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The Development of Social Cognition in Adolescence: An Integrated Perspective

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Highlights

- We review the development of social cognition and the social brain network during human adolescence.
- Social cognitive development is discussed in the context of other developing neural systems.
- We examine the role of social cognitive development in adolescent-typical behaviours.

Abstract

Social cognitive processes are critical in navigating complex social interactions and are associated with a network of brain areas termed the ‘social brain’. Here, we describe the development of social cognition, and the structural and functional changes in the social brain during adolescence, a period of life characterised by extensive changes in social behaviour and environments. Neuroimaging and behavioural studies have demonstrated that the social brain and social cognition undergo significant development in human adolescence. Development of social cognition and the social brain are discussed in the context of developments in other neural systems, such as those implicated in motivational-affective and cognitive control processes. Successful transition to adulthood requires the rapid refinement and integration of these processes and many adolescent-typical behaviours, such as peer influence and sensitivity to social exclusion, involve dynamic interactions between these systems. Considering these interactions, and how they vary between individuals and across development, could increase our understanding of adolescent brain and behavioural development.

Keywords: Social Cognition, Mentalising, Humans, Adolescence, Social Brain, Development

Highlights

- We review the development of social cognition and the social brain network during human adolescence.
- Social cognitive development is discussed in the context of other developing neural systems.
- We examine the role of social cognitive development in adolescent-typical behaviours.

1. Introduction

Adolescence can be defined as the period of life between puberty and the achievement of self-sufficiency and independence (Blakemore and Mills, 2014). This transitional period of development has long been associated with physical, social, behavioural and cognitive changes. More recently, advances in brain imaging technology have enabled increased understanding of structural and functional changes in the human brain during this developmental period (Blakemore and Mills, 2014; Casey et al., 2008; Ernst and Fudge, 2009; Lenroot and Giedd, 2006), and how they relate to social cognitive development. This review integrates recent research on the development of social cognition in adolescence within the context of other aspects of adolescent neurocognitive development, such as motivational and affective processing, decision-making and cognitive control.

2. The Social Brain

Social cognition refers to the ability to make sense of the world through processing signals generated by other members of the same species (Blakemore and Mills, 2014; Frith, 2007) and encompasses a wide range of cognitive processes that enable individuals to understand and interact with one another (Adolphs, 1999; Frith and Frith, 2007). These include social perceptual processes such as face processing (Farroni et al., 2005), biological motion detection (Pelphrey and Carter, 2008), and joint attention (Carpenter et al., 1998), in addition to more complex social cognitive processes involving inference and reasoning, such as mentalising, the process of mental state attribution. Such social cognitive processes enable us to understand and predict the mental states, intentions and actions of others, and to modify our own accordingly (Frith and Frith, 2007). Social cognition thus plays a critical role in the successful negotiation of complex social interactions and decisions (Crone, 2013).

A wide network of brain areas, referred to as the 'social brain' network, is involved in social perception and cognition (Adolphs, 2009; Frith, 2007). Regions within the social brain network include the posterior superior temporal sulcus (pSTS), temporoparietal junction (TPJ), dorsomedial prefrontal cortex (dmPFC; medial aspects of BA10), anterior temporal cortex (ATC), and the inferior frontal gyrus (IFG; Frith and Frith, 2007; Van Overwalle, 2009; **Figure 1**).

Electrophysiological and functional magnetic resonance imaging (fMRI) studies consistently report the involvement of the pSTS in the perception of biological motion and eye gaze (Puce and Perrett, 2003), and in grasping the intentionality and appropriateness of biological motion (Pelphrey et al., 2004). Therefore, the pSTS may be involved in decoding complex social gestures. The TPJ is involved in different aspects of social cognition, including in situations that require inferring the mental states of others, as opposed to information known about others (Saxe and Kanwisher, 2003; Saxe et al., 2009). In contrast, the dmPFC is activated in multiple conditions, including when inferring the mental states of others, when reflecting on knowledge of another's traits, and when reflecting on the traits of oneself (Frith, 2007). Frith (2007) has proposed that the underlying similarity between tasks that activate the dmPFC is their involvement in handling communicative intentions, which requires a second order representation of a mental state, whether one's own or another person's. The ATC is involved in interpreting social narratives (Olson et al., 2013, 2007), processing social scripts (Frith, 2007; Frith and Frith, 2003) and integrating social memories with emotion (Olson et al., 2007; Pfeifer and Peake, 2012). The IFG, which is associated with a range of cognitive processes, has been implicated in action observation (Rizzolatti et al., 2001; Shaw et al., 2012) and understanding social situations (Carter et al., 2012).

While the coactivation of these regions has been demonstrated in many neuroimaging experiments involving social cognition tasks, the individual contributions and integration of these anatomically distinct regions to social cognitive processes are debated, as is their specificity for processing social information (see Adolphs, 2010, for discussion).

3. The Social Brain in Adolescence

Many social changes occur during adolescence. These include the fact that, compared with children, adolescents form more complex and hierarchical peer relationships and are more sensitive to acceptance and rejection by their peers (Brown, 2004; Steinberg and Morris, 2001). Although the factors that underlie these social changes are likely to be multi-faceted, one possible contributing factor is the development of the social brain. Certain social cognitive processes, such as face processing (Farroni et al., 2005), biological motion detection (Pelphrey and Carter, 2008) and joint attention (Carpenter et al., 1998), are present from an early age (see Baillargeon et al., 2010). However, more complex aspects of social cognition and the structure and function of associated brain networks continue to develop across adolescence and into early adulthood.

3.1. Structural Development of the Social Brain in Adolescence

Areas within the social brain network are among the regions that undergo the most protracted development in humans (Barnea-Goraly et al., 2005; Giedd et al., 1999; Gogtay et al., 2004; Shaw et al., 2008; Sowell et al., 2004, 1999), showing changes throughout adolescence before relatively stabilizing in the early to mid-twenties. Mills et al. (2014) examined the structural developmental trajectories (grey matter volume, cortical thickness and surface area) of brain areas associated with mentalising. In a sample of 288 individuals with at least two brain scans between the ages of 7 and 30 years, they found that grey matter volume and cortical thickness decreased in medial Brodmann area 10 (dmPFC), TPJ, and pSTS from childhood into the early twenties. In contrast, the ATC increased in grey matter volume until early adolescence (~12 years), decreasing thereafter, whereas cortical thickness increased until early adulthood (~19 years). Surface area in all four regions followed a cubic trajectory, reaching a peak in late childhood or early adolescence, before decreasing into the early twenties (Mills et al., 2014; **Figure 2**).

The underlying cellular changes associated with a reduction in grey matter volume are still debated (Paus et al., 2008; Poldrack, 2010), and to date no studies have directly tested the relationship between developmental changes in underlying cellular or synaptic anatomy and structural MRI measures. Despite these limitations, it is thought that reductions in grey matter volume might reflect, at least in part, increases in white matter integrity and/or synaptic reorganisation (Paus et al., 2008). Histological studies of post-mortem human brain tissue provided evidence that the prefrontal cortex (PFC) continues to undergo synaptic pruning during adolescence (Huttenlocher and Dabholkar, 1997; Petanjek et al., 2011).

3.2. Development of Social Cognition and Social Brain Function in Adolescence

Recent neuroimaging and behavioural studies have shown developments in a number of social cognitive abilities and functional changes in associated brain networks across adolescence.

