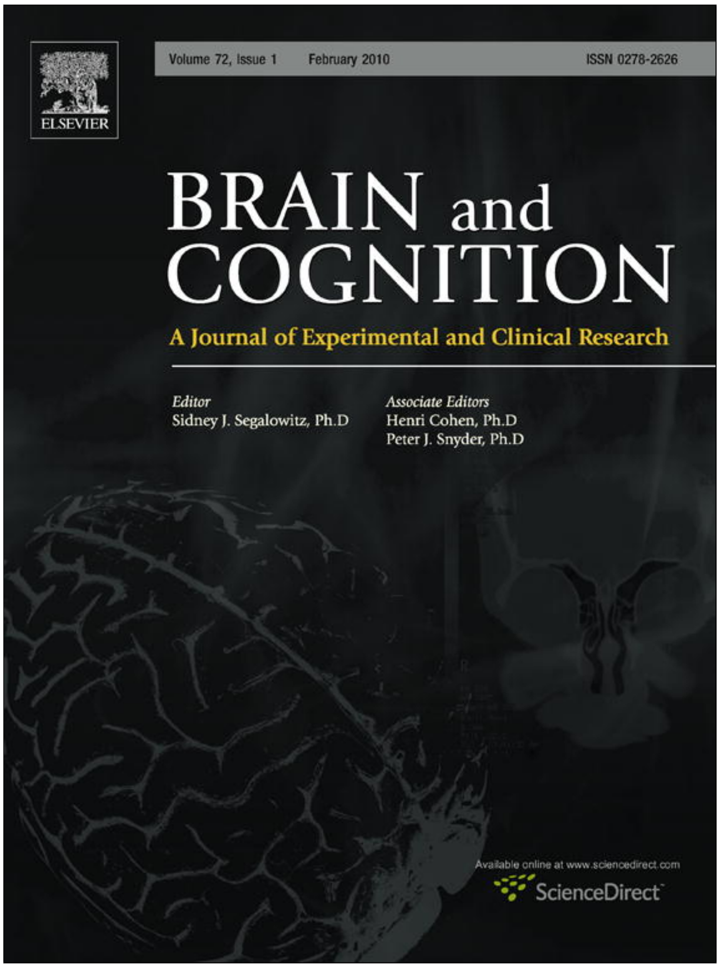
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Review Article

Social brain development and the affective consequences of ostracism in adolescence

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ABSTRACT

Recent structural and functional imaging studies have provided evidence for continued development of brain regions involved in social cognition during adolescence. In this paper, we review this rapidly expanding area of neuroscience and describe models of neurocognitive development that have emerged recently. One implication of these models is that neural development underlies commonly observed adolescent phenomena such as susceptibility to peer influence and sensitivity to peer rejection. Experimental behavioural evidence of rejection sensitivity in adolescence is currently sparse. Here, we describe a study that directly compared the affective consequences of an experimental ostracism manipulation (Cyberball) in female adolescents and adults. The ostracism condition led to significantly greater affective consequences in the adolescents compared with adults. This suggests that the ability to regulate distress resulting from ostracism continues to develop between adolescence and adulthood. The results are discussed in the context of models of neurocognitive development.

1. Introduction

Human adolescence is a period of physical, psychological and social transition between childhood and adulthood (Spear, 2000). In recent years it has been established that substantial neural development also occurs during this period of life (see Paus, 2005 for a review; Gogtay & Thompson, 2010; Paus, this issue; Giedd & Lenroot, 2010; Schmithorst, 2010). There are significant changes in grey matter and white matter volumes in brain regions responsible for complex human behaviours, notably the prefrontal cortex and temporo-parietal regions (Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 1999). These regions are involved in a variety of cognitive functions, including social cognition, mentalising (the attribution of mental states to oneself and to other people) and self-related processing. In this paper, we review developmental functional imaging studies of social cognition, mentalising and self-processing, and discuss recent models of adolescent neurocognitive development. We then describe a behavioural study that investigated affective reactions to an instance of experimentally induced ostracism in adolescents, compared with adults. Finally, we evaluate how the results of our study can inform models of adolescent development.

2. Developmental functional imaging studies of the social brain

2.1. The social brain

The social brain is defined as the network of brain regions subserving social cognition, i.e. those enabling us to recognise others, and to evaluate our own and others' mental states (intentions, desires and beliefs), feelings, enduring dispositions and actions (Brothers, 1990; Frith & Frith, 2007). Many different brain regions are involved in social cognition, including medial prefrontal cortex (mPFC), anterior cingulate cortex (ACC), inferior frontal gyrus, posterior superior temporal sulcus (pSTS), temporo-parietal junction (TPJ), the amygdala and anterior insula (see Fig. 1). Some of these brain regions are activated during the attribution of mental states to oneself and to others. This ability, known as mentalising or theory of mind, enables us to understand other people's behaviour and actions in terms of underlying mental states such as intentions, desires and beliefs (Frith & Frith, 2007). Social cognitive processes underlying mentalising range from basic perceptual processes such as biological motion and face perception (Frith, 2007; Pelphrey & Carter, 2008) to those enabling us to perceive and understand emotional responses in ourselves and others (Olsson & Ochsner, 2008), to more abstract meta-representational abilities enabling us to hold an 'intentional stance', i.e. the idea that others' act on the basis of their mental states (Dennett, 1987).

Using functional imaging and a wide range of stimuli, several studies have shown remarkable consistency in identifying the

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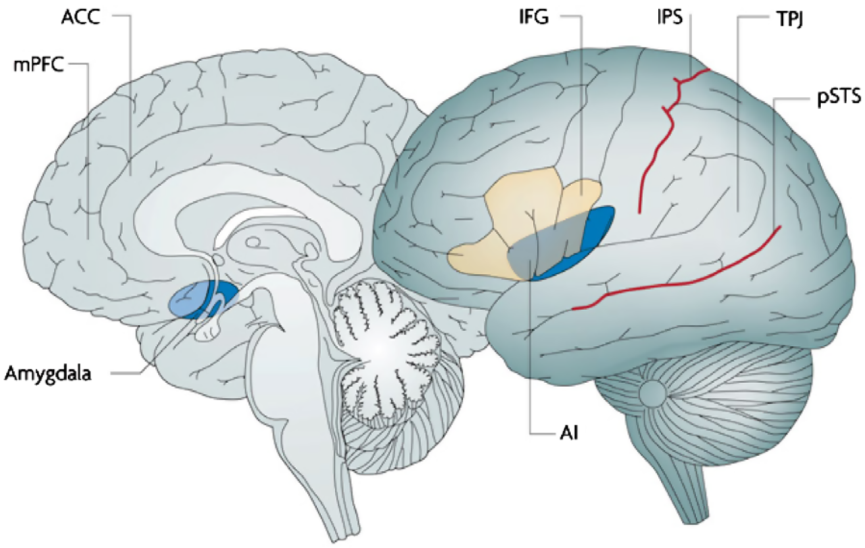


Fig. 1. Regions of the social brain. Studies using social cognitive tasks show consistent activation of a network of brain regions including the medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), posterior superior temporal sulcus (pSTS), amygdala, anterior cingulate cortex (ACC), anterior insula (AI), inferior frontal gyrus (IFG) and interparietal sulcus (IPS). See Frith and Frith (2007) for reviews of the function of these regions. Reproduced, with permission, from Blakemore (2008).

brain regions that are involved in mentalising. These studies have used stimuli such as stories (Fletcher et al., 1995; Gallagher et al., 2000; Saxe & Kanwisher, 2003), sentences (den Ouden, Frith, Frith, & Blakemore, 2005), cartoons (Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Gallagher et al., 2000) and animations (Castelli, Happe, Frith, & Frith, 2000) designed to elicit the attribution of mental states. In each case, the mentalising task resulted in the activation of a network of regions including the amygdala, pSTS/TPJ, the temporal poles and the mPFC. Each of these is hypothesised to contribute to different sub-processes involved in mentalising (Frith, 2007). For example, the amygdala is involved in processing emotional facial expressions (Morris et al., 1998); the pSTS/TPJ is involved in predicting complex movements (Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004); the temporal poles are thought to bind highly processed perceptual inputs with an emotional response (Olson, Plotzker, & Ezzyat, 2007); and the mPFC may have a special role in understanding our own and others' communicative intentions, particularly the anterior rostral subregion (Frith, 2007).

There is considerable overlap between these social brain regions and regions that are still developing structurally in adolescence. Adolescence is an interesting time to investigate the development of social cognition because this period of life is characterised by changes in social behaviour (Brown, 2004) and in self-awareness (Harter, 1990; Sebastian, Burnett, & Blakemore, 2008). Adolescence is a time during which peers, rather than parents, become influential in shaping social behaviour (Steinberg and Silverberg, 1986). In early adolescence, children become increasingly self-conscious and more aware of, and concerned with, others' opinions (Parker, Rubin, Erath, Wojslawowicz, & Buskirk, 2006; Vartanian, 2000). Thus, social brain functions, including mentalising and self-awareness, might be expected to develop during adolescence. In the next section, we review recent neuroimaging studies that have investigated the functional development of the social brain in adolescence.

