al.*, 2008; Passarotti *et al.*, 2009; Pfeifer *et al.*, 2011), although this effect appears to vary by emotion or task design in ways that are not yet clear, and is still absent in some studies (Williams *et al.*, 2006; Yurgelun-Todd and Killgore, 2006; Rahko *et al.*, 2010). The paradigms used have all varied slightly, and have included passive viewing of static and dynamic faces, affect matching and various attentional directions (e.g. to gender or facial features). Future research should attempt to clarify emotion- and task-specific effects in the developmental trajectory of amygdala response to facial affect.

The differences noted above between early and recent studies, specifically the recent identification of developmental changes in amygdala reactivity (peaks during adolescence, relative to childhood or adulthood), may have resulted from various methodological improvements, including scanning sequences that allow researchers to obtain better signal in medial temporal and orbitofrontal regions, or the use of larger samples and longitudinal designs. Recent yields from the IMAGEN study (Schumann *et al.*, 2010), a multi-site imaging genetics study with thousands of adolescent participants, have benefited from several of these and other advances. One manuscript reported a combined participant total of over 1100 adolescents, allowing researchers to create sharply defined probability maps delineating the networks responding to angry and neutral facial expressions specifically in 13.5- to 15.5-year-olds (Tahmasebi *et al.*, 2011). The large sample also made it possible to look at sex differences, finding that girls' responses to neutral faces exceeded those of boys across multiple regions, whereas boys' responses to angry faces exceeded those of girls in the right amygdala. Another manuscript reporting on 470 adolescents from the IMAGEN sample (averaging 14.5 years of age) found that boys' responses to angry faces exceeded those of girls in the right amygdala (Schneider *et al.*, 2011), but also noted that the bilateral amygdala responses to angry and neutral faces were equivalent when collapsing across genders. Together these studies suggest that both angry and neutral faces are highly salient to adolescents, in ways that may differ by gender. Such studies represent exciting progress since the earliest attempts in the field to look at gender differences in adolescent emotion processing (Killgore *et al.*, 2001; McClure *et al.*, 2004; Yurgelun-Todd and Killgore, 2006).

More recent studies investigating age-related changes have also identified other regions of interest that change over development in response to emotions, expanding the focus beyond the amygdala. For example, a longitudinal study surveying children at age 10 years, and again in early adolescence at age 13 years, identified increases in ventral striatum to emotional expressions across happy, sad, angry and fearful expressions, and increases in ventromedial PFC (VMPFC) to happy, sad, fearful and neutral expressions (Pfeifer *et al.*, 2011). Several other studies have likewise observed increases in activity during emotion tasks in various subregions of PFC with development from childhood to adolescence (Yurgelun-Todd and Killgore, 2006; Deeley *et al.*, 2008; Hare *et al.*, 2008; Passarotti *et al.*, 2009). One hypothesis ventured by some of these studies is that the increasing responses in PFC indicate greater exertion of cognitive control in affective contexts. However, this speculation has often relied heavily on reverse inference, that is, assuming that the activation of a certain brain region implies the involvement of a particular cognitive process (Poldrack, 2006, 2011).

A related area of inquiry that has received surprisingly little attention is the development of the neural systems directly supporting emotion regulation, and not just reactivity, in adolescence. In adults, emotional reappraisal engages lateral and/or medial PFC and this is functionally associated with changes in amygdala activity (Ochsner and Gross, 2007). Reappraisal is a particularly adaptive form of emotion regulation that involves reframing the meaning of a stimulus in order to change the emotional response it elicits, like imagining that an ill person in a hospital bed is not dying, but instead receiving a treatment that will make them healthy again. Very few studies have examined emotion regulation processes at the neural level in adolescents (see Levesque *et al.*, 2004, for an fMRI study of young girls aged 8–10 years regulating the emotions elicited by sad films). This might in part be due in part to the ethical complexities of exposing minors to potentially traumatic stimuli (such as the International Affective Picture System; IAPS; Lang *et al.*, 2008), which is often necessary in emotional reappraisal studies. However, one study looked at the regulation of responses to disgust (Pitskel *et al.*, 2011), by asking children and adolescents (aged 7–17 years) to look, up-regulate (pretend it is right in front of you) or down-regulate (pretend it is fake) their experience of disgust elicited by disgusting IAPS stimuli. Although other fMRI studies summarized above suggest emotion reactivity peaks in adolescence (greater than during childhood or adulthood), insula activation elicited by the specific emotion of disgust significantly decreased with age in the passive viewing condition, and there were no significant relationships between age and self-report ratings of disgust in this (or any other) condition. Together these results suggest that, unlike for some other