3.2.1. Face Processing

A vast array of social information can be extracted from the faces of those around us, including identity, emotional expression and direction of eye gaze. In adolescence, new aspects of face processing become increasingly important, as more complex social cognitive abilities develop, such as judgements of attractiveness or social status, which rely on the successful detection and interpretation of communicative signals from face processing. Newborn infants appear to be capable of detecting human faces (Farroni et al., 2005). Basic face perception abilities develop gradually (Mondloch et al., 2006) and are mirrored at the neural level by slowly emerging cortical networks (Cohen Kadosh et al., 2011; Scherf et al., 2007).

A small number of studies have suggested that face-processing abilities continue to improve during adolescence (Monk et al., 2003; Pfeifer et al., 2011; Yurgelun-Todd and Killgore, 2006), with some studies observing a dip in face-processing proficiency in early adolescence (Carey et al., 1980; Thomas et al., 2007). While the core face-processing network appears to be present from around 7 years of age, face-processing abilities and the brain systems that support them continue to show age-related changes between adolescence and adulthood. For example, recruitment of the PFC during face-processing tasks increases between childhood and adolescence and then decreases between adolescence and adulthood (reviewed in Blakemore, 2008).

There is also evidence that face-processing systems become increasing specialised, particularly in relation to more complex aspects of face-processing such as detecting socially-relevant information. Cohen et al (2011; 2013) used a series of fMRI target detection tasks (detection of facial identity, expression, or eye-gaze direction) to investigate the developmental changes in the functional connectivity of the face processing network when performing tasks involving face-property specific processes. Children, adolescents and young adults all activated the core face-processing network across all different tasks, however the extent to which network connectivity was selectively modulated according to face-processing task demands increased between the ages of 7 and 11 years (Cohen Kadosh et al., 2011). In adults, detecting a facial identity was associated with selective strenghtening of the functional connectivity between the inferior occipital gyrus (IOG) and the fusiform gyrus, whereas detecting an emotional expression modulated connectivity between the IOG and the STS. No such modulation was found in children. A follow-up study indicated that with age there were also increases in task-specific activations that were additionally associated with changes in grey and white matter volume. These changes were distinct from more widespread activations that varied as a function of individual task performance (Cohen Kadosh et al., 2013). Thus, changes in face-processing during the first three decades of life appear to be related both to continued structural development of underlying brain areas and individual task performance, which might reflect changing cognitive strategies across development and experience (Cohen Kadosh et al., 2013).

3.2.2. Mentalising

Mentalising describes the ability to make attributions about the mental states of others, including their beliefs, thoughts, desires, intentions and feelings. There is a rich literature on the development of mentalising in childhood, pointing to changes in the ability to understand others' mental states during the first five years of life (Frith and Frith, 2007). While certain aspects of mentalising are present in infancy (Baillargeon et al., 2010), it is not until around the age of four years that children begin to explicitly understand that someone else can hold a belief that differs from their own, and which can be false (Barresi and Moore, 1996). Until fairly recently, there was a shortage of studies looking into mentalising after childhood, as it was generally assumed that these abilities were already mature by mid-childhood in typically developing children. However, adolescence is marked by substantial changes in social competence and social behaviour, as well as structural development within the social brain (Mills et al., 2016). These changes may be paralleled by changes in the neural processing of mentalising.

Neuroimaging studies of mentalising have consistently found associations with activity within the dmPFC, TPJ, pSTS, and ATC (**Figure 1**), suggesting these regions are key to the process of mental state attribution. A number of developmental fMRI studies of mentalising report decreases in dmPFC recruitment between adolescence and adulthood (reviewed in Blakemore, 2008).

These studies have used a variety of tasks that require mental state attribution, such as understanding irony (Wang et al., 2006), thinking about social emotions such as guilt (Burnett et al., 2009), understanding intentions (Blakemore et al., 2007), thinking about the preferences and dispositions of oneself or a fictitious story character (Pfeifer et al., 2009) and making attributions about the emotional states of others (Gunther Moor et al., 2012; Overgaauw et al., 2015). An example of such a task is the Reading the Mind in the Eyes Test (RMET; Baron-Cohen et al., 2001a, 2001b), which assesses the ability to perceive, categorise and make attributions about other people's mental and affective states, based only on photographs of their eyes. Gunther Moor et al. (2012) used fMRI to compare brain activation while performing the RMET between early adolescents (10 to 12 years), mid adolescents (14 to 16 years) and young adults (19 to 23 years), relative to a control condition (age and gender categorisations of the same stimuli). Whereas participants of all ages showed increased activation in the pSTS during the task, participants in the youngest group exhibited additional engagement of the dmPFC (Gunther Moor et al., 2012). A follow-up study in which the same participants were re-tested two years later indicated that these cross-sectional differences reflected longitudinal changes within individuals. Specifically, dmPFC activation during the RMET followed a quadratic developmental trajectory, being lowest during mid-adolescence (Overgaauw et al., 2015).

In some studies, higher activity in more posterior regions of the social brain, such as the pSTS/TPJ (Blakemore et al., 2007), and in the ATC (Burnett et al., 2009), was observed in adults as compared to adolescents. There is also evidence for developmental differences in functional connectivity between dmPFC and other parts of the social brain network, such as the pSTS, ATC and TPJ (Burnett and Blakemore, 2009; Klapwijk et al., 2013).

Why adolescents recruit the dmPFC more than adults in social cognitive tasks is still an empirical question. It has been suggested that the decrease in recruitment of the dmPFC across adolescence may relate to changes in neuroanatomy or maturing neurocognitive strategies (Blakemore, 2008). It has been hypothesised that developmental changes in brain function may reflect—and/or contribute to—changes in brain structure (Cohen Kadosh et al., 2011; Crone and Richard Ridderinkhof, 2011; Scherf et al., 2012). However, the relationship between structural and functional changes is currently not well understood as few studies have directly compared structural and functional data within the same individuals (Cohen Kadosh et al., 2013; Dumontheil et al., 2010b; Lu et al., 2009; Olesen et al., 2003; van den Bos et al., 2012b). While decreases in functional activity can co-occur with reductions in grey matter volume (Cohen Kadosh et al., 2013; Lu et al., 2009), they are not always associated (Dumontheil et al., 2010b). These mixed results suggest that age-related changes in blood oxygen level dependent signal do not entirely reflect structural maturation, and may instead reflect the maturation of neurocognitive strategies, such as an increased recruitment of cognitive control systems between adolescence and adulthood during social interactions (Dumontheil et al., 2012; Mills et al., 2015; van den Bos et al., 2011; discussed further in Sections **3.2.3** and **3.2.4**).

3.2.3. Perspective-Taking

The ability to take another person's point of view into account, i.e. perspective-taking, is an important determinant of successful social functioning in everyday life (Fett et al., 2011). Fundamental aspects of perspective-taking develop during childhood (Barresi and Moore, 1996; Leslie, 1987; Perner and Davies, 1991). However, the ability to use these social competencies online continues to develop throughout adolescence.

The Director task has been used to investigate the ability to use perspective-taking to guide decisions in a referential communicative context (Apperly et al., 2008; Brown-Schmidt and Hanna, 2011; Fett et al., 2014b; Keysar et al., 2003, 2000). Participants are instructed to move objects around a set of shelves by a director, who cannot see some of the objects that the participant can see (**Figure 3**; Apperly et al., 2010; Dumontheil et al., 2010a). Correct interpretation of the instructions requires participants to use the director's perspective and only move objects that the director can see. Adult participants frequently make errors in this task, suggesting that, despite possessing the ability to use mentalising to understand that the director's perspective differs from their own, they often fail to use this information to guide decisions (Keysar et al., 2003, 2000).