2.2. Development of the mentalising network

A number of neuroimaging experiments have investigated the development of mentalising during adolescence and have consistently shown that mPFC activity decreases between adolescence and adulthood. One fMRI study investigated the development of communicative intent, using a task in which participants had to decide whether a speaker was being sincere or ironic (Wang, Lee, Sigman, & Dapretto, 2006). Understanding irony requires separating the literal from the intended meaning of a comment. In children/young adolescents (aged 9–14) the mPFC and left inferior frontal gyrus were more active during this task than in adults (aged 23–33). The authors interpreted the increased mPFC activity in young adolescents as a reflection of the need to resolve the discrepancy between the literal and intended meaning of an ironic remark. The region of the mPFC that was more active in young adolescents than in adults lies within the dorsal mPFC, an area that is consistently activated by mentalising tasks in adults (Amodio & Frith, 2006; Gilbert et al., 2006) (see Fig. 2; green dots).

A similar region of the dorsal mPFC in the right hemisphere was found to be more active in adolescents than in adults in an fMRI study that involved thinking about one's own intentions (Blakemore, den Ouden, Choudhury, & Frith, 2007). Adolescents (aged 12–18) and adults (aged 22–38) were presented with scenarios about intentional causality (involving intentions and consequential actions) or physical causality (involving natural events and their consequences). The right dorsal mPFC was more active in adolescents than in adults during intentional causality relative to physical causality (Fig. 2; blue dots). Conversely, a region in the right STS was more active in adults than in adolescents when they were thinking about intentional causality compared with physical causality. In this intentional causality study, the scenarios pertained to the self insomuch as they asked about participants' own hypothetical intentions. In another developmental study that focused on the processing of self-related sentences (Pfeifer, Lieberman, & Dapretto, 2007), children (aged 9.5–10.8) and adults (aged 23–31.7) read phrases about academic skills and social competence. In the *self* condition, participants were asked to indicate whether the phrases accurately described them. In the *other* condition they were asked to indicate whether the phrases accurately described a fictional, familiar other person (Harry Potter). The mPFC and ACC were more active in the children than in adults during self-knowledge retrieval compared with other-knowledge retrieval (see Fig. 2; yellow dots). The authors suggested that, compared with adults, early adolescents might rely more on 'on-line' self-reflective processing performed by the mPFC.

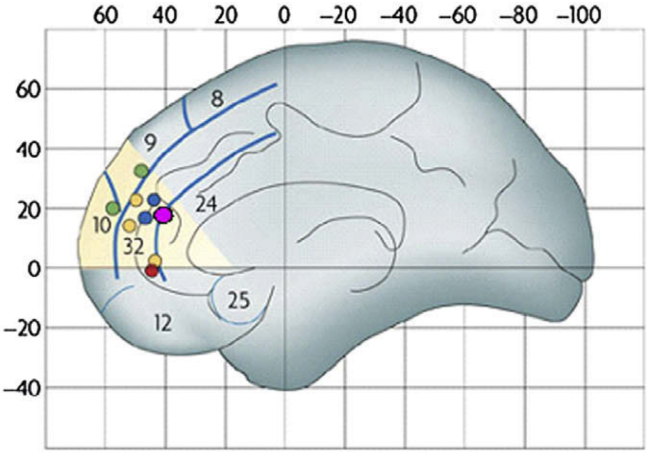


Fig. 2. Activation of the medial prefrontal cortex (mPFC) during mentalising tasks decreases during adolescence. The yellow shaded area indicates a section of the dorsal mPFC that is activated in studies of mentalising. The coloured dots indicate voxels in which decreased activity is observed between late childhood and adulthood during participation in social cognition tasks. The red dot represents the area of activation that was higher in adolescents than in adults during the animations task used by Wang et al. (2006). The green dots represent areas that were more active in adolescents than in adults during an irony-comprehension task (Moriguchi, Ohnishi, Mori, Matsuda, & Komaki, 2007). The blue dots represent areas of activation that were higher in adolescents than in adults during intention understanding (Blakemore et al., 2007). The yellow dots represent areas that were more active in children than in adults in a self–other evaluation task (Pfeifer et al., 2007). The pink dot represents the area of activation that was higher in adolescents than in adults in a social emotion task (Burnett et al., in press). The blue lines indicate approximate borders between Brodmann areas, which are numbered on the diagram. Adapted, with permission, from Blakemore (2008). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To summarise, as yet there have only been a handful of developmental neuroimaging studies of mentalising. However, there does seem to be some consistency: the studies to date point to a developmental shift in the neural strategy for mentalising. In particular, the studies have found that activity in mPFC decreases between adolescence and adulthood. There are several different explanations for changes in neural activity during social cognition tasks. One possibility is that adolescents and adults use different cognitive strategies to perform social cognition tasks. Another possibility is that the functional differences are a consequence of the structural development that takes place during this period of life (see Blakemore, 2008, for discussion).

2.3. Behavioural development of mentalising during adolescence

In the developmental neuroimaging studies of mentalising reviewed above, which showed that activity in mPFC decreased between adolescence and adulthood, task performance was equated across age groups. Equating performance between groups is critical for the interpretation of the functional neuroimaging data: if performance between groups was significantly different, it would be impossible to know whether a group difference in neural activity was the cause, or simply a consequence of, the difference in performance. However, matching performance in this way negates important differences between adolescents and adults in terms of social cognition. If the neural substrates for social cognition change during adolescence, what are the consequences for social cognitive behaviour? Most developmental studies of social cognition focus on early childhood, possibly because children perform adequately in even quite complex mentalising tasks by age five (Frith & Frith, 2007). It is a challenge therefore to design a task on which older children and adolescents do not perform at ceiling level.

Recently, we used a computerised version of a mentalising task on which even adults make significant errors (Keysar, Lin, & Barr, 2003). We gave our version of this task to 177 female participants divided into five age groups: child I (7.3–9.7 years); child II (9.8–11.4); adolescent I (11.5–13.9); adolescent II (14.0–17.7) and adults (19.1–27.5) (Dumontheil, Apperly, & Blakemore, in press). Participants viewed a set of shelves containing objects, which they were instructed to move by a "director" who could see some but not all of the objects. In the critical condition, participants need to use the director's perspective and move only objects that the director can see, in order to make the correct response. The task involves both mentalising (taking another's perspective), and executive functions (the need for speeded response selection). The results demonstrated improvement on this task even between the adolescent II and adult groups. Thus, while theory of mind tasks are passed by age four, these new data indicate that the interaction between theory of mind and executive functions continues to develop in late adolescence (Dumontheil et al., in press).

2.4. Development of the affective processing network

The social brain also includes regions involved in processing information about the affective states of self and other. However, not all affective processing involves social stimuli, and a distinction can be drawn between social emotions, which require the understanding of mental states (e.g. embarrassment and guilt), and basic emotions, which do not (e.g. disgust, fear). A recent fMRI study investigated changes during adolescence of the neural processing of social emotion compared with basic emotion (Burnett, Bird, Moll, Frith, & Blakemore, in press). Adult (age 22–32) and adolescent (age 10–18) participants read scenarios that described either social emotions (guilt or embarrassment) or basic emotions (fear or disgust). Like the fMRI studies of mentalising reviewed above, activity in the dorsal MPFC during social relative to basic emotion was higher in the adolescent group than in the adult group (Fig. 2, pink dot), while the opposite developmental pattern was found in the left temporal pole.

One of the most important ways in which we have access to others' emotions is through interpreting facial expressions. Several behavioural studies have shown developmental changes in this ability during the course of adolescence (Herba, Landau, Russell, Ecker, & Phillips, 2006; McGivern, Andersen, Byrd, Mutter, & Reilly, 2002; Thomas, De Bellis, Graham, & LaBar, 2007), and functional neuroimaging studies have also found evidence of developmental change. Thomas et al. (2001) compared young adolescents (mean age 11 years) with adults using fMRI during the passive viewing of fearful and neutral faces. They found that while adults activated the amygdala only to fearful faces, adolescents activated the amygdala more to neutral faces, possibly because the latter were more ambiguous, or possibly because the amygdala is less selective earlier in development. However, there are conflicting findings in this area. For example Guyer et al. (2008) found greater amygdala activation to fearful faces in adolescents (aged 9–17 years) than in adults. Development of prefrontal cortex response to faces has also been found. Yurgelun-Todd and Killgore (2006) reported increased activity in a number of lateral and superior prefrontal regions (bilaterally for girls and right sided for boys) in response to fearful faces between the ages of 8 and 15. Thus, frontal activity increased between childhood and adolescence in this study. It would be interesting to compare adult responses within a similar design, as it might be predicted that PFC activity would decrease again, in line with studies of mentalising.

Another important social cognitive skill is the ability to allocate attention appropriately in a socio-emotional context. In one study, adolescents (aged 9–17 years) showed activation of the ACC and left OFC during passive viewing of fearful faces relative to neutral faces, whereas adults (aged 25–36) did not (Monk et al., 2003). When attention was directed to a non-emotional aspect of fearful (relative to neutral) faces, activity in the ACC was higher in adolescents compared with adults. Therefore, as in the mentalising studies reviewed above, frontal activity tended to decrease between adolescence and adulthood. In addition, the findings suggest that, whereas adults modulate brain activity based on attention demands, adolescents modulate activity based on the emotional nature of a stimulus. This suggests that the neural basis of the ability to pay attention to a non-salient stimulus (in this case, the nose of a fearful face) in the presence of emotionally evocative, attention-grabbing stimuli (the eyes of a fearful face) is still undergoing maturation between adolescence and adulthood.