emotions, adolescents are not necessarily more reactive to disgust than children. The left angular gyrus was involved in both up- and down-regulation of disgust across the entire sample, perhaps due to the necessary use of pretense (related to simulation and false belief, both of which can engage lateral parietal cortex). Connectivity analyses suggested that the VMPFC diminished responses in amygdala and insula during down-regulation. The results also suggested that down-regulation may increase with development given significant negative correlations between age and amygdala activity in that condition, but since there were no behavioral differences in self-report ratings of reappraisal effectiveness, this hypothesis needs to be further validated.

Studying emotion regulation in adolescence at the neural level is now further extended by a contribution to this issue that likewise tackled the issue of exposing minors to distressing content (McRae et al., this issue). In this fMRI study, 38 participants aged 10–22 years were asked to engage in reappraisal of negative IAPS stimuli, in contrast to passive viewing of negative and neutral stimuli. Parents of participants under age 18 years were allowed to pre-screen stimuli in advance and rule out up to one dozen if so desired. One noteworthy behavioral result from this study illustrated that younger participants self-reported higher negative affect during reappraisal trials than older participants, which suggests this emotion regulation ability improves with development. After equating performance as closely as possible across the sample, the authors found both linear and quadratic effects of age on the neural correlates of reappraisal processes. Activity in ventrolateral PFC (VLPFC) during emotion regulation increased linearly with age. Quadratic effects were observed in posterior cingulate during emotion regulation (greatest in the 14- to 17-year-olds compared with 10- to 13-year-olds and 18- to 23-year-olds), as well as in medial PFC during emotion reactivity (least in the 14- to 17-year-olds). The authors hypothesized these results possibly reflect changes in adolescents' use of social cognitive processing during reappraisal, but also cautioned that this interpretation relies on reverse inference, and future work is needed to explore this new hypothesis.

Another noteworthy area of study with respect to adolescent emotion processing is the relationship between neural responses it elicits and various measures of individual differences in development, including autonomic system reactivity (Yang et al., 2007), risky behavior and susceptibility to peer influence (Pfeifer et al., 2011), or negative affect and depressive symptomatology (Forbes et al., 2010). In this issue, Whittle and colleagues (Whittle et al., this issue) review the limited number of studies looking at atypical brain function during adolescent depression, which rely primarily on facial expressions of emotions. Their fMRI study makes an interesting advance by exposing adolescents to videoclips of their own mothers' affective behavior (in comparison to similar videoclips of an unfamiliar mother), an important contribution because the stimuli are much more salient and naturalistic than the commonly used static emotional facial expressions of adults. Collapsed across own and unfamiliar mother conditions, positive (vs. neutral) affective behavior elicited activity in bilateral superior temporal sulcus and amygdala, while negative (vs. neutral) affective behavior also elicited activity in medial PFC and dorsal anterior cingulate cortex (ACC). There was more activity in rostral and dorsal ACC, as well as in precuneus and posterior cingulate, during responses to their own mother's positive (vs. neutral) affective behavior; however, a reduction in this pattern specific to rostral anterior cingulate cortex (ACC) was correlated with increased depressive symptoms. It is perhaps to soon to fully interpret these kinds of brain–behavior correlations, but it is critical to continue cataloguing them in order to build up hypotheses about task-dependent function in these regions, in ways that will also inform the study of developmental disorders and psychopathology.