In a sample of participants aged 7 to 27 years, Dumontheil et al. (2010a) used a computerised adaptation of the Director task. To differentiate between the general impact of cognitive control demands on task performance and effects that specifically impact the social components of the task, a control condition was added in which the director was absent and participants had to use a non-social rule to guide their decisions while following the (otherwise) identical instructions as in the director condition. Although accuracy improved until mid-adolescence in both conditions, accuracy in the director condition continued to improve after mid-adolescence. Similar findings were also observed in a more recent study (Symeonidou et al., 2015). These findings suggest that the ability to use another's perspective to guide decisions continues to develop in late adolescence, over and above developmental improvements in more general cognitive control processes recruited by both conditions.

This improvement may be due to increased motivation to take account of another's perspective as well as improved integration of social cognition and cognitive control systems (Dumontheil et al., 2010a). Using a variant of the Director task adapted for fMRI (Apperly et al., 2010; Dumontheil et al., 2010a), in which the cognitive demands of the task were also manipulated, Dumontheil et al. (2012)

demonstrated demonstrated developmental differences in brain areas associated with both social cognitive and more domain-general cognitive control processes. In both social and non-social conditions, adults recruited fronto-parietal regions associated with cognitive control more than adolescents. When social cues were needed to accurately perform the task both adults and adolescents (11 to 16 years) recruited the dmPFC, however, adolescents also recruited the dmPFC when social cues were not needed. The authors suggest that this engagement of the dmPFC for irrelevant social stimuli may reflect the use of social brain regions even when they are not necessary, consistent with a pattern of increasing specialisation within networks supporting social cognition.

Developmental improvements in cognitive control (see Section **4**) likely influence—and are influenced by—social cognitive processing during adolescence. For example, although attending to social cues is largely automatic (Spunt and Lieberman, 2013), taking another person's perspective when it differs from one's own requires the inhibition of our own, egocentric perspective (Surtees and Apperly, 2012), an effortful process that requires cognitive control resources. A recent behavioural study demonstrated that when under high cognitive load (simultaneously remembering three 2-digit numbers), adults and adolescents were slower at taking another person's perspective in the Director task than when under low cognitive load (remembering one 3-digit number), suggesting that taking another's perspective is cognitively demanding (Mills et al., 2015). Further evidence for the role of more general cognitive control resources in perspective-taking comes from a recent developmental study (9 to 29 years) that found inhibitory control ability, measured using a go-nogo task, partly accounted for errors on the director task over and above age-related variance (Symeonidou et al., 2015).

3.2.4. Social Decision-Making

Another line of research into the dynamic and interactive aspects of social cognition has employed tasks from the field of behavioural economics to simulate more complex aspects of social exchanges

(Belli et al., 2012; Evans and Krueger, 2011; van den Bos et al., 2011; 2010). These paradigms can be used to study the development of social preferences for fairness, trustworthiness, or cooperation, and the cognitive and neural mechanisms that underlie social decision-making.

Three such games are the Ultimatum Game, the Trust Game and the Dictator Game. The first two games require an understanding of others' intentions, as a successful outcome is not only dependent on one's own behaviour, but also on the behaviour of others (Colman, 1995; Heifetz, 2012). In the Ultimatum Game (Güth et al., 1982), one player decides how to split an amount of money with a second player, who decides whether to accept or reject this offer. If accepted, the money is split accordingly, but if rejected both players receive nothing. In the Trust Game, the first player invests an amount of money to a second player, who can then choose either to divide it equally between them (reciprocate), or keep more for themselves (defect). In contrast, in the Dictator Game (Kahneman et al., 1986), and other allocation game variants (e.g. Fehr et al., 2008), the second player is forced to accept the split offered by the first player, so allocators do not need to consider the behaviour of the other.

Behavioural studies indicate that an understanding and social preference for fairness norms is well-developed by the age of 7 to 8 years (Fehr et al., 2008; Güroğlu et al., 2009b). Several studies have shown no age differences in costly prosocial behaviour (fair allocations in the Dictator Game) between the ages of 9 to 18 years (Gummerum et al., 2014; Güroğlu et al., 2009a, 2009b). Developmental studies of sharing find increases in equity preference during childhood, followed by decreases with age in adolescence (Luengo Kanacri et al., 2013; Meuwese et al., 2015).

Even though a basic sense of fairness in bargaining is observed in young children, the understanding of intentionality in social interactions develops gradually over the course of adolescence and early adulthood (Güroğlu et al., 2009b; van den Bos et al., 2010). Age-related changes in social behaviour beyond childhood, such as increases in trust and reciprocity during social interactions (Belli et al., 2012; Fett et al., 2014a; van den Bos et al., 2010), may be associated with the increasing tendency to consider others' viewpoints and intentions. Indeed, compared to adults, children and adolescents are less effective in analysing the intentionality of partners' behaviour and mental states during social interaction (Güroğlu et al., 2009b; Sutter, 2007).

In an fMRI study, young adolescents (12 to 14 years), older adolescents (15 to 17 years), and emerging adults (18 to 22 years) played the role of the second player in the Trust Game (van den Bos et al., 2011). An anonymous first player would give them an amount of money, which they could either divide equally between themselves and the first player (reciprocate), or keep more for themselves (defect). Participants' tendency to take the perspective of the first player into account was investigated by examining their sensitivity to the degree of risk (i.e. the amount of money that could be lost) taken by the first player. Older adolescents and emerging adults were more likely to reciprocate when the first player stood to lose more money by trusting the second player, and less likely to reciprocate when the first player stood to lose a relatively small amount of money, whereas the younger adolescents did not differentiate. These findings suggest that adolescence is not necessarily characterized by general increases in prosocial behaviour, but an increase in sensitivity to the perspective of others.

These forms of perspective-taking behaviour were associated with increased involvement of the left TPJ and the right dorsolateral PFC (dlPFC), which the authors suggest indicates a role for both social cognitive and cognitive control systems in the development of social behaviour in adolescence. When participants observed that the first player trusted them, recruitment of the left TPJ increased with age, and this level of activation correlated with participants' sensitivity to the first player. All participants showed greater recruitment in the dmPFC when making self-oriented choices (defecting), but only young adolescents engaged this region when making reciprocal choices. This heightened activation in the dmPFC for reciprocal choices decreased between early and late adolescence and remained stable into early adulthood, possibly reflecting a shift away from engaging in social interactions from an egocentric perspective, although the precise psychological mechanisms cannot be ascertained from neural activity patterns (van den Bos et al., 2011). Participants also showed increased engagement of the right dlPFC with age when receiving trust, which the authors speculate may indicate a regulatory role of right dlPFC in social exchange, for example, in the inhibition of more egocentric behaviour.

Fett et al. (2014b) investigated the relationship between perspective-taking and social processes such as trust and reciprocity in adolescence, using two variants of the Trust Game and the Director task. Adolescents (13 to 18 years) with a higher perspective-taking tendency (measured as accuracy on the Director task) demonstrated greater trust towards others (initial investment in the Trust Game) and higher levels of trust during co-operative interactions (higher investments). While all adolescents modified their behaviour in response to unfair interactions (decreased investments and more malevolent reciprocity) when they were treated unfairly, high perspective-takers did so more drastically, suggesting a greater decrease in trust. The authors propose that increases in perspective-taking tendencies in adolescence are therefore associated with specific developmental changes in trust and reciprocity, as opposed to simply generalised increases in prosocial behaviour. Although this study did not include adult participants, the behavioural patterns of high perspective-takers were similar to those observed in adults in another study using this paradigm (Fett et al., 2014a).