Related to this is the ability to regulate one's own emotions, which is a prerequisite for successful social interaction. Studies in adults have shown that the regulation of emotions depends on the PFC, particularly ventrolateral regions, and its connections with limbic regions such as the amygdala (see Ochsner & Gross, 2005, 2007 for a review). Several studies have suggested functional change in this network between childhood and adulthood. Lévesque et al. (2004) found that 8–10 year olds activated more prefrontal loci than adults when asked to suppress emotional reactions to sad film clips (Lévesque et al., 2003) (though note that the children and adults were not directly compared in the same study).

More recently, Hare et al. (2008) scanned children, adolescents and adults (age range 7–32) during a go-nogo task involving fearful, happy, and calm facial expressions. Amygdala reactivity to fearful faces was greater in adolescents than in younger or older participants, and correlated with reaction time delays to fearful compared with happy expressions. In contrast, ventral PFC activity did not differ with age. Activity in ventral PFC was negatively correlated with reaction time difference, suggesting a regulatory role, and stronger amygdala–ventral PFC connectivity was associated with greater amygdala habituation over trials. The authors argue that increased limbic activation relative to ventral PFC regulation could contribute to the increased emotional reactivity and poor decision making associated with adolescence.

Another approach is to look at how a measured behavioural difference in putative affective processing is reflected at the neural level. Grosbras et al. (2007) divided young adolescents (mean age 10 years), into groups with Low and High resistance to peer influence, as measured by the Resistance to Peer Influence (RPI) questionnaire (Steinberg & Monahan, 2007). These groups were then compared in terms of their neural response to emotional and neutral stimuli (passive viewing of angry and neutral hand gestures/facial expressions). For the angry stimuli only, individuals with High RPI showed more co-ordinated activity across premotor and prefrontal regions than those with Low RPI. The authors suggested that High RPI adolescents may spontaneously engage executive processes in response to socially relevant stimuli, while Low RPI adolescents do not. By taking an individual differences approach, this study was able to suggest a neural mechanism that might account for differences in sensitivity to peer influence in early adolescence.

While most of the above studies have used stimuli that tap into a specific affective process (e.g. face or gesture processing), Guyer, McClure-Tone, Shiffrin, Pine, and Nelson (in press) used an ecologically valid chat-room paradigm in order to investigate neural responses to anticipated peer evaluation in adolescents aged 9–17. Participants were asked to think about how peers in the chat-room would evaluate them, and these peers had previously been rated as being of either high or low interest to the participant. For peers of high interest, relative to low, significant interactions between age and sex were seen. Specifically, in females only, there was increasing activation with age in regions involved in affective processing including the nucleus accumbens, hypothalamus, hippocampus and insula. This differential response between males and females mirrors behavioural data showing greater concern regarding peer evaluation among adolescent females than males (La Greca & Lopez, 1998), and neural data showing increasing sensitivity to social stimuli with age in female adolescents (McClure et al., 2004).

To summarise, there is some indication of functional development in brain regions involved in processing social stimuli between adolescence and adulthood. In particular, PFC activity during mentalising and face-processing tasks decreases with age, while PFC regions involved in emotion regulation exert increasing top–down control between adolescence and adulthood. In contrast, regions such as the amygdala, which are involved in the initial emotional response to a stimulus may be more active and less selective during adolescence than at other points during the lifespan. They may also show increased modulation by social salience, for example in the chat-room paradigm in adolescent females. In the following section, we describe recent models of adolescent neurocognitive development that have been proposed to link neurobiological changes initiated at the onset of puberty with socio-emotional development. These models provide an important theoretical framework in what has previously been a predominantly data-driven field.

3. Models of adolescent social neurocognitive development

Recently, several cognitive models have been proposed to account for behaviour associated with neurocognitive development during adolescence. These focus on the links between the development of executive functions (enabling flexible behaviour in pursuit of a goal) and aspects of social cognition such as affect regulation, with a view to explaining adolescent behavioural phenomena such as risk-taking in the presence of peers. These models have yet to incorporate explicitly the development of mentalising.

3.1. The Social Information Processing Network (SIPN) model

The SIPN model posits that social information processing occurs by way of three interacting neural "nodes", which afford the detection of social stimuli that are then integrated into a larger emotional and cognitive framework (Nelson, Leibenluft, McClure, & Pine, 2005). The detection node, comprising the intraparietal sulcus, the STS, the fusiform face area as well as temporal and occipital regions, deciphers social properties of the stimulus such as biological motion (Haxby, Hoffman, & Gobbini, 2002; Pelphrey & Carter, 2008). The affective node, comprising limbic areas including the amygdala, ventral striatum, hypothalamus and OFC, is thought then to process the emotional significance of the social stimulus (Whalen et al., 1998; Winston, Strange, O'Doherty, & Dolan, 2002). Finally, the cognitive-regulatory node, consisting of much of the PFC, is responsible for response inhibition, goal-directed behaviour and complex social behaviours (Frith, 2007). Changes in social cognitive behaviour during adolescence are proposed to result from the remodelling of these networks, particularly the affective and cognitive-regulatory nodes, and connectivity between nodes. Remodelling may result in part from the effect of pubertal gonadal steroids on limbic regions, which are densely innervated by gonadal steroid receptors (Ernst, Romeo, & Andersen, 2009; McEwen, 2001; Nelson et al., 2005); and partly from the gradual maturation of the prefrontal cortex, which continues into the late teens and early twenties (Gogtay et al., 2004; Sowell et al., 1999).

The focus of the SIPN model is on how social stimuli are imbued with emotional significance. The mentalising studies described above (which often do not include an affective component) suggest that the development of non-affective strategies for understanding our own and others' mental states may also represent an important contributor to changes in social cognition and behaviour during adolescence.

3.2. Subcortical/cortical developmental mismatch models

Casey, Jones, and Hare (2008) have noted that children (and adults) do not exhibit heightened emotional sensitivity or increased risk-taking as do adolescents. This is suggestive of a non-linear maturational trajectory for the brain networks subserving these processes. In a recent review, these researchers suggested that the limbic system (including the amygdala and nucleus accumbens) matures earlier than the PFC, with the result that individuals are more greatly affected by the emotional context when making decisions. The greatest mismatch in the development of these systems occurs during adolescence.

A similar model proposed by Steinberg (2005, 2008), focuses on the importance of social reward during adolescence. According to this model, the changing reward value of positive social feedback from peers and the development of executive functions interact to explain well-documented phenomena such as adolescent risk-taking and susceptibility to peer pressure. Remodelling of the dopamine system (Andersen, Thompson, Rutstein, Hostetter, & Teicher, 2000; Teicher, Andersen, & Hostetter, 1995) is hypothesised to increase the salience of social rewards such as peer approval, while gonadal steroid release is suggested to lead to an increasing sensitivity to social stimuli, via effects on oxytocin receptors (Chibbar, Toma, Mitchell, & Miller, 1990; Insel, Young, Witt, & Crews, 1993). Concurrently, there is relatively gradual development of prefrontal cognitive control mechanisms, and of connectivity between prefrontal and limbic regions (Hare et al., 2008). Therefore, the PFC may not be as efficient at regulating social and emotional responses as at other points in the lifespan.

An important strength of both of these models is that they suggest neurobiological explanations for why adolescents may be particularly sensitive to social reward, and why this might result in increased risk-taking. Self-report studies have shown that adolescents find spending time with peers particularly rewarding and are particularly influenced by their peers (Csikszentmihalyi, Larson, & Prescott, 1977; Larson & Richards, 1991). Susceptibility to peer influence is thought to contribute to adolescents' greater propensity to engage in risky activities, compared with other age groups (Steinberg, 2005, 2008). Empirical support for this theory comes from a recent behavioural study measuring the incidence of risky driving events in a car simulation video game, in which adolescents and adults played either alone or with two friends present. For adolescents, the presence of peers more than doubled the number of risks taken, whereas for adults the presence of peers had little effect on risky driving (Gardner & Steinberg, 2005).

This result has been interpreted as reflecting increased reward salience of peers during adolescence, mediated by the remodelling of dopaminergic circuitry (Steinberg, 2008). However, it is possible that the continuing development of social cognitive abilities such as mentalising (and its neural substrates) may also contribute. For example, as individuals improve in their ability to represent abstract social goals and the mental states of others during adolescence, they become more aware of others' reactions to them (Parker et al., 2006). They also become more aware of the importance of succeeding in social situations, and of the social costs of failure (Davey, Yücel, & Allen, 2008). This might contribute to the increased salience of peers, though this may not be restricted to reward salience but would also stretch to include an increased salience of potential negative consequences of social interaction. This increased salience could be further compounded by the relative immaturity of prefrontal regions involved in emotion regulation, resulting in heightened affective responses to negative social interactions.

Indeed, another well-documented phenomenon during adolescence is sensitivity to peer rejection (Kloep, 1999; Larson & Richards, 1994; O'Brien & Bierman, 1988). All the models discussed are compatible with the hypothesis that brain development might underlie this sensitivity. However, to date, studies have not explored rejection sensitivity empirically, comparing adolescents with adults to ascertain whether affective consequences of a rejection episode really are greater during adolescence, or whether the phenomenon could result from differences in environment (or some other systematically varying external factor) with age. In the next section, we describe a study that investigated the affective consequences of ostracism in adolescence.

4. Ostracism in adolescence

As peer relationships become more important in adolescence, the potential negative consequences of rejection or victimisation by peers increase. For example, Crick et al. (1999) have studied the effects of relational aggression (aggression based on damage, or the threat of damage, to interpersonal relationships) on children and adolescents. Often this takes the form of socially excluding the victim using the 'silent treatment', or by spreading rumours about the victim. Being a victim of relational aggression is associated with social-psychological adjustment problems, including internalising problems (e.g. depression), and externalising problems (e.g. lack of self-control).