Finally, the most recently emerging interest in this particular area of study is disentangling effects of chronological age from the effects of puberty (i.e. the significant increase in various hormones associated with sexual maturation, and the physical changes that occur as a consequence of these neuroendocrine changes). Adolescence is traditionally defined by the onset of puberty, but pubertal stage and chronological age are not tightly correlated within early adolescence, and it is likely that at least some aspects of adolescent brain development are triggered by puberty (while others might be more associated with age). In a recent study, Forbes and colleagues (2011) sampled from a narrow age range (11–13 years) and assessed pubertal development (using Tanner staging conducted by pediatric experts). They found that amygdala responses to neutral faces, and VLPFC responses to fear faces, were greater in pre/early puberty than mid/late puberty. A contribution to the current special issue by Moore and colleagues (this issue) expanded this line of inquiry via a longitudinal study, in which 45 participants were followed from age 10 to 13 years. Amygdala reactivity to emotional facial expressions was correlated with pubertal development at both time-points, measured in this case via self-report on the Pubertal Development Scale (PDS; Petersen et al., 1988), and was independent of chronological age. Correlations between pubertal development and responses to affective faces in the amygdala, hippocampus, and temporal pole were stronger in early adolescence than late childhood. Future studies should attempt to reconcile these differences by exploring these factors carefully. One important goal will be to delineate pubertal influences on gender differences in neural responses to particular emotional expressions during adolescence, as identified by the recent large-scale studies discussed above. Nevertheless, Moore et al. (this issue) represents an important and novel contribution to the literature that paves the way for further investigation into the dissociable effects of puberty vs age on affective brain development.

In summary, those studies in the special issue which focus primarily on affective processing illustrate provide the following insights. First, it will be useful in the future to continue diversifying the elicitors of affect, from the commonly used facial expressions of emotion to more intense (McRae *et al.*, this issue), dynamic and personally relevant stimuli (Whittle *et al.*, this issue). Second, it will be critical to expand our focus beyond the study of simple emotion reactivity during adolescence, to explicitly modelling emotion regulation processes and their development (McRae *et al.*, this issue). Finally, it is clear that independent of chronological age, pubertal development has unique effects on brain function (Moore *et al.*, this issue), thus future fMRI studies across a range of socioemotional processes should attend to this important predictor of change.

fMRI studies of mentalizing during adolescence

Theory of mind, or mentalizing, is the process that enables us to understand other people's actions and behavior in terms of the underlying mental states that drive them (Frith and Frith, 2007). While there have been many studies attempting to identify the neural systems underlying mentalizing abilities in adults (for reviews, see Amodio and Frith, 2006; Carrington and Bailey, 2008), studies focusing on the development of mentalizing are much fewer in number, especially in adolescent samples. However, interest in this area is growing rapidly with the realization that many of the sociocognitive changes in adolescence are likely to be influenced by development of the social brain beyond childhood. For example, one recent study implicated several mentalizing regions, such as dorsomedial PFC (DMPFC) and temporo-parietal junction (TPJ), in making reflected self-appraisals (reporting what you think others think about you) during both adolescence and adulthood (Pfeifer *et al.*, 2009). Interestingly, adolescents also used these same mentalizing regions during direct self-appraisals (reporting what you think about yourself), significantly more than adults, who did not engage these regions during direct self-appraisals. This suggests the sociocognitive processes involved in mentalizing subserve self-perception in a unique way during adolescence.

One remarkably consistent finding across the studies investigating the neural correlates of mentalizing in adolescents is that, despite a wide variety of tasks, one particular region associated with mentalizing appears to be more active in adolescents than adults: DMPFC (for reviews and a meta-analysis, see Blakemore 2008, 2010). For example, one of the first developmental fMRI studies of mentalizing investigated changes in the neural systems supporting the understanding of communicative intent, using a task in which participants had to decipher a speaker's intention (whether they were being sincere or ironic; Wang *et al.*, 2006). The DMPFC (as well as left inferior frontal gyrus) was more active during this task in late childhood and early adolescence (9–14 years of age) than in adults (aged 23–33 years).