Recent behavioural findings add support to this conclusion. In a series of allocation games, in which the identity of the interaction partner was manipulated (friends; antagonists; neutral classmates; anonymous peers), younger adolescents (9 and 12 years) showed similar levels of prosocial behaviour to all interaction partners (Güroğlu et al., 2014). However, older adolescents (15 and 18 years) showed increasing differentiation in prosocial behaviour according to their relation with the partner, displaying the most prosocial behaviour (both costly and non-costly) towards friends. This suggests that with age, *who* you are interacting with becomes more important. The age-related increase in non-costly prosocial behaviour towards friends was mediated by self-reported perspective-taking skills.

4. Cognitive Control and Affective-Motivational Processing in Adolescence

Developmental changes in social cognition and the structure and function of the social brain occur in the context of developments in a broad range of cognitive processes and the neural networks which support them. Several influential models of adolescent neurocognitive development have been proposed that focus on the relations between regulatory and affective-motivational processes and their associated neural circuits (Casey et al., 2008; Ernst and Fudge, 2009; Ernst et al., 2006; Steinberg, 2008).

Cognitive control and motivational-affective responding are mutually influential processes. Cognitive control can be defined as the ability to actively guide behaviour, and involves the coordination of a heterogeneous set of sub-processes mediated by the PFC (Casey et al., 2001; Miller and Cohen, 2002; (Casey et al., 2001; Miller and Cohen, 2001; Norman and Shallice, 1986). These sub-processes, including inhibitory control, performance monitoring and working memory, continue to mature into late adolescence and early adulthood (Casey et al., 1997; Crone et al., 2006; Durston et al., 2002; Luna et al., 2015, 2004, 2001; Rubia et al., 2006), and during this period there is a steady increase in the ability to use cognitive control to guide thoughts and actions (Asato et al., 2006; Huizinga et al., 2006; Luna et al., 2010).

Dual-systems models hypothesise that cognitive control mechanisms, mediated by the PFC, develop later and more slowly than mechanisms of emotional responsiveness and motivation, such as the amygdala and ventral striatum (VS; Casey et al., 2008; Somerville et al., 2010; Steinberg, 2010).

Extending the dual-systems models, Ernst et al.'s (Ernst and Fudge, 2009; Ernst et al., 2006) triadic model advocates three neural systems, and the interplay between them, as important in understanding adolescent development: 1) a reward/approach processing system; 2) an avoidance processing system; and 3) a regulatory system exerting top-down cognitive control over reward and avoidance systems. A key tenet of these models is that adolescent behaviour and cognition is associated with changes in the balance between the different circuits (Ernst and Fudge, 2009; Ernst et al., 2006; Somerville et al., 2010). Individual differences in the developmental trajectories of neural circuits and the cognitive processes they subserve are proposed to interact with environmental factors, manifesting in a unique neurocognitive developmental profile. This variation may confer increased vulnerability for some adolescents. These models have given rise to a large number of behavioural and neuroimaging studies of the development of affective-motivational and regulatory processes during adolescence.

4.1. Interactions between Cognitive Control and Affective Processing in Adolescence

When cognitive control processes interact with affective information, as is typical in everyday life, there are two key types of interplay, both of which can be termed types of emotional regulation. The first is the explicit top-down regulation of affective responses by cognitive control (reviewed in Ochsner and Gross, 2005), and the second is the bottom-up modification or disruption of cognitive control processes by affective information. Neural models of emotional regulation implicate a network of extensively interconnected brain regions, including the PFC, amygdala and VS (Ochsner and Gross, 2005). These connections demonstrate marked maturational changes during adolescence (Cunningham et al., 2002) and developmental studies of functional connectivity suggest age-related increases in connectivity between the vmPFC and both the amygdala and VS during the processing of affective information (Gee et al., 2013; Guyer et al., 2008; Pfeifer et al., 2011; Somerville et al., 2013; Spielberg et al., 2015, 2014; van den Bos et al., 2012a).

Experimental studies investigating emotional regulation in adolescence have largely focused on inhibitory control, the ability to suppress behaviour that is prepotent or goal-irrelevant, in the context of affectively valenced information. These studies have demonstrated improvements in the ability to resist interference from affective information between adolescence and adulthood (Cohen Kadosh et al., 2014; Cohen-Gilbert and Thomas, 2013; Dreyfuss et al., 2014; Hare et al., 2008; Ladouceur et al., 2006; Lewis et al., 2006; Somerville et al., 2011; Tottenham et al., 2011). Adolescents exhibit decreased responses to emotional stimuli in the vmPFC (Barbalat et al., 2013; Etkin et al., 2006; Hare et al., 2008). The vmPFC plays an important role in affect regulation and in the formation and pursuit of socio-affective goals (Davey et al., 2008), and its functional connectivity with the amygdala is associated with the habituation of emotional stimuli (Barbalat et al., 2013; Etkin et al., 2006; Hare et al., 2008). In another study, age-dependent activation changes in PFC regions to distracting emotional stimuli correlated with trait emotional ability (Perlman et al., 2014).

4.2. Interactions between Cognitive Control and Affective-Motivational Processing in Adolescence

Adolescence is associated with heightened risk-taking behaviour, such as alcohol and tobacco-use, unsafe sexual behaviour, violent and non-violent crime and dangerous driving (Eaton et al., 2012; Smith et al., 2014b; Steinberg, 2008). A popular hypothesis is that adolescents have a disproportionately developed “hot” motivational system compared with a relatively immature “cold” cognitive control system that is not yet strong enough to consistently restrain potentially hazardous impulses (Albert and Steinberg, 2011; Casey and Jones, 2010; Casey et al., 2011; Somerville et al., 2010). Therefore heightened reward sensitivity in adolescence can manifest in suboptimal decisions when faced with real-life gambles, like choosing to drink and drive especially when with friends.

Experimental evidence supports the idea that in “hot” (i.e., affective) contexts, adolescents show less advantageous choice behaviour (van Duijvenvoorde et al., 2010) and are more likely than children and adults to make risky decisions (Burnett et al., 2010; Cauffman et al., 2010; Figner et al., 2009; reviewed in Blakemore and Robbins, 2012). In contrast, “cold” (i.e. non-affective) tasks tend to elicit either no change or decreases in risk-taking with age (Crone et al., 2008; Figner et al., 2009; Paulsen et al., 2011; Rakow and Rahim, 2010). Studies using risky decision making and probabilistic reward paradigms mostly supports the hypothesis that adolescents are biased to taking risks due to heightened reward sensitivity (reviewed in van Duijvenvoorde et al., this issue). There is also evidence supporting the idea that in such “hot” situations, adolescents do not engage regulatory prefrontal regions to the same extent as adults (Geier and Luna, 2009). However, reward also appears able to enhance some aspects of cognitive control in adolescence to a greater extent than in adulthood (Geier and Luna, 2009, 2012; Geier et al., 2010; Jazbec et al., 2006; Padmanabhan et al., 2011), suggesting the relationship between motivational processing and cognitive control is a complex one.