Several studies using self-report methods have found hypersensitivity to peer acceptance and rejection in adolescents compared with younger children or adults (Kloep, 1999; Larson & Richards, 1994; O'Brien & Bierman, 1988). O'Brien and Bierman (1988) studied both preadolescent and adolescent attitudes to peer relationships and found that, while both groups felt that peers provided companionship and support, adolescents (aged 13–17) reported that peer evaluations were more important in determining their sense of personal self-worth than did younger children. Peer rejection was commonly viewed as an indication of their 'unworthiness' as an individual, and this peer effect on self-evaluation was most apparent in girls aged 13–15. This sensitivity appears to decline between mid-adolescence and adulthood. For example, Kloep (1999) found that the extent to which adolescent girls worried about peer acceptance reached a peak at age 15–16, and declined sharply thereafter.

Research in adults has led to the development of models of the psychological consequences of ostracism (see Williams, 2007 for a review). Most of these have necessarily focused on short term, isolated instances of exclusion by others. Williams (1997, 2001) proposed a need threat account, in which ostracism threatens four fundamental psychological needs: self-esteem, belonging, control and a sense of meaningful existence. Several studies have found that these needs are threatened (a construct termed 'need threat') following ostracism (Williams, Cheung, & Choi, 2000; Zadro, Boland, & Richardson, 2006; Zadro, Williams, & Richardson, 2004), and that people attempt to refortify these needs, for example, by conforming more to group norms (Williams et al., 2000). This theory has been generated on the basis of data from adult participants, and it is unknown whether adolescents react to ostracism in the same way.

The current study examined the affective consequences of an experimental ostracism manipulation in adolescents compared with adults. Ostracism was manipulated using Williams et al.'s (2000) 'Cyberball' paradigm. In this task, participants play a ball game over the internet with two other players, whose actions are pre-programmed. However, participants are led to believe they are playing with real individuals. After a few throws, the other players stop throwing the ball to the participants. This paradigm was chosen because it reliably induces feelings of rejection in adults (Eisenberger, Lieberman, & Williams, 2003; Williams et al., 2000; Zadro et al., 2004, 2006). The affective consequences of exclusion (low mood and anxiety) were measured via self-report. Additionally, we compared adults and adolescents on Williams et al.'s (2000) need threat scale.

In the current study we chose to test females for a number of reasons. Social anxiety has been found to be greater in adolescent girls than in boys, with higher social anxiety levels associated with poorer social functioning (La Greca & Lopez, 1998). This is likely related to the greater extent to which self-worth is determined by positive peer evaluations in adolescent girls than boys (O'Brien & Bierman, 1988). Furthermore, it has been found that girls are both more likely to use (Cairns, Cairns, Neckerman, & Ferguson, 1989) and to be subjected to (Crick & Nelson, 2002), relational aggression, and that adjustment problems are more strongly related to relational aggression in girls than in boys. Finally, adolescence is a key time for the emergence of mood disorders such as depression and anxiety (Costello et al., 2002; Paus, Keshavan, & Giedd, 2008), and it is at this time that the pattern of higher incidence in girls compared to boys is first seen (Angold et al., 1998). Therefore, it is particularly important to characterise social information processing and self-perception in adolescent girls.

To investigate whether the effects of ostracism change during the course of adolescence, we included two adolescent groups, which differed in terms of pubertal stage (verified by questionnaire): young adolescents (aged 11–13) and mid-adolescents (aged 14–15). Previous studies looking at the importance attached to peer evaluations in every-day life have shown that it peaks between 13 and 16 years in girls (Kloep, 1999; O'Brien & Bierman, 1988). This study aimed to explore whether a similar trend would be seen in an experimental paradigm. We predicted that the consequences of social rejection on affective measures of mood and anxiety would be greater in adolescents than in adults on the basis of previous reports of hypersensitivity to rejection in adolescence. Similarly, the four needs might also be differentially threatened by ostracism between the groups. However, an alternative possibility is that the four needs would be threatened equally across all age groups. One study (Zadro et al., 2006) has shown that the extent to which the four needs are threatened is not moderated by individual differences such as social anxiety immediately following ostracism, and that it is only after some time (45 min) that differences in coping strategy based on individual differences emerge. Therefore, the study further aims to explore whether there are developmental differences in the initial experience of need threat.

5. Methods

5.1. Participants

The study included 77 female participants divided into three groups: young adolescents (YA) ($N = 26$, age range: 11.9–13.9, mean = 12.8, SD = .59); mid-adolescents (MA) ($N = 25$, age range: 14.0–15.8, mean = 15.0, SD = .53), and adult ($N = 26$, age range: 22.2–47.1, mean = 27.4, SD = 6.2). Participants were asked to complete an adapted version of a developmental questionnaire (Carskadon & Acebo, 1993). Only 61% of participants returned their questionnaires; therefore Tanner stage data were used to confirm a developmental difference between the groups, and was not used a variable in subsequent analyses. Approximate Tanner stages were calculated from the questionnaire data; the two adolescent groups differed by one Tanner stage with a mean of 2.47 (SD = .67) in the YA group and 3.36 (SD = .84) in the MA group.

All three groups were matched on standard age-appropriate measures of verbal ability (one-way ANOVA: $F(2, 74) = 1.31$, $p = .28$). Adolescents were tested using the British Picture Vocabulary Scale (BPVS-II: Dunn, Dunn, Whetton, & Burley, 1997). Adults completed the National Adult Reading Test (NART-2; Nelson & Willison, 1991). Age Group means were YA: 116.3 (SD = 14.87), MA: 121.3 (SD = 17.43), and adult: 115.7 (SD = 5.58). Most of the adults in our sample were university students, and the school from which the adolescents were drawn is an academically selective school from which over 90% go onto higher education. This suggests that the groups were of similar socio-economic background. No participant had a history of neurological or psychiatric disorder, determined by self and/or parent report.

5.2. Design

The design was a 3×3 factorial with factors Age (YA, MA, Adult) and Condition (baseline, inclusion, ostracism).

5.3. Ostracism manipulation

Cyberball (Williams & Jarvis, 2006; Williams et al., 2000) was used. In order to deflect attention from the true motivation of the study, participants were told that the aim of the task was to look at 'mental visualisation ability'. Ethical permission for this minor deception was obtained from the local research ethics committee.

Players were represented on the computer screen by cartoon drawings, with the participant's character always located at the bottom centre (see Fig. 3a). They could choose to throw the ball to the players on either their left or their right by pressing corresponding keyboard buttons. The game comprised 70 throws, lasting around 3 min. The probability that the other players would throw the ball to the participant systematically varied according to condition. Inclusion always preceded ostracism in order to avoid negative spill-over effects, which would have been theoretically more problematic than spill-over effects from inclusion in terms of the hypotheses. This same fixed-order strategy has been used whenever Cyberball has been employed in within-subjects designs (Eisenberger, Way, Taylor, Welch, & Lieberman, 2007; Eisenberger et al., 2003). In the inclusion condition, participants were in possession of the ball 33% of the time (equal inclusion). In the ostracism condition the confederates were initially programmed to throw the ball to the participant with equal probability; however, after the first eight throws, they stopped throwing it to the participant altogether for the remainder of the game (around 50 throws).

5.4. Dependent measures

5.4.1. Mood

Participants rated how good/bad, happy/sad, friendly/unfriendly and tense/relaxed they were currently feeling, on a scale of 1–7. These anchors comprised the mood section of the need threat questionnaire, devised by Williams et al. (2000). Mood ratings were taken at baseline (before Cyberball) as well as after inclusion and ostracism.

5.4.2. Anxiety

Anxiety levels were measured using the state/trait anxiety inventory (Spielberger, 1983). This consists of 20 statements for each subscale (State (STAI-S) and Trait (STAI-T)). Participants rated how much each statement described them on a scale from 1 to 4. Trait scores were measured only at baseline, while state anxiety was measured both at baseline, and after inclusion and ostracism.