Meanwhile, adults relied more than adolescents on the fusiform gyrus for mentalizing. This anterior-to-posterior shift was observed again the following year in an fMRI study that involved thinking about one's own intentions (Blakemore *et al.*, 2007). Adolescents (aged 12–18 years) and adults (aged 22–38 years) were presented with scenarios requiring assessments of either intentional causality (involving intentions and consequential actions) or physical causality (involving natural events and their consequences). While the DMPFC was more active in adolescents than in adults during intentional causality judgments relative to physical causality judgments, the right posterior superior temporal sulcus (pSTS) was more active in adults than in adolescents.

In a contribution to this issue, Gunther Moor and colleagues (Gunther Moor *et al.*, this issue) compared brain activity in three age groups (10–12, 14–16 and 19–23 years) while participants carried out the 'mind in the eyes' paradigm (Baron-Cohen *et al.*, 2001a, 2001b). This task involves making judgements about the mental states and emotions a person is feeling based only on photographs of their eyes, rather than analysis of verbal statements. At all ages, greater activity was found in the pSTS during the reading the mind in the eyes task, relative to a control condition that involved making age and gender judgments about the same facial stimuli. However, only the youngest group showed significant additional involvement of the MPFC in mentalizing during this task. Once again, this new finding is consistent with the anterior-to posterior shift in brain regions supporting mentalizing. Including more than two age groups in investigations, like this one does, may allow us to ultimately gain traction on when this anterior-to-posterior shift occurs during adolescence. At least for this particular task, a reduction in MPFC signal appears to take place by 14–16 years of age. Future studies should continue to investigate this interesting question, which could have significant implications for adolescent interpersonal behavior.

The anterior-to-posterior developmental shift in brain regions supporting mentalizing has also been supported by research examining social emotion processing. Comparing adolescent and adult processing of social emotions is of relevance because, unlike basic affective states like joy and anger, phenomena like guilt and embarrassment require mentalizing. A study in adolescents (11–18 years) and adults (23–32 years) showed that, once again, DMPFC was more active in adolescents than adults (Burnett *et al.*, 2008). Furthermore, in this same sample, DMPFC was functionally connected with two other regions associated with mentalizing, TPJ and pSTS, significantly more in adolescents than adults (Burnett *et al.*, 2009). Another contribution to the special issue likewise investigates the intersection of affect and mentalizing (Sebastian *et al.*, this issue). Specifically, Sebastian and colleagues investigated distinct and overlapping neural substrates of cognitive mentalizing

(understanding thoughts and intentions) and affective mentalizing (understanding emotions), using a theoretical framework proposed by Shamay-Tsoory and colleagues (2010). A group of adolescents (aged 11–16 years) and adults (aged 24–40 years) were scanned while looking at cognitive and affective mentalizing cartoons. Both types of cartoons activated the social brain network (including DMPFC, pSTS/TPJ and temporal poles), while the affective mentalizing cartoons activated VMPFC to a greater extent than did cognitive mentalizing cartoons. Affective mentalizing was associated with increased VMPFC activity in the adolescents relative to the adults. This extends the pattern of greater DMPFC activity in children and adolescents, suggesting that the precise aspect of medial PFC that peaks during development is task-sensitive. It also highlights the importance of tracking more precisely subdivisions of interest within medial PFC (e.g. dorsal, anterior rostral and ventral; for example, see Pfeifer and Peake, 2012).

Another advance in this area of study is the use of neuroeconomics paradigms to elicit mentalizing processes, which participants presumably rely on to understand the behavior of their interaction partners. Investigations of reciprocal behavior using the 'trust game' (Berg et al., 1995), in which participants choose to share or hoard money (displaying trust or distrust in their partner), identify mentalizing regions at work including TPJ and DMPFC (van den Bos et al., 2009). In a recent follow-up exploring developmental trajectories (van den Bos et al., 2011), decreases in medial PFC/rostral ACC were observed in choices to reciprocate (sharing money following their partner's decision to trust them and share money). While all age groups studied used this region when defecting (hoarding money despite their partner's decision to trust them and share money), only early adolescents (ages 12–14 years) also did so when reciprocating. Meanwhile, left TPJ responses during reciprocate and defect trials (relative to trials where the first player did not trust the second player, which precluded the opportunity to reciprocate or defect) increased in a linear fashion from early adolescence to late adolescence (ages 15–17 years), and early adulthood (ages 18–22 years).