While the models outlined above have been instrumental in increasing our understanding of adolescent neurocognitive development, they are not without limitations. Crone and Dahl (2012) argue that developmental neuroimaging studies do not support a simple model of frontal cortical immaturity as an explanation of adolescent behaviour and cognition. Indeed, based on a recent meta-analysis, they suggest that the degree of variability in fMRI studies of cognitive control is difficult to reconcile with such a model (Luna et al., 2010). Several research groups argue instead for a more nuanced understanding of the interactions between cognitive, affective and social processing in understanding how these systems develop, and how this relates to adolescent behaviour (Casey et al., 2015; Crone and Dahl, 2012; Nelson and Guyer, 2011; Nelson et al., 2015; Pfeifer and Allen, 2015, 2012; Schriber and Guyer, 2015; van den Bos and Eppinger, 2015). Crone and Dahl (2012) propose that adolescents show flexibility in PFC recruitment and cognitive control that is particularly sensitive to social and affective context. Cognitive control is hypothesised to be less automatic during adolescence, giving rise to greater variation in performance, but also to more creative and adaptive responses. This flexibility is conceptualised as both advantageous in learning to navigate the complex and rapidly changing social challenges of adolescence, and as having the potential to confer risks and vulnerabilities in the face of individual risk factors and risky environments. A more nuanced approach is also consistent with the Social Information Processing model of adolescent development (Nelson et al., 2005), which proposes that hormonally induced changes to socio-affective systems result in increased salience of social contexts in adolescence.

5. Interactions between the Social Brain, Cognitive Control and Affective-Motivational Processing in Adolescence

Adolescence is a time of pronounced social-cognitive and social-affective development (Crone and Dahl, 2012), in which social factors increase in salience and value (Blakemore and Mills, 2014). While there is a growing body of work investigating the interplay between cognitive control and motivational-affective processing, less is known about the way in which these processes interact with social cognitive processes, social contexts and stimuli. Social interactions are a key source of elicited motivational-affective responses: social cues can elicit robust affective responses, and those around us can be a salient source of potential rewards and punishments. Socio-affective context, such as the heightened motivational salience of peers or the affective appraisal of the value of an outcome, appears to exert a great influence on the extent to which cognitive control systems are recruited in adolescence (Christakou, 2014). This context can be external, for example, one’s social context, or internal, such as one’s affective state.

5.1 Social Cognition and Affective Processing

The perception, understanding and interpretation of others’ emotions is a fundamental aspect of social interaction and requires the integration of a range of perceptual, social cognition and affective skills (Garcia and Scherf, 2015). These include basic aspects of affective processing, such as emotion perception and recognition, and more complex social cognitive processes, such as the ability to understand the affective states of others, sometimes referred to as affective mentalising.

Affective mentalising requires the integration of both social cognition and affective processing networks. Sebastian et al. (2012) examined the development of affective (understanding emotions) and cognitive mentalising (understanding thoughts, perspectives and intentions) and their neural substrates during adolescence using cartoon vignettes. Both types of mentalising were associated with activation in social brain network regions (including dmPFC, pSTS/TPJ and ATC), however affective mentalising also elicited activation in the vmPFC, which was greater in adolescents compared to adults. These findings extend the pattern of decreased dmPFC activation between childhood and adulthood to aspects of mPFC of more typically associated with affective processing and highlights the importance of considering the integration, overlap and interplay of multiple developing brain regions and networks when investigating the development of complex social skills and behaviours during adolescence.

5.2. Affective Consequences of Social Interactions

Social affect refers to the interaction between our emotions and our behaviour in the context of communication with others. The highly rewarding nature of peer interactions during adolescence is believed to increase the impact of both positive and negative aspects of such interactions (Rubin et al., 2006). Social situations can evoke strong emotional responses, and there is evidence this is particularly great in adolescence.

Studies of peer rejection in adolescence, using a range of experimental paradigms, repeatedly find that peer rejection is associated with worsened mood, increased distress and increased anxiety in adolescents compared to child and adult groups, particularly in younger adolescents (reviewed in Platt et al., 2013). Similarly, Silvers et al. (2012) found that compared to older adolescents and adults, young adolescents had greater difficulty regulating their emotions when presented with socio-affective stimuli compared to non-social affective stimuli. Studies of the neural bases of emotional regulation in the context of social rejection have implicated prefrontal regions, notably the right ventrolateral PFC (vlPFC). Compared to adults, adolescents show reduced activation of this region during experimental manipulations of social rejection, such as the Cyberball game (Bolling et al., 2011; Masten et al., 2009; Sebastian et al., 2010, 2011). It has been suggested that developmental increases in vlPFC activation may be associated with increased regulation of social distress following exclusion. Consistent with this hypothesis, within adolescents, greater right vlPFC activation during exclusion has been associated with higher levels of parent-reported interpersonal competence, lower self-reported distress (Masten et al., 2009), and lower self-reported resistance to peer influence (Sebastian et al., 2011). Furthermore, Bolling et al. (2011) found age-related increases in functional connectivity between the right vlPFC and the ventral ACC, an effect which was only found during social exclusion, and not during a similar task in which social expectancies were violated, but particpants were not exlcuded (Bolling et al (2011).

Emotion regulation strategies play a key role in mastering complex social interactions and the emotions they evoke (Gross and John, 2003; Gross, 2002; Ochsner et al., 2002), an important component of which are social cognitive skills. For example, emotional reappraisal (cognitively changing one’s interpretation of an emotion-eliciting situation) requires the integration of cognitive control processes and the ability to take another person’s perspective (Gross, 2014), both of which continue to develop in adolescence (McRae et al., 2012a, 2012b).

5.3. Social Context and Peer Influence

Social context can impact decision-making, such as the propensity to engage in prosocial or risky behaviours. Studies of social context in adolescence have largely focused on the impact of peer influence on adolescent risk-taking behaviour. The presence of peers affects how likely adolescents are to take risks in a driving-simulation game (Gardner and Steinberg, 2005). While adolescents (13 to 16 years), young adults (18 to 22 years), and adults (24+ years) take around the same number of driving risks when alone, in the presence of their friends adolescents take significantly more risks, whereas peer presence had no impact on risk-taking in adults and an intermediate effect in young adults (Gardner and Steinberg, 2005). Adolescents are also sensitive to the presence of peers when performing other experimental tasks involving risky and reward-related decisions (O'Brien et al., 2011; Smith et al., 2015, 2014a).

Increased sensitivity to the presence of peers found in risky and reward-related decision-making appears to extend to other aspects of cognition. Using a modified version of the Iowa Gambling Task (IGT), Silva et al. (2015) demonstrated that the presence of peers had a facilitative effect on the ability to learn from rewarding and punishing feedback in late adolescent males (18 to 22 years). In contrast, another study found that the presence of peers had a detrimental effect on female adolescents' performance of a high-level cognitive task (relational reasoning; Wolf et al., 2015). Pairs of female friends were randomly assigned as either a participant or an observer. The participant then performed the task in three social contexts; alone, observed by their friend, or observed by an experimenter. Social context affected adolescent, but not adult, performance, an effect that was also influenced by the participants' age and task difficulty. Older adolescents (14.9-17.8 years) exhibited poorer performance when being observed by their friend relative to the experimenter, independent of task difficulty, while younger adolescents (10.6-14.2 years) only showed this effect for easier reasoning trials (Wolf et al., 2015). Together, these studies suggest that peer presence can result in both enhanced and impaired performance. Further research is needed to understand whether differences between the two studies (e.g. participant age and sex, cognitive task, task difficulty and the presence or absence of feedback) influenced the direction of the performance effects observed. However, the fact that the impact of social context on performance varied according to the identity of the observer (Wolf et al., 2015) suggests that the source of social influence is a critical factor in understanding the effects of social context in adolescence.