5.4.3. Need threat

The extent to which inclusion and ostracism affected the four needs was measured using the need threat questionnaire (Williams et al., 2000). The need threat scale consists of 12 statements;

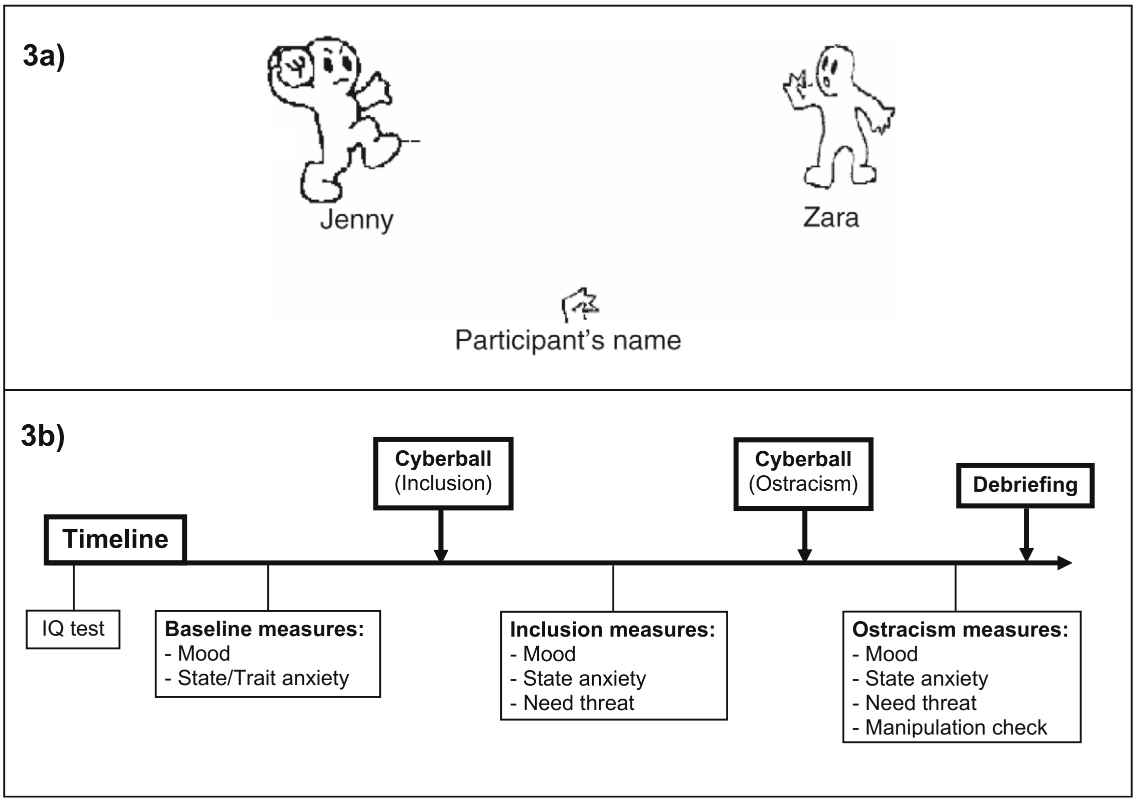


Fig. 3. The Cyberball game and a schematic of the experimental procedure. (3a) The Cyberball game: participants are represented by a cartoon at the bottom of the screen, and computerised characters stand on either side. In the ostracism condition, the other characters do not throw the ball to the participant. (3b) A schematic of the time course of the experiment. On arrival, participants completed an IQ test and the baseline measures. They then played Cyberball (first inclusion, then ostracism). After each run of Cyberball they completed a battery of self-report measures.

three questions pertaining to each need (self-esteem, belonging, control and meaningful existence). Participants rated how much each statement described their reaction during Cyberball on a scale from 1 to 5.

5.4.4. Manipulation check

At the end of the experiment, we wanted to be sure that participants realised that they had been included/ostracised. Participants rated the truth of two statements on a scale from 1 to 5 for each of the two times they had played Cyberball ("I was ignored" and "I was excluded"). They were also asked to estimate what proportion of the time they had received the ball, given that 33% was an equal share.

5.5. Procedure

See Fig. 3b for a schematic of the experimental procedure. Participants initially completed a measure of verbal ability; then baseline self-report measures. These consisted of current mood ratings, and the STAI. Participants then played Cyberball (inclusion condition). They were told that they would be playing with two other girls over the internet, and that it was important for them to visualise the experience as much as possible. Afterwards, they filled out mood, state anxiety and need threat questionnaires. Participants then played Cyberball in the ostracism condition, this time with two different 'girls', and again completed the questionnaires. At the end of the experiment, they completed the manipulation check measures, and were then fully debriefed as to the aims of the study. It was made clear that the computerised characters in Cyberball were not real. No participant expressed regret at having taken part.

6. Results

Data from one adult were excluded from state anxiety analyses, because she did not complete the measure after all three conditions. Data were analysed using mixed model ANOVAs, with Age (YA, MA, adult) as the between-subjects factor, and Condition (either (baseline, inclusion and ostracism) or (inclusion and ostracism) as appropriate) as the within-subjects factor. Corrections for multiple comparisons were made using Bonferroni corrections, and Greenhouse Geisser corrections were used to correct for non-sphericity.

6.1. Manipulation check

All age groups realised that they were included and ostracised in the appropriate conditions. Overall, participants estimated that they received the ball 35.01% (SD = 11.72) of the time in the inclusion condition, and 7.66% (SD = 5.39) in the ostracism condition. These mean estimates were fairly accurate, with actual percentages of 33% and 11%, respectively. In a mixed model ANOVA, there was a main effect of Condition, with significantly higher estimates of possession after inclusion than ostracism ($F(1, 74) = 475.18$, $p < .001$, partial eta squared ($\eta_p^2 = .87$)). There was no main effect of Age, and no Age × Condition interaction.

Amalgamating responses to the items 'I felt ignored' and 'I felt excluded', all participants reported feeling more excluded in the ostracism condition ($M = 4.64$, SD = .49) than in the inclusion condition ($M = 1.68$, SD = .78), ($F(1, 74) = 779.95$, $p < .001$, $\eta_p^2 = .91$). There was no significant main effect of Age, and no Age × Condition interaction. As the possible range of scores was 1–5, with five meaning participants felt excluded, the mean scores suggest participants reacted to the two conditions appropriately.

6.2. Mood

For two of the mood anchors (good/bad and happy/sad), and for overall mood, there was a main effect of Condition (good/bad: *F*(1.60, 118.14) = 15.09, *p* < .001, $\eta_p^2 = .17$); happy/sad: *F*(1.53, 112.91) = 10.91, *p* < .001, $\eta_p^2 = .13$) and overall mood: *F*(1.59, 117.46) = 16.29, *p* < .001, $\eta_p^2 = .18$). Post-hoc tests showed significantly lower mood after ostracism than after either baseline or inclusion (all *ps* < .008). There were no main effects of Age. There were significant interactions between Age and Condition for these three anchors (good/bad: *F*(3.19, 118.14) = 3.01, *p* = .03, $\eta_p^2 = .08$; happy/sad: *F*(3.05, 113) = 2.78, *p* = .044, $\eta_p^2 = .07$ and overall mood: *F*(3.18, 117.5) = 3.00, *p* = .031, $\eta_p^2 = .08$). Simple effects analyses showed that in all cases the interaction was due to significantly lower mood after ostracism than baseline and inclusion in both adolescent groups (all *ps* < .05). In contrast, there were no differences between conditions for adults (Fig. 4).

The remaining mood anchors (friendly/unfriendly and tense/relaxed) did not show an interaction between Condition and Age. For friendly/unfriendly, there was a main effect of Condition (*F*(1.57, 116) = 21.45, *p* < .001, $\eta_p^2 = .23$), due to participants feeling significantly less friendly after ostracism compared with both baseline and inclusion (all *ps* < .001), but no main effect of Age. For tense/relaxed, there was a main effect of Condition (*F*(1.79, 132.72) = 5.11, *p* = .009, $\eta_p^2 = .12$), due to participants reporting feeling significantly less relaxed after ostracism in all age groups compared with baseline (*p* = .022), but no significant difference between ostracism and inclusion. There was also a main effect of Age (*F*(2, 74) = 5.08, *p* = .009, $\eta_p^2 = .12$). This was due to MA being significantly less relaxed than adults across conditions (MA: *M* = 3.84, SD = 1.49; Adults: *M* = 4.81, SD = 1.44; *p* = .011), with a marginal effect in the same direction for YA (YA: *M* = 4.23, SD = 1.61; *p* = .051).

6.3. State and trait anxiety

A one-way ANOVA comparing Age groups found no differences in trait anxiety (measured at baseline).

For state anxiety, a mixed model ANOVA showed that there was a main effect of Condition (*F*(1.7, 124.23) = 8.96, *p* < .001, $\eta_p^2 = .11$), and a main effect of Age (*F*(2, 73) = 7.60, *p* = .001, $\eta_p^2 = .17$) (see Fig. 5). Post-hoc tests showed that the main effect of Condition was due to significantly greater anxiety after ostracism (*M* = 39.74, SD = 10.12), compared with both baseline (*M* = 36.82, SD = 8.15; *p* = .014) and inclusion (*M* = 36.45, SD = 8.70; *p* < .001). The main effect of Age was due to significantly greater anxiety in the MA group (*M* = 41.72, SD = 7.26) than in adults across conditions (*M* = 33.63, SD = 7.89; *p* = .001). The Age × Condition interaction was not significant (*F*(3.4, 124.23) = 1.22, *p* = .31, $\eta_p^2 = .03$). However, because we had an a priori hypothesis that the effect of ostracism on anxiety would be greater in adolescents than adults, we conducted planned comparisons, but used Bonferroni correction to be conservative. The results suggested that the main effect of Condition was driven by the reactions of the YA group. Anxiety was significantly higher after ostracism than either at baseline (*p* = .034) or after inclusion (*p* < .001) in this group, while anxiety in the MA and adult groups did not differ significantly between conditions.

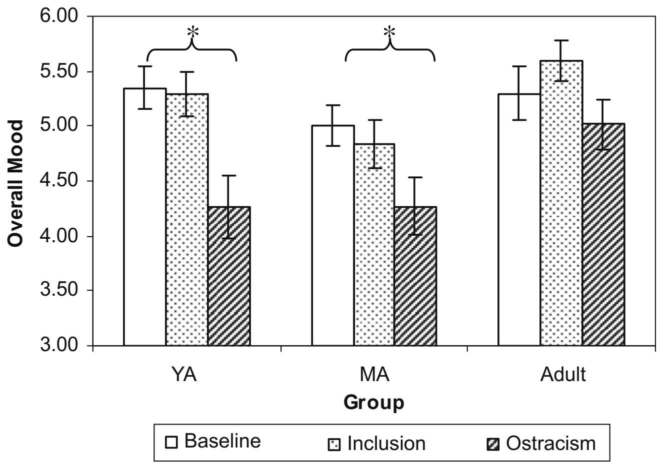
6.4. The four needs

For the need threat questionnaire, internal consistency between the three items for each need (self-esteem, belonging, control, and meaningful existence) was high (Cronbach's α all >.80). Therefore a single mean score was calculated for each need and this was used in subsequent analyses.