Although the focus of many of the developmental mentalizing studies has been on DMPFC and TPJ functioning, other regions have been implicated in mentalizing when considered from a different theoretical perspective. In particular, one line of research has emphasized a more "embodied" route to mentalizing, wherein we understand the intentions behind others' actions via a neural mechanism that co-activates to our own and others' actions (also called the action-observation network, or mirror neuron system). Shared neural representations have been identified for various goal-directed actions as well as emotions. The brain regions implicated in shared representations vary according to the specific action or emotion, but include areas such as the inferior frontal gyrus, premotor cortex

and supplementary motor areas, inferior parietal lobule, and somatosensory cortex (Caspers et al., 2010; Keysers et al., 2010), as well as dorsal anterior cingulate cortex (ACC) and anterior insula. Although a handful of studies have explored shared neural representations as mentalizing mechanisms in neurotypical preadolescent children (e.g. Grosbras et al., 2007; Pfeifer et al., 2008), the following contribution to the special issue extends this line of work firmly into adolescence.

In another longitudinal contribution to the special issue, Shaw and colleagues (this issue) closely examine the functioning of the action-observation network from age 10 to 13 years with three waves of data, acquired once every 1.5 years. The authors conducted an activation likelihood estimate (ALE) analysis of action-observation and imitation studies, which identified a priori regions of interest (ROIs) in frontal, parietal and occipito-temporal areas, as well as the amygdala. Participants viewed neutral (ambiguous) and angry hand and face actions. Percent BOLD (blood-oxygenation-level dependent) signal change and ratio of active to quiescent voxels within the ROIs were calculated at each timepoint, for each participant, to represent magnitude and extent of the neural response, respectively. Linear and nonlinear (quadratic) trends in development were then interrogated. Most of the ROIs demonstrated significant linear age-related decreases in their magnitude and extent of activation measures. However, the data were examined not only by chronological age but also by pubertal stage (after covarying out chronological age). Interestingly, they observe that when pubertal stage is the predictor instead of chronological age, some linear trends are replaced by nonlinear trends: U-shaped in frontal and occipito-temporal ROIs, and inverted U-shaped in parietal ROIs. Like the contribution from Moore et al. (this issue), this study utilizes a longitudinal design and demonstrates trajectories that are specific to pubertal development, independent of chronological age. Together, these two papers illustrate the value of a longitudinal design and the importance of assessing puberty, not just chronological age, during adolescence.

In summary, the contributions to the special issue focusing primarily on mentalizing illustrate two important points. First, the well-validated linear age-related decline in DMPFC responses during mentalizing (Gunther Moor et al., this issue) is now joined by linear and non-linear patterns of developmental change in other regions associated with simulation (e.g., premotor cortex; Shaw et al., this issue). Furthermore, affective contributions to or influences on mentalizing and simulation also undergo significant change during adolescence (Sebastian et al., and Shaw et al., this issue).

fMRI studies of peer relations during adolescence

Compared with children, adolescents are more sociable, form more complex and hierarchical peer relationships and are more sensitive to acceptance and rejection by peers

(Steinberg and Morris, 2001). Thus, knowledge about the neural systems supporting peer relations is essential to understanding adolescent development. Yet, this topic of inquiry has been the most recent to emerge, perhaps in part due to a need for paradigms that allow participants to have 'real' social interactions in the scanner. One well-known paradigm that accomplishes this is the 'cyberball' game (Williams *et al.*, 2000), in which participants are led to believe they are playing an online game of 'catch' with confederates. During this game, participants are included for some period(s) of time, but eventually also excluded. In adults, this leads to dorsal ACC (and often anterior insula) activation, increasingly so, to the extent that participants feel distressed by the social rejection, while VLPFC is engaged presumably to downregulate the negative affective response (Eisenberger *et al.*, 2003). The first study that employed this paradigm in adolescents found that 13-year-olds activated the insula more during social exclusion than inclusion (Masten *et al.*, 2009). Unlike in adults, there was no main effect of exclusion on either dorsal ACC or VLPFC activity. However, activity in VLPFC (as well as ventral striatum and DMPFC) was negatively correlated with activity in dorsal and ventral ACC, insula and amygdala. A follow-up study of these same participants indicated that greater ventral ACC activity during social exclusion at age 13 years predicted higher levels of depressive symptoms 1 year later, after controlling for initial levels of depressive symptoms (Masten *et al.*, 2011).