Social context also modulates risk attitudes adopted by adolescents (Engelmann et al., 2012). A recent study investigated the development of social influence on risk perception from late childhood to adulthood, by asking participants to rate the riskiness of everyday situations (Knoll et al., 2015; **Figure 4**). After recording their rating, individuals were informed about the ratings of a social-influence group (teenagers or adults) before rating each situation again. All age groups showed a significant social-influence effect, changing their risk ratings in the direction of the provided ratings, and this social-influence effect decreased with age. Most age groups adjusted their ratings more to conform to the ratings of the adult social-influence group than to the ratings of the teenage social-influence group. Only young adolescents were more strongly influenced by the teenage social-influence group than they were by the adult social-influence group, which suggests that, to early adolescents, the opinions of other teenagers about risk matter more than the opinions of adults.

Research on the mechanisms supporting social influence in adults suggests that social norms and context can influence reward and value signals (Zaki et al., 2011), and it has been hypothesised that the presence of peers may be associated with alterations in brain regions implicated in motivational-affective processing during adolescence, due to increases in the salience of peers (Nelson et al., 2015, 2005; Spear, 2010). In an fMRI version of the driving-simulation game, social context was manipulated by having the participant either play alone, or with two friends present outside of the scanner who communicated with the participant over an intercom. Compared to adolescents (14 to 18 years) and young adults (19 to 22 years), adults (24 to 29 years) showed greater activity in lateral PFC when making decisions in the driving game, regardless of social context. In contrast, relative to both adult groups, adolescents showed increased recruitment of the VS and lateral orbitofrontal cortex when making decisions in the presence of peers compared to when playing alone (Chein et al., 2011).

In contrast to the presence of peers, parents can have a protective effect on risk-taking in adolescence. Telzer et al. (2015) showed that adolescents demonstrated reduced risk-taking behaviour when their mothers were present compared with when alone. Safe decision-making was associated with greater recruitment of the vlPFC and greater functional coupling between the VS and vlPFC, while risky decision-making was associated with decreased activation in the VS. The authors propose that heightened adolescent sensitivity in neural circuitry that is associated with greater risk-taking can also be redirected toward thoughtful, more deliberative and safe decisions.

Peer influence is largely associated with negative outcomes, however recent evidence highlights that peers can also have a positive influence on behaviour. A recent study demonstrated that prosocial feedback from peers was associated with increased prosocial behaviour compared to either no feedback, or antisocial feedback, which was associated with decreased prosocial behaviour (van Hoorn et al., 2014). The tendency to moderate behaviour in line with the values of the people we are with likely involves both regulatory and social cognitive processes. Greater neural activity within cognitive control regions during a response inhibition task predicted safer decisions in the driving game, specifically when in the presence of a peer who expressed risk-averse attitudes, as compared to a risk-promoting peer (Cascio et al., 2014). The authors suggest that the ability to override risky tendencies in the presence of cautious peers may therefore be associated with individual differences in systems involved in top-down cognitive control.

In everyday life, the attitudes and values of those around us are not always explicitly expressed but must instead be inferred using social cognitive processes. Studies investigating the relationship between risk-taking and social exclusion in adolescence suggest that in addition to cognitive control processes, social cognition processes may also be uniquely implicated in adolescents' vulnerability to peer influence on risk-taking. Falk et al. (2014) used the Cyberball game (Williams, 2007) to examine whether neural activation during simulated social exclusion predicted peer influence on risky decisions in the driving-game one week later. Activity in the social brain network (dmPFC, right TPJ, PCC) during social exclusion was positively associated with increased risk-taking when playing the game in the presence of a peer, relative to alone. In a further study, participants completed the driving-game, while in the implied presence of two online peers, before and after being socially excluded by these peers (Peake et al., 2013; **Figure 5**). Exclusion was associated with greater behavioural risk-taking among adolescents with low self-reported resistance to peer influence (RPI). When making risky decisions after social exclusion, adolescents who had lower RPI exhibited higher levels of activity in right TPJ, and this response was a significant mediator of the relationship between RPI and greater risk-taking after social exclusion. Lower RPI was also associated with lower levels of activity in lateral PFC during crashes following social exclusion, but this did not mediate the relationship between RPI and greater risk-taking after social exclusion.

Adolescence is a period of life characterised by increased self-awareness and the emergence of a socially integrated self-identity (Sebastian et al., 2008; Meeus, 2011). It has been proposed that increased awareness of others' perspectives during adolescence might also be related to the 'imaginary audience'. This term describes the phenomenon whereby adolescents believe that others are constantly observing and evaluating them (Elkind, 1967), even if this is not actually the case. The New Look Theory (Lapsley, 1991; 1993) suggests that the phenomenon may result from a combination of two processes. First, adolescents need to develop their own identity as separate from their parents (separation-individuation). As they begin to question who they are and how they fit in, they may become increasingly self-conscious, leading to the imaginary audience. Second, the development of social perspective taking results in adolescents becoming increasingly aware that others have the capacity to evaluate them. This may subsequently lead them to overestimate the extent to which this actually occurs (Lapsely & Murphey, 1985). It should be noted that more recent studies suggest that the imaginary audience peaks in adolescence but persists into young adulthood, and that even older adults exhibit some phenomena associated with it (Frankenberger, 2000).

6. Implications and Future Directions

The successful transition to adulthood requires the rapid refinement of socio-affective and regulatory abilities, social cognition, decision-making and planning in complex social contexts (Nelson et al., 2015, 2005). Many adolescent-typical social behaviours, such as peer influence and sensitivity to social exclusion, involve the co-ordination of social cognition, motivational-affective processes and cognitive control, and the neural systems that support them. While all of these systems show profound development during adolescence, the precise timings and trajectories of structural developments in brain areas within these networks show substantial variation between individuals (Mills et al., 2014). Understanding the interactions between these systems will be crucial in understanding how individual differences in neurocognitive development during adolescence relate to variation in behaviour and cognition.

Many of the behavioural and cognitive changes associated with adolescence, such as increased exploration, novelty-seeking, emotional lability and social salience assist the transition to an independent adult role, however they can also confer vulnerability (Eldreth et al., 2013); half of all lifetime cases of mental health disorder begin by age 14 (Kessler et al., 2005). Increasing our understanding of the development of these abilities, and the way in which they interact with each other, may also give insight as to why some adolescents are successful in making this transition, while others experience difficulties. It may also allow the identification of developmental ‘windows’ in which individuals may be particularly vulnerable, knowledge which is vital for understanding who is at greatest risk, and how to design effective early interventions (see Andersen et al., this issue). Indeed, it has been suggested that adolescence may represent an optimal period in which to intervene (Eldreth et al., 2013).