The four needs were only measured after inclusion and ostracism, as the questions pertained directly to the Cyberball experience. In separate mixed model ANOVAs for each need, there were main effects of Condition for all four needs, with lower need fulfilment after ostracism (*self-esteem:* *F*(1, 74) = 87.68, *p* < .001, $\eta_p^2 = .54$; *belonging:* *F*(1, 74) = 136.81, *p* < .001, $\eta_p^2 = .65$; *control:* *F*(1, 74) = 57.62, *p* < .001, $\eta_p^2 = .44$ and *meaningful existence:* *F*(1, 74) = 101.17, *p* < .001, $\eta_p^2 = .58$. For self-esteem, there was a main effect of Age (*F*(1, 74) = 8.34, *p* = .001, $\eta_p^2 = .18$). Post-hoc tests showed that this was due to significantly lower self-esteem across conditions in the MA group (*M* = 2.83, SD = .54) compared to adults (*M* = 3.39, SD = .69; *p* < .001). There were no other main effects of Age, or interactions between Age and Condition.

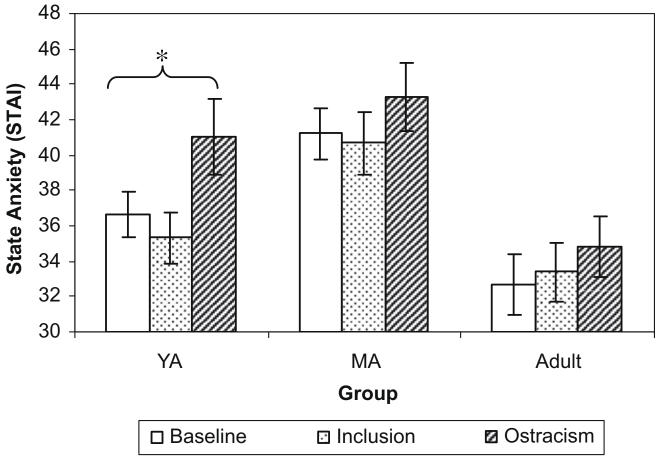
7. Discussion

This study used an experimental ostracism manipulation (Cyberball) to investigate the hypothesis that adolescents are



* Significant at p < .05, corrected

Fig. 4. Overall mood ratings for each group under each condition. Mood was significantly lowered by the ostracism condition compared with baseline and inclusion in the two adolescent groups (YA and MA). Mood was lowered by ostracism in the adult group, but this was not significant.



* Significant at p < .05, corrected

Fig. 5. State anxiety scores for each group under each condition. There was a main effect of Condition, with higher anxiety after ostracism in all groups. However, planned comparisons showed that anxiety was significantly greater after ostracism in the YA group only. There was also a main affect of Group, due to higher mean state anxiety in the MA group compared to adults across conditions.

hypersensitive to peer rejection. On some measures, affective reactions to ostracism were greater in adolescents than in adults. We found evidence for significantly lowered overall mood after ostracism in both YA and MA groups, and significantly higher state anxiety in the YA group, but no differences between conditions on either measure for adults. In contrast, each of Williams' (1997, 2001) 'four needs' (self-esteem, belonging, control and meaningful existence) was significantly threatened by ostracism in all groups. Importantly, we found no group differences on any manipulation check measure. Therefore, we found no evidence of a difference between the groups' more general experience of being included and ostracised.

7.1. Effects of ostracism on self-reported affective measures (mood and anxiety)

Both YA and MA adolescents rated all moods (good, happy, friendly and relaxed) as less positive after ostracism compared with both baseline and inclusion conditions. In contrast, adults felt less friendly and less relaxed after ostracism, but did not feel any less good or happy. This stronger effect in the adolescents indicates hypersensitivity to rejection, and also sheds light on previous studies looking at the effects of ostracism on mood in adults. Inconsistent results have been seen with regard to mood effects following ostracism in adults. While some studies have shown lowered mood after ostracism (Stroud, Salovey, & Epel, 2002; Williams et al., 2000), others have not (Twenge, Baumeister, Tice, & Stucke, 2001; Zadro et al., 2004). Our finding of lowered mood on only some anchors (friendly/unfriendly and tense/relaxed) suggests that not all mood states are equally affected by ostracism in adults. Therefore, differences in how mood state has been measured in previous studies may contribute to the inconsistencies seen. The current data further suggest that adolescents may be more sensitive than adults to the acute effects of short term ostracism on mood, and that these effects may be more broad in scope, affecting a wider range of measured mood states.

Following the Cyberball ostracism condition, there was a general increase in state anxiety across age groups relative to baseline and inclusion conditions. However, planned comparisons showed that this difference was only significant in YA. This suggests a heightened reactivity to ostracism in this group, particularly compared to adults who reported comparable levels of anxiety to YA at baseline and after inclusion. Although trait anxiety (measured at baseline) did not differ between age groups, we did find age differences in state anxiety at baseline. Specifically, the MA group were significantly more anxious than adults. This is in line with previous work showing that social anxiety is at its peak at age 15, which also corresponds to the peak onset of social phobia (Erath, Flanagan, & Bierman, 2007; Mancini et al., 2005). This high baseline anxiety makes anxiety levels reported after inclusion and ostracism difficult to interpret in MA since it may have masked the effects of ostracism on anxiety.

7.2. Effects on the four needs

In line with Williams' need threat model of ostracism, each of the four needs was significantly threatened by the ostracism condition, regardless of age group. This supports the idea that need threat is an automatic, reflexive process that occurs independently of individual differences in variables such as social anxiety (Williams, 2007; Zadro et al., 2006). The current results further suggest that developmental stage (at least between adolescence and adulthood) does not significantly affect the experience of need threat, and that increased need threat does not explain increased sensitivity to social ostracism in adolescence. Although the finding of lower self-esteem across conditions in the MA group was not explicitly predicted, there are studies showing that girls are particularly likely to suffer decreasing self-esteem over the course of adolescence (Zimmerman, Copeland, Shope, & Dielman, 1997).

7.3. Methodological considerations

While results are consistent with our hypothesis that adolescents would be hypersensitive to the affective consequences of ostracism, there are alternative interpretations. The use of a fixed-order within-subjects design meant that participants were aware of the questionnaire measures that were being employed following the inclusion condition, i.e. before they were ostracised. It could be argued that adolescents were more sensitive than adults to demand characteristics that this situation might create. However, we think this is unlikely; most notably because adolescents did not respond in the same way on all measures. They showed hypersensitivity specifically on the affective measures, but not on the need threat questionnaire. However, future studies could eliminate this possibility by including physiological measures of affective arousal such as skin conductance responses or cortisol levels (Blackhart, Eckel, & Tice, 2007).

In the current study, we did not have an accurate measure of pubertal stage across all participants, and adolescent groups differed on both age and pubertal stage. Future studies could explore sensitivity to ostracism in individuals matched for age but differing in pubertal status to explore whether the effect is tied to pubertal development.

7.4. Implications for adolescent social cognitive development

The current data replicate and extend previous findings in a number of ways. Previous studies have used interviews and experience-sampling methods to explore how adolescents respond to peer rejection in the context of their every-day lives (Coleman, 1974; Kloep, 1999; Larson & Richards, 1994; O'Brien & Bierman, 1988). The current study complements these studies, demonstrating hypersensitivity to general rejection (not necessarily by peers) in an experimental context in adolescent females. The ostracism manipulation was brief and without lasting consequences, yet hypersensitivity, particularly on mood measures, was still seen. Furthermore, as Cyberball was played over the internet, external factors such as school environment, social status among peers or participants' physical appearance cannot fully account for the effect. It would be interesting to study whether the same effect would be seen in adolescent males. A recent study in adults showed lowered mood in both males and females following a social rejection task, but only females showed increased cortisol levels, associated with a stress response (Stroud et al., 2002). This complements developmental self-report studies suggesting that adolescent females are more upset by negative peer evaluations and relational aggression than males (O'Brien & Bierman; Crick & Nelson, 2002). However, adolescent males and females have not been directly compared on sensitivity to ostracism in an experimental context.

7.5. Implications for models of adolescent neurocognitive development

The results of this study are in line with predictions derived from the neurobiological models discussed above. Although the models differ in terms of the precise developmental trajectories of different neural systems, all have in common the idea that relatively protracted development of prefrontal regulatory systems, possibly in conjunction with a more rapidly developing limbic system, may underlie commonly observed phenomenon such as risk-taking in the presence of peers. These models would also predict adolescent hypersensitivity to peer rejection in an experimental context. The continued development of mentalising might also contribute to this effect by increasing the extent to which adolescents are aware of others' appraisals and of the importance of succeeding in social situations, and by increasing the extent to which adolescents use social comparison to build a self-concept (Damon & Hart, 1988; Davey et al., 2008; Harter, 1990; Parker et al., 2006; Ruble, Boggiano, Feldman, & Loebl, 1980).