Other studies of social rejection using adolescents have modified the traditional cyberball paradigm to alternate between epochs of inclusion and exclusion more rapidly, which may lead to greater statistical power than the original design, a single epoch of inclusion and a single epoch of exclusion (Sebastian *et al.*, 2010, 2011; Bolling *et al.*, 2011a). In one such study, female adolescents (14–17 years) and young adults (24–39 years) both engaged ventral ACC (as well as VMPFC and orbitofrontal cortex) more during social exclusion than inclusion, and the VLPFC response was attenuated in adolescents (Sebastian *et al.*, 2011). This general replication was paired with an interesting extension, which was that only in adolescents, greater VMPFC responses during exclusion than inclusion were associated with greater susceptibility to peer influence. Another study sampled across a wider age range of children and adolescents (7–17 years), and also compared cyberball with a second game called 'cybershape', which violates social expectancies (by not following rules), but does not cause social exclusion of the participant (Bolling *et al.*, 2011a, 2011b). In this study, social exclusion (but not rule violation) resulted in activity in ventral ACC and insula, consistent with other studies in adolescents, but it also engaged posterior cingulate and retrosplenial cortex. Responses in VLPFC, as well as several mentalizing regions, increased with age during social exclusion. It is noteworthy

that, although Bolling *et al.* (2011a) included mostly male participants, and Sebastian *et al.* (2011) included solely female participants, there was significant overlap of effects across studies. This suggests that responses to peer rejection share common ground in adolescence across both genders: specifically, ventral ACC and insula are responsive to social exclusion, but ventrolateral PFC is less engaged than in adults (Sebastian and Blakemore, 2011).

Of course, the cyberball paradigm is not the only method available for studying peer relations using neuroimaging techniques. One variation is called the 'social judgment' task (Somerville *et al.*, 2006; Gunther Moor *et al.*, 2010), in which participants guess whether unfamiliar, age-matched peers will like them. In one study spanning from 8 to 25 years of age, expecting to be liked engaged VMPFC and striatum more with age (Gunther Moor *et al.*, 2010). Ventral ACC and VLPFC (among other regions) were also increasingly involved in processing social rejection feedback (being disliked) with age. These findings are nicely consistent with those using cyberball, although the authors note that the responses to peer evaluations did not peak in early or middle adolescence, as might be expected.

Another approach, the 'chatroom' task, slightly changes the focus from anticipated social evaluations (expecting to be liked/disliked) to interest in peer interactions. Participants think they are in a multisite investigation of internet-based communication (chat room behavior). They view pictures of age-matched peers, rate their interest in interacting with each peer, and guess how interested each peer is in interacting with them. One study of 9- to 17-year-olds using the chatroom task found that activity in ventral striatum and insula increased with age when girls, but not boys, attempted to gauge a high-interest peer's interest in them (Guyer *et al.*, 2009). This knowledge is extended by another contribution to the special issue, which focused on participants' receipt of feedback that high and low interest peers were (or were not) interested in interacting with them, and subsequent ratings of distress caused by each acceptance or rejection (Guyer *et al.*, this issue). Across both high- and low-interest peers, responses were greater in ventral striatum, right pSTS/TPJ and fusiform gyrus during acceptance, compared to rejection. Meanwhile, responses were greater in VLPFC following both kinds of feedback for low-interest peers. However, there were significant interactions between feedback and age, gender and level of interest in peers. For example, in girls but not boys, activity in the insula increased with age during acceptance *vs* rejection from high-interest peers. This result (insula activity during acceptance, rather than rejection) may differ from the patterns described above because of using multiple peers, and specifically contrasting between those who were of high or low interest to the participant.