Social processing and context may be particularly relevant in understanding adolescent mental health risk. Silk et al. (2012) propose that sensitivity to social threat is a core vulnerability that predisposes adolescents to early anxiety and later depression. Social reward processing has also been emphasized as an important factor in the development of adolescent depression (Davey et al., 2008). Furthermore, the age-of-onset distribution for Social Anxiety Disorder differs notably from other anxiety disorders. Social Anxiety Disorder onset rates increase considerably at age 10, with approximately 50% of cases beginning by age 13, and 90% of cases beginning by age 23 (Beesdo et al., 2010; Stein, 2006). It has been hypothesised that the normative cognitive, socio-affective and environmental changes of adolescence place individuals at elevated vulnerability to Social Anxiety Disorder, especially when these changes interact with existing risk factors (Caouette and Guyer, 2014). While, adolescence is typically associated with increased salience of social reward and motivation to approach peers to gain social affiliation, individuals at increased risk for Social Anxiety Disorder may experience approach-avoidance conflict in these situations, due to being simultaneously highly invested in what their peers think of them and extremely fearful of humiliation or rejection (Caouette and Guyer, 2014; Lucock and Salkovskis, 1988). Recent research highlights the importance of investigating developmental changes in connectivity and integration within and between neural networks in identifying mechanisms and predictors of risk in adolescence (Lichenstein et al, this issue; Guyer et al., 2014 Dev Psy; Jarcho et al 2015). For example, experimental studies suggest that adolescents with or at risk of Social Anxiety Disorder exhibit atypical activity and connectivity in reward-related brain circuits during the anticipation of social rewards (Guyer et al., 2014, 2008).

As adolescents approach adulthood, they need to become equipped to navigate the social complexities of their community. It has been suggested that adolescence is a time of heightened cultural susceptibility (Choudhury, 2010; Fiske, 2009) and that pubertal maturation increases the salience of the social environment in adolescence (Crone and Dahl, 2012; Peper and Dahl, 2013). A further proposition is that adolescence represents a period of heightened neural plasticity, during which time the brain is particularly amenable to change and the effects of experience and intervention (Fuhrmann et al. 2015). Psychology and intervention research highlights the importance of reducing situations in which high-risk behaviours such as gang affiliation and criminal behaviour are rewarded through positive peer feedback (Dishion and Tipsord, 2011). Indeed, interventions that segregate adolescents engaging in problem behaviours into groups can actually increase high-risk behaviour (Dishion and Tipsord, 2011; Dishion et al., 2012; Ellis et al., 2012). The social augmentation hypothesis proposes that peer exclusion in adolescence can lead to neuroanatomical alterations in reward sensitivity, thereby increasing susceptibility to peer influence (Dishion et al., 2012). However, recent evidence suggests that social context can also have positive effects on behaviour, such as learning, mental reasoning and engaging in prosocial behaviour. Interventions targeting adolescent criminal or health behaviour should harness these positive effects of sensitivity to social context.

In sum, understanding the way in which developments in social cognition and the social brain during adolescence interact dynamically with other developing systems and abilities in the context of social interaction is crucial in understanding adolescent brain and behavioural development during this important period of biological and social transition.

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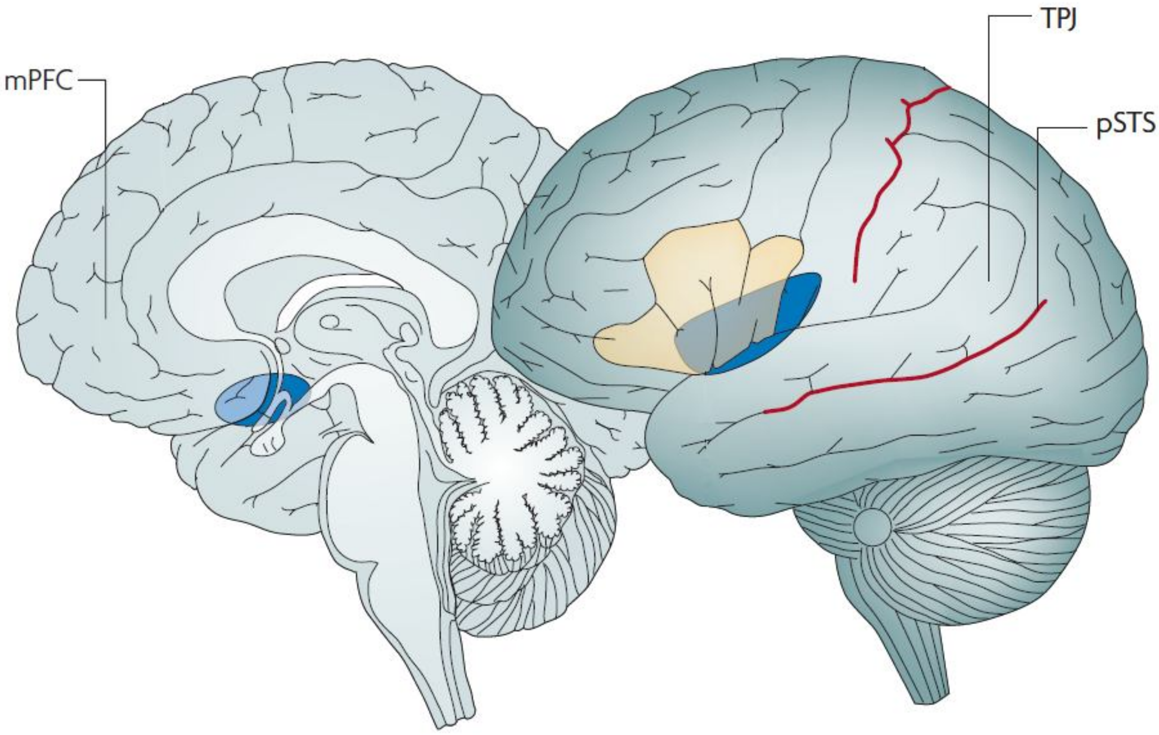

Figure 1: Regions of the social brain network: areas of the brain that may be sensitive to social cognitive processes necessary to navigate the adolescent social environment. Regions that are involved in social cognition include the dorsal medial prefrontal cortex (dmPFC) and temporoparietal junction (TPJ), which are involved in thinking about mental states; the posterior superior temporal sulcus (pSTS), which is involved in observing faces and biological motion; the anterior temporal cortex (ATC), which is involved in applying social knowledge; and the inferior frontal gyrus (IFG), which is involved in understanding the actions and emotions of others. Adapted from Blakemore (2008).