Functional imaging studies are needed in order to elucidate the neural bases of sensitivity to ostracism in adolescence. In adults, there is evidence suggesting that the neural substrates for social pain overlap with those underlying physical pain (Eisenberger et al., 2003). Using a range of paradigms, evidence has been found for the involvement of the dorsal anterior cingulate cortex (dACC) (Eisenberger et al., 2003, 2007), subgenual/ventral ACC (Somerville, Heatherton, & Kelley, 2006), right ventrolateral PFC (Eisenberger et al., 2003), medial PFC, posterior cingulate, and insula (Kross, Egner, Ochsner, Hirsch, & Downey, 2007). These regions overlap considerably with those continuing to develop structurally and functionally during adolescence (Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008). One recent study has shown a similar pattern of activation in adolescents aged 12.4–13.6 years (Masten et al., 2009) to that seen in adults on the Cyberball task (Eisenberger et al., 2003, 2007), and additionally showed the involvement of the subgenual ACC, which was not activated in previous studies of adults using the same task. However, adults and adolescents were not compared within the same study, and this will be an important next step in elucidating the neural correlates of increased sensitivity to social pain such as ostracism in adolescence.

8. Conclusions

We began this article by summarising recent work that has explored the link between social cognition and functional brain development during adolescence. This work suggests that many aspects of social cognition and their neural substrates, including face processing, social emotion processing and mentalising, are still developing during the second decade of life. These findings are compatible with neurocognitive models of adolescence, and also make specific predictions about adolescent sensitivity to negative social experiences. We conducted an experimental manipulation to explore the affective consequences of ostracism in adolescence. While the effects of ostracism on need threat were broadly similar between age groups, as predicted by Williams' need threat model, mood was more negatively affected after an episode of ostracism in both groups of adolescents than in adults, while anxiety was greater in the YA group. These experimental findings complement self-report studies showing hypersensitivity to social rejection during adolescence. The research discussed in this review shows that an iterative approach between data and theoretical models can be helpful in formulating and testing experimental hypotheses, particularly within a relatively new field such as social developmental cognitive neuroscience.

References

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*(4), 268–277.

Andersen, S. L., Thompson, A. T., Rutstein, M., Hostetter, J. C., & Teicher, M. H. (2000). Dopamine receptor pruning in prefrontal cortex during the periadolescent period in rats. *Synapse, 37*(2), 167–169.

Angold, A., Costello, E. J., & Worthman, C. M. (1998). Puberty and depression: The roles of age, pubertal status and pubertal timing. *Psychological Medicine, 28*(1), 51–61.

Blackhart, G. C., Eckel, L. A., & Tice, D. M. (2007). Salivary cortisol in response to acute social rejection and acceptance by peers. *Biological Psychology, 75*(3), 267–276.

Blakemore, S.-J. (2008). The social brain in adolescence. *Nature Reviews Neuroscience, 9*(4), 267–277.

Blakemore, S.-J., den Ouden, H., Choudhury, S., & Frith, C. (2007). Adolescent development of the neural circuitry for thinking about intentions. *Social, Cognitive and Affective Neuroscience, 2*(2), 130–139.

Brothers, L. (1990). The social brain: A project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience, 1*, 27–51.

Brown, B. B. (2004). Adolescents' relationships with peers. In R. M. Lerner & L. Steinberg (Eds.), *Handbook of adolescent psychology* (2nd ed.). Hoboken, N J: John Wiley & Sons.

Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage, 11*(2), 157–166.

Burnett, S., Bird, G., Moll, J., Frith, C., & Blakemore, S.-J. (2009). Development during adolescence of the neural processing of social emotion. *Journal of Cognitive Neuroscience, 21*(9), 1736–1750.

Cairns, R. B., Cairns, B. D., Neckerman, H. J., & Ferguson, L. L. (1989). Growth and aggression: I. Childhood to early adolescence. *Developmental Psychology, 25*, 320–330.

Carskadon, M. A., & Acebo, C. (1993). A self-administered rating scale for pubertal development. *Journal of Adolescent Health Care, 14*, 190–195.

Casey, B. J., Jones, R. M., & Hare, T. A. (2008). The adolescent brain. *Annals of the New York Academy of Sciences, 28*(1), :62–77.

Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage, 12*, 314–325.

Chibbar, R., Toma, J., Mitchell, B., & Miller, F. (1990). Regulation of neural oxytocin gene expression by gonadal steroids in pubertal rats. *Molecular Endocrinology, 4*, 2030–2038.

Coleman, J. C. (1974). *Relationships in adolescence*. London: Routledge & Kegan Paul.

Costello, E. J., Pine, D. S., Hammen, C., March, J. S., Plotsky, P. M., et al. (2002). Development and natural history of mood disorders. *Biological Psychiatry, 52*(6), 529–542.

Crick, N. R., & Nelson, D. A. (2002). Relational and physical victimization within friendships: Nobody told me there's be friends like these. *Journal of Abnormal Child Psychology, 30*(6), 599–607.

Crick, N. R., Werner, N. E., Casas, J. F., O'Brien, K. M., Nelson, D. A., & Grotpeter, J. K. (1999). Childhood aggression and gender: A new look at an old problem. In D. Bernstein (Ed.), *Nebraska symposium on motivation*. Lincoln: University of Nebraska Press.

Csikszentmihalyi, M., Larson, R., & Prescott, S. (1977). The ecology of adolescent activity and experience. *Journal of Youth and Adolescence, 6*, 281–294.

Davey, C. G., Yücel, M., & Allen, N. B. (2008). The emergence of depression in adolescence: Development of the prefrontal cortex and the representation of reward. *Neuroscience and Biobehavioral Reviews, 32*(1), 1–19.

Damon, W., & Hart, D. (1988). *Self-understanding in childhood and adolescence*. New York: Cambridge University Press.

den Ouden, H. E., Frith, U., Frith, C., & Blakemore, S. J. (2005). Thinking about intentions. *Neuroimage, 28*(4), 787–796.

Dennett, D. C. (1987). *The intentional stance*. Cambridge, MA: The MIT Press.

Dumontheil, I., Apperly, I. A., & Blakemore, S. J. (in press). Online usage of theory of mind continues to develop in late adolescence. *Developmental Science*. doi:10.1111/j.1467-7687.2009.00888.x.

Dunn, L. M., Dunn, L. M, Whetton, C., & Burley, J. (1997). British picture vocabulary scale (2nd ed.).

Eisenberger, N. I., Lieberman, M. D., & Williams, K. D. (2003). Does rejection hurt? An fMRI study of social exclusion. *Science, 302*(5643), 290–292.

Eisenberger, N. I., Way, B. M., Taylor, S. E., Welch, W. T., & Lieberman, M. D. (2007). Understanding genetic risk for aggression: Clues from the brain's response to social exclusion. *Biological Psychiatry, 61*(9), 1100–1108.

Erath, S. A., Flanagan, K. S., & Bierman, K. L. (2007). Social anxiety and peer relations in early adolescence: Behavioral and cognitive factors. *Journal of Abnormal Child Psychology, 35*(3), 405–416.

Ernst, M., Romeo, R. D., & Andersen, S. L. (2009). Neurobiology of the development of motivated behaviors in adolescence: A window into a neural systems model. *Pharmacology, Biochemistry and Behaviour* (advance online publication).

Fletcher, P. C., Happé, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., et al. (1995). Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition, 57*(2), 109–128.

Frith, C. D. (2007). The social brain? *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 362*(1480), 671–678.

Frith, C. D., & Frith, U. (2007). Social cognition in humans. *Current Biology, 17*, R724–R732.

Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia, 38*, 11–21.

Gardner, M., & Steinberg, L. (2005). Peer influence on risk taking, risk preference, and risky decision making in adolescence and adulthood: An experimental study. *Developmental Psychology, 41*(4), 625–635.

Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., et al. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience, 2*(10), 861–863.

Giedd, & Lenroot (2010). Sex differences in the adolescent brian. *Brain and Cognition*, 72(1), 46–55.

Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Lawrie, S. M., et al. (2006). Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. *Journal of Cognitive Neuroscience, 18*(6), 932–948.

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., 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.

Gogtay, & Thompson (2010). Mapping gray matter development: Implications for typical development and vulnerability to psychopathology. *Brain and Cognition*, *72*(1), 6–15.

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. *Journal of Neuroscience, 27*(30), 8040–8045.

Guyer, A. E., McClure-Tone, E. B., Shiffrin, N. D., Pine, D. S., & Nelson, E. E. (in press). Probing the neural correlates of anticipated peer evaluation in adolescence. *Child Development*.

Guyer, A. E., Monk, C. S., McClure-Tone, E. B., Nelson, E. E., Roberson-Nay, R., et al. (2008). A developmental examination of amygdala response to facial expressions. *Journal of Cognitive Neuroscience, 20*(9), 1565–1582.

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.

Harter, S. (1990). Developmental differences in the nature of self-representations: Implications for the understanding, assessment, and treatment of maladaptive behaviour. *Cognitive Therapy and Research, 14*(2), 113–142.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry, 51*, 59–67.

Herba, C. M., 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.

Insel, T., Young, L., Witt, D., & Crews, D. (1993). Gonadal steroids have paradoxical effects on brain oxytocin receptors. *Journal of Neuroendocrinology, 5*, 619–628.

Keysar, B., Lin, S., & Barr, D. J. (2003). Limits on theory of mind use in adults. *Cognition, 89*(1), 25–41.

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.