In another contribution to the special issue, the features of cyberball and chatroom or social judgment tasks were

blended, in a new paradigm called 'chatroom interact' (Silk et al., this issue). Here participants viewed photographs of age-matched peers, and then also engaged in simulated live interactions, where both self and other were viewable on screen. This study used pupillary reactivity to peer feedback (acceptance and rejection) as an index of brain activity in regions associated with cognitive control and emotion regulation, including dorsolateral PFC, ACC, and amygdala. Pupil dilation was greater in response to rejection than acceptance, and this effect increased with age (across participants 9- to 17-years old). Closeness to and connection with peers in everyday life was measured multiple times over the course of multiple days, and participants who reported higher levels of closeness/connection during peer interactions demonstrated less pupil dilation during rejection. Interestingly, following rejection, participants tended to avoid looking at themselves on screen, but following acceptance, participants tended to center their gaze on themselves. Pupillary responses were strongly correlated with eye gaze position during the first second following feedback, such that participants with greater pupil dilation during and leading up to the rejection tended to avert their gaze away from the self more. Together, these results suggest that peer evaluations affect not only physiological responses but also patterns of attention, especially in older adolescents. Another contribution to the special issue dovetails with this study by examining how time spent with friends was associated with neural responses to exclusion during cyberball (Masten et al., this issue). Seniors in high school (ages 17–18 years) completed a nightly diary for two weeks, recording how much time they spent with friends outside of school. Two years later, the participants completed an fMRI scan. Average time spent with friends during high school was negatively correlated with activity in anterior insula activity during exclusion. Together, these two studies suggest aspects of friendship quality may act as a buffer against negative affective reactions to peer rejection. Both studies also took the important step of assessing qualities of adolescents' interactions with real peers and friends in their everyday lives. Future studies should endeavor to examine how the relationship between various indicators of peer relationship qualities and neural responses to different kinds of peer interactions changes throughout adolescence.

Yet, another distinct approach to understanding peer relations during adolescence at the neural level has been to look at responses to peer influence. In particular, these studies examine the impact of peer influence on adolescent risk-taking behavior, which represents another productive area of developmental neuroscience research that is beyond the scope of this introduction (for a recent review, see Somerville et al., 2010). The interest in pairing peer influence with risk-taking is due to the robust finding in behavioral studies that, unlike adults, adolescents are particularly prone to taking risks when peers are present (Steinberg,

2008). In one fMRI study (Chein et al., 2010) participants played the 'stoplight task', a driving game in which participants have to decide whether or not to go and risk crashing at yellow lights (Gardner and Steinberg, 2005). Two friends of each participant were allowed in the console room and communicated with the participant over the intercom when they were watching. The results showed that there was an interaction between age group and social context in responses from ventral striatum and orbitofrontal cortex. These two regions were significantly more active in adolescents (ages 14–18 years) during decision-making events (when stoplights turned yellow), compared to two young adult groups (ages 19–22 and 24–29 years). Meanwhile, the older group of young adults relied more on lateral PFC during the decision-making events, across both social contexts (alone and with peers).

In a related contribution to the special issue, Segalowitz and colleagues (this issue) extend this line of work by focusing on adolescent males (aged 15 years), playing a similar driving game while undergoing electroencephalography (EEG). Source estimation of a specific event-related potential (ERP) component associated with responses to negative performance feedback, the feedback-related negativity (FRN), was the dependent variable of interest. In the peer condition, two friends were allowed to encourage, advise and generally 'egg on' the participant. First, the FRN was observed to be stronger when participants were alone, compared with when they were being influenced by peers. In addition, weaker FRNs were associated with higher trait surgency (measured by positive affect, sensation-seeking and behavioral approach). The FRN was localized to VMPFC, rostral ACC and dorsal ACC during the peer influence condition using Low Resolution Electromagnetic Tomography (LORETA). Weaker intracerebral current source densities in rostral ACC and VMPFC during the peer influence condition correlated with higher trait surgency. The authors suggest that a diminished FRN, reflective of diminished medial PFC activity, reflects diminished regulatory control in the context of peer influence, particularly for high surgency boys. As noted by the authors, this should not be generalized to adolescent girls without further investigation. However, this study begins to elucidate some of the individual difference factors that may moderate susceptibility to peer influence during the teenage years.

In summary, the common message of the studies in the special issue focusing primarily on peer relations is 2-fold. First, real peer contexts appear to influence multiple indices of adolescents' neural responses to peer interactions or social exclusion (Masten et al., this issue; Segalowitz et al., this issue; Silk et al., this issue). Second, peer interactions of various types are highly likely to arouse an affective response in adolescents, and/or influence how they direct their attention or process feedback (Guyer et al., this issue; Masten et al., this issue; Segalowitz et al., this issue; Silk et al., this issue).

ISSUES, FUTURE DIRECTIONS AND CONCLUSIONS

From a bird's-eye view, several important themes emerge in this special issue on Adolescence that are relevant for future research. One theme reflects a tension between the ability to chart linear and non-linear developmental trajectories by significantly expanding participant age ranges, and the difficulty of categorizing and defining age groups appropriately. For example, in studies like Gunther Moor *et al.* and McRae *et al.* (both this issue), the group labelled young adults included very young individuals (aged 19–23, 18–22 and ≥18 years, respectively). Meanwhile, Masten *et al.* (this issue) defined their 18-year-old participants as adolescents. In other words, the same chronological age is variably defined as adolescents by some and young adults by others. We know relatively little about how brain activation associated with these various aspects of affective or mentalizing processes and peer relations changes during the third decade (ages 20–29 years). We think this issue calls for continued careful selection not only of age labels, but also of participant ages, to help ensure that comparison groups are most relevant to defining developmental trajectories. In particular, researchers might consider justifying their choice of age labels by incorporating indices of pubertal development, independent functioning in society, or other markers that help to identify adolescent group membership with better precision.

A second theme focuses on the methodologies and analyses used in developmental neuroscience. The special issue reveals the field's increasing use of longitudinal studies, either with multiple waves of fMRI for each participant (Moore *et al.* and Shaw *et al.*, this issue), or drawing connections between behavioral data collected at one timepoint and imaging data collected at another timepoint (Masten *et al.*, this issue). It is also becoming more common for wider age ranges to be sampled continuously (Guyer *et al.* and Silk *et al.*, this issue) and discontinuously (Gunther Moor *et al.* and Sebastian *et al.*, this issue), a practice that is useful to continue as it allows researchers to test for both linear and non-linear age-related trends (McRae *et al.*, this issue; Shaw *et al.*, this issue.). Another recent advance in the field illustrated twice in this special issue is the specific consideration of pubertal development as an instigator of neural change, independent from chronological age (Moore *et al.* and Shaw *et al.*, this issue).

A third and final theme deals with the intertwined nature of social, cognitive, and affective processes in adolescence. Early studies in the field were typically more compartmentalized, tending to focus primarily on one topic (such as affect or mentalizing). In the special issue, many studies crossed topical boundaries. For example, Sebastian *et al.* (this issue) compared cognitive and affective theory of mind; Segalowitz *et al.* (this issue) related peer influence to risk-taking; Shaw *et al.* (this issue) examined shared neural representations for actions with and without affect; Whittle *et al.* (this issue) utilized parent interactions to elicit affect.

We applaud this less compartmentalized approach, while remaining mindful of methodological challenges such as maintaining clear definitions of each ontological construct (Lenartowicz *et al.*, 2010).

In conclusion, the special issue of *Social Cognitive and Affective Neuroscience* on Adolescence presents an exciting and invigorating collection of papers. Core findings are extended and strengthened, methodological techniques are advanced and constructs are interrelated to better reflect the richness and complexity inherent in the everyday lives of teenagers.

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