Kross, E., Egner, T., Ochsner, K., Hirsch, J., & Downey, G. (2007). Neural dynamics of rejection sensitivity. *Journal of Cognitive Neuroscience, 19*(6), 945–956.

La Greca, A. M., & Lopez, N. (1998). Social anxiety among adolescents: Linkages with peer relations and friendships. *Journal of Abnormal Child Psychology, 26*(2), 83–94.

Larson, R., & Richards, M. H. (1991). Daily companionship in late childhood and early adolescence: Changing developmental contexts. *Child Development, 62*, 284–300.

Larson, R., & Richards, M. H. (1994). *Divergent realities: The emotional lives of mothers, fathers, and adolescents*. New York: Basic Books.

Lévesque, J., Eugène, F., Joanette, Y., Paquette, V., Mensour, B., et al. (2003). Neural circuitry underlying voluntary suppression of sadness. *Biological Psychiatry, 53*(6), 502–510.

Lévesque, J., Joanette, Y., Mensour, B., Beaudoin, G., Leroux, J. M., et al. (2004). Neural basis of emotional self-regulation in childhood. *Neuroscience, 129*(2), 361–369.

Mancini, C., Van Ameringen, M., Bennett, M., Patterson, B., & Watson, C. (2005). Emerging treatments for child and adolescent social phobia: A review. *Journal of Child and Adolescent Psychopharmacology, 15*, 589–607.

Masten, C. L., Eisenberger, N. I., Borofsky, L. A., Pfeifer, J. H., McNealy, K., Mazziotta, J. C., et al. (2009). Neural correlates of social exclusion during adolescence: Understanding the distress of peer rejection. *Social, Cognitive and Affective Neuroscience, 4*(2), 143–157.

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.

McEwen, B. S. (2001). Invited review: Estrogen effects on the brain: Multiple sites and molecular mechanisms. *Journal of Applied Physiology, 91*, 2785–2801.

McGivern, R. F., Andersen, J., Byrd, D., Mutter, K. L., & Reilly, J. (2002). Cognitive efficiency on a match to sample task decreases at the onset of puberty in children. *Brain and Cognition, 50*, 73–89.

Monk, C. S., McClure, E. B., Nelson, E. E., Zarahn, E., Bilder, R. M., et al. (2003). Adolescent immaturity in attention-related brain engagement to emotional facial expressions. *Neuroimage, 20*(1), 420–428.

Moriguchi, Y., Ohnishi, T., Mori, T., Matsuda, H., & Komaki, G. (2007). Changes of brain activity in the neural substrates for theory of mind during childhood and adolescence. *Psychiatry and Clinical Neurosciences, 61*(4), 355–363.

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*, 47–57.

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, H. E., & Willison, J. R. (1991). National adult reading test (2nd ed.).

O'Brien, S. F., & Bierman, K. L. (1988). Conceptions and perceived influence of peer groups: Interviews with preadolescents and adolescents. *Child Development, 59*(5), 1360–1365.

Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences, 9*(5), 242–249.

Ochsner, K. N., & Gross, J. J. (2007). Cognitive emotion regulation: Insights from social cognitive and affective neuroscience. *Current Directions in Psychological Science, 17*(2), 153–158.

Olson, I. R., Plotzker, A., & Ezzyat, Y. (2007). The enigmatic temporal pole: A review of findings on social and emotional processing. *Brain, 130*(7), 1718–1731.

Olsson, A., & Ochsner, K. N. (2008). The role of social cognition in emotion. *Trends in Cognitive Sciences, 12*(2), 65–71.

Parker, J. G., Rubin, K. H., Erath, S. A., Wojslawowicz, J. C., & Buskirk, A. A. (2006). A developmental psychopathology perspective. In *Developmental psychopathology* (2nd ed.. In D. Cicchetti & D. J. Cohen (Eds.). *Theory and methods* (vol. 1, pp. 96–161). New York: Wiley.

Paus, T. (2005). Mapping brain maturation and cognitive development during adolescence. *Trends in Cognitive Sciences, 9*, 60–68.

Paus, T., Keshavan, M., & Giedd, J. N. (2008). Why do many psychiatric disorders emerge during adolescence? *Nature Reviews Neuroscience, 9*(12), 947–957.

Pelphrey, K. A., & Carter, E. J. (2008). Brain mechanisms for social perception: Lessons from autism and typical development. *Annals of the New York Academy of Sciences, 1145*, 283–299.

Pelphrey, K. A., Morris, J. P., Michelich, C. R., Allison, T., & McCarthy, G. (2005). Functional anatomy of biological motion perception in posterior temporal cortex: An fMRI study of eye, mouth and hand movements. *Cerebral Cortex, 15*, 1866–1876.

Pfeifer, J. H., Lieberman, M. D., & Dapretto, M. (2007). I know you are but what am I?!: Neural bases of self- and social knowledge retrieval in children and adults. *Journal of Cognitive Neuroscience, 19*(8), 1323–1337.

Ruble, D. N., Boggiano, A. K., Feldman, N. S., & Loebl, H. H. (1980). Developmental analysis of the role of social comparison in self-evaluation. *Developmental Psychology, 16*, 105–115.

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *Neuroimage, 19*(4), 1835–1842.

Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia, 42*, 1435–1446.

Schmithorst (2010). White matter development during adolescence as shown by diffusion MRI. *Brain and Cognition*, *72*(1), 16–26

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. J., Lerch, J. P., Ekstrand, K., Lenroot, R., et al. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *Journal of Neuroscience, 28*, 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.

Sowell, E. R., Thompson, P. M., Holmes, C. J., Batth, R., Jernigan, T. L., & Toga, A. W. (1999). Localizing age-related changes in brain structure between childhood and adolescence using statistical parametric mapping. *Neuroimage, 9*, 587–597.

Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Reviews, 24*(4), 417–463.

Spielberger, C. (1983). *Manual for the State-Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychologists Press.

Steinberg, L. (2005). Cognitive and affective development in adolescence. *Trends in Cognitive Sciences, 9*(2), 69–74.

Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review, 28*(1), 78–106.

Steinberg, L., & Monahan, K. C. (2007). Age differences in resistance to peer influence. *Developmental Psychology, 43*(6), 1531–1543.

Steinberg, L., & Silverberg, S. B. (1986). The vicissitudes of autonomy in early adolescence. *Child Development, 57*(4), 841–851.

Stroud, L. R., Salovey, P., & Epel, E. S. (2002). Sex differences in stress responses: Social rejection versus achievement stress. *Biological Psychiatry, 52*(4), 318–327.

Teicher, M. H., Andersen, S. L., & Hostetter, J. C. Jr. (1995). Evidence for dopamine receptor pruning between adolescence and adulthood in striatum but not nucleus accumbens. *Brain Research: Developmental Brain Research, 89*(2), 167–172.

Thomas, K. M., Drevets, W. C., Whalen, P. J., Eccard, C. H., Dahl, R. E., et al. (2001). Amygdala response to facial expressions in children and adults. *Biological Psychiatry, 49*(4), 309–316.

Thomas, L. A., De Bellis, M. D., Graham, R., & LaBar, K. S. (2007). Development of emotional facial recognition in late childhood and adolescence. *Developmental Science, 10*(5), 547–558.

Twenge, J. M., Baumeister, R. F., Tice, D. M., & Stucke, T. S. (2001). If you can't join them, beat them: Effects of social exclusion on aggressive behavior. *Journal of Personality and Social Psychology, 81*, 1058–1069.

Vartanian, L. R. (2000). Revisiting the imaginary audience and personal fable constructs of adolescent egocentrism: A conceptual review. *Adolescence, 35*, 639–661.

Wang, A. T., Lee, S. S., Sigman, M., & Dapretto, M. (2006). Developmental changes in the neural basis of interpreting communicative intent. *Social Cognitive and Affective Neuroscience, 1*, 107–121.

Whalen, P. J., Rausch, 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*, 411–418.

Williams, K. D. (1997). Social ostracism. In R. M. Kowalski (Ed.), *Aversive interpersonal behaviors* (pp. 133–170). New York: Plenum.

Williams, K. D. (2001). *Ostracism: The power of silence*. New York: Guilford Press.

Williams, K. D. (2007). Ostracism. *Annual Review of Psychology, 58*, 425–452.

Williams, K. D., & Jarvis, B. (2006). Cyberball: A program for use in research on ostracism and interpersonal acceptance. *Behavior Research, Methods, Instruments and Computers, 38*, 174–180.

Williams, K. D., Cheung, C. K., & Choi, W. (2000). Cyberostracism: Effects of being ignored over the internet. *Journal of Personality and Social Psychology, 79*(5), 748–762.

Winston, J. S., Strange, B. A., O'Doherty, J., & Dolan, R. J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience, 5*, 277–283.

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*, 194–199.

Zadro, L., Boland, C., & Richardson, R. (2006). How long does it last? The persistence of the effects of ostracism in the socially anxious. *Journal of Experimental Social Psychology, 42*, 692–697.

Zadro, L., Williams, K. D., & Richardson, R. (2004). How low can you go? Ostracism by a computer is sufficient to lower self-reported levels of belonging, control, self-esteem, and meaningful existence. *Journal of Experimental Social Psychology, 40*, 560–567.

Zimmerman, M. A., Copeland, L. A., Shope, J. T., & Dielman, T. E. (1997). A longitudinal study of self-esteem: Implications for adolescent development. *Journal of Youth and Adolescence, 26*(2), 117–141.