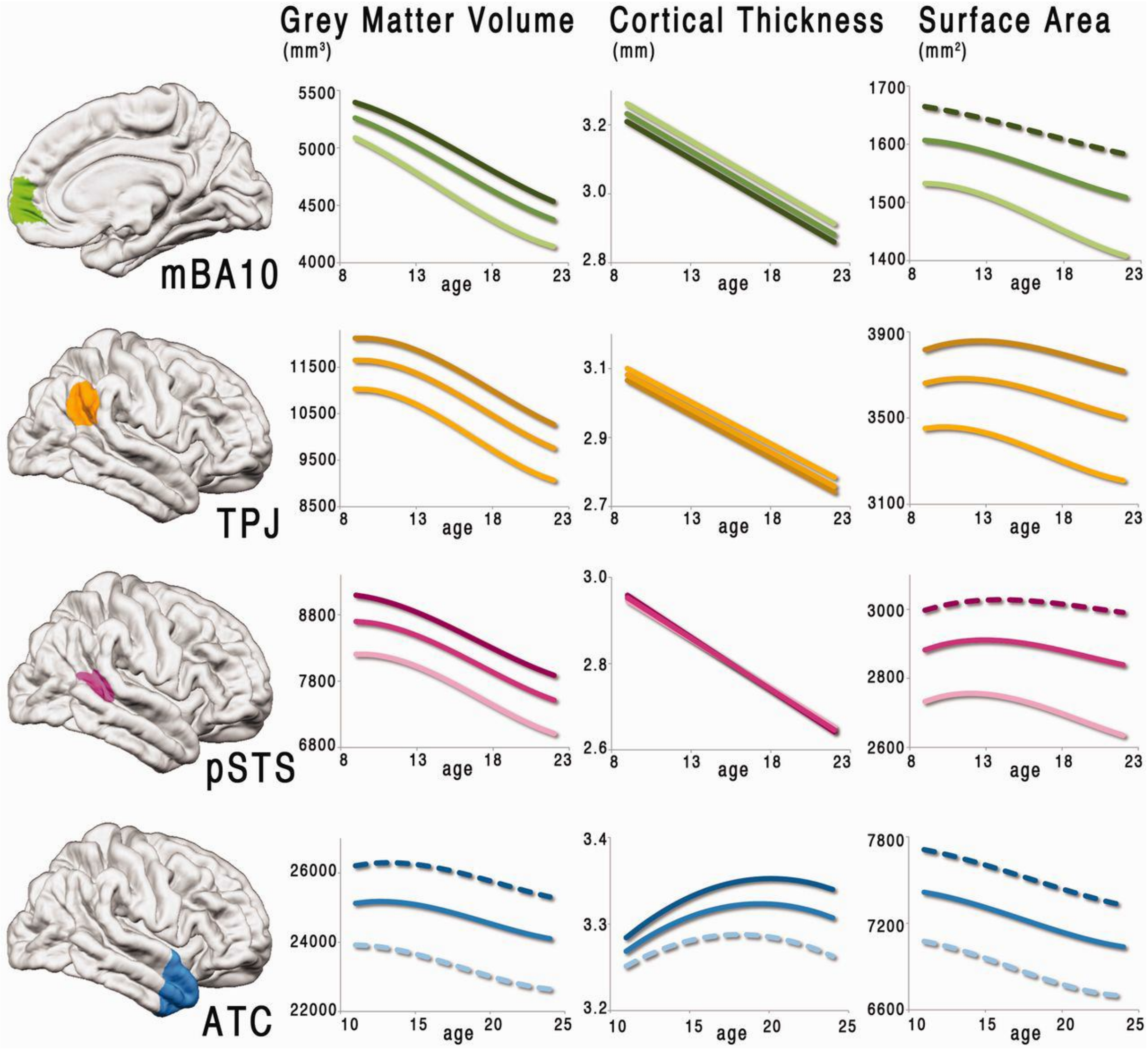

Figure 2: Structural developmental trajectories of brain areas associated with mentalising across adolescence (grey matter volume, cortical thickness, surface area). The best fitting models for all participants are shown for each region of interest (combined hemispheres). Models are fitted to the middle 80% of the sample (ages 9–22 years for mBA10, TPJ and pSTS; ages 11–24 years for ATC). The lighter lines show the fitted models applied to females only, and the darker lines show the fitted models applied to males only. Solid lines indicate the fitted model was significant ($P < 0.05$), whereas dashed lines indicate the fitted model was not significant ($P \geq 0.05$). **mBA10:** medial Brodmann area 10; **TPJ**: temporoparietal junction; **pSTS:** posterior superior temporal sulcus; **ATC:** anterior temporal cortex. Reproduced from (Mills et al., 2014).

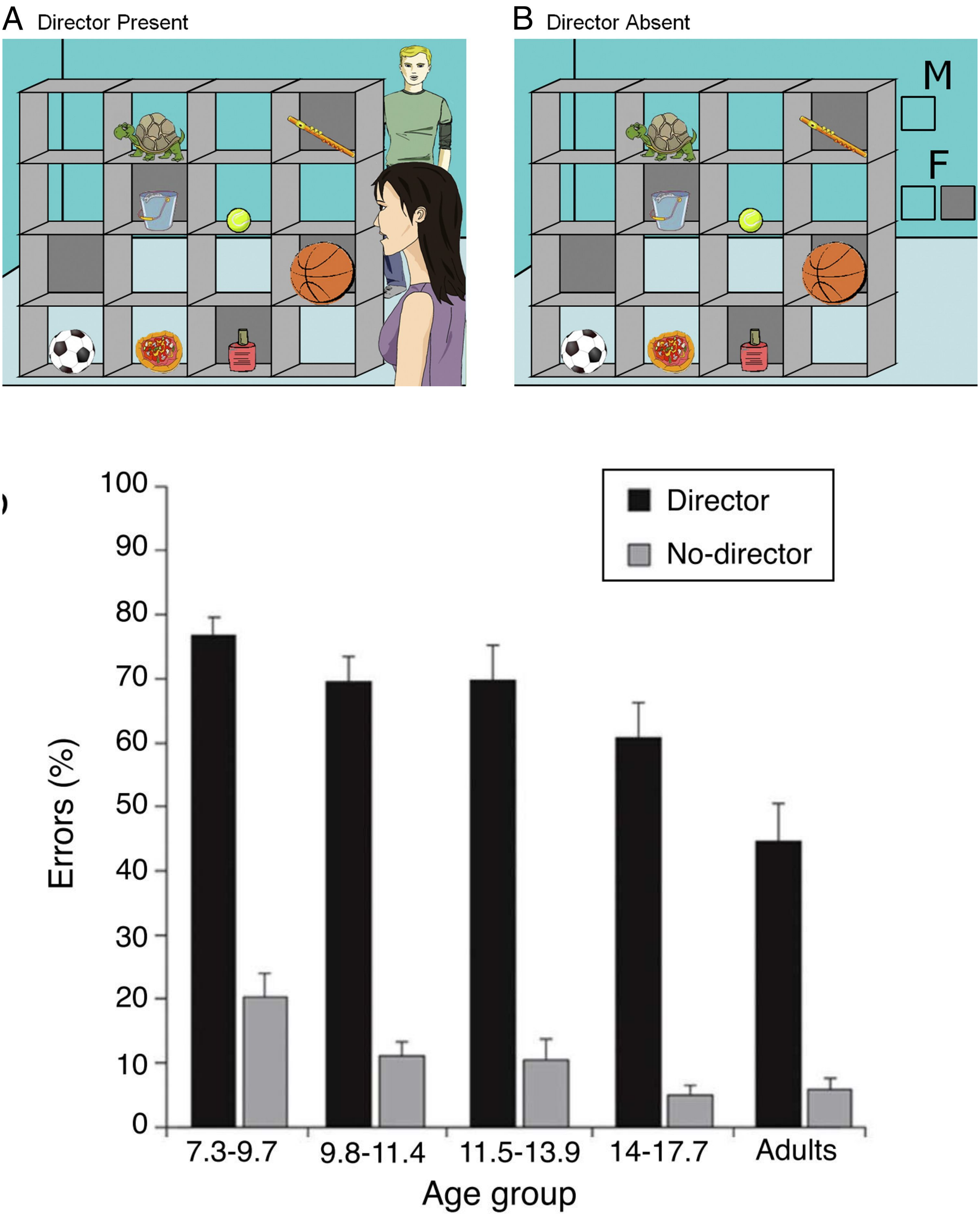

Figure 3: Example stimuli from the Director task, including a social (A: Director) and non-social control condition (B: No-Director). In this example, in both conditions participants hear the

instruction: 'Move the large ball up' in either a male or a female voice. In both examples, if the voice is female, the correct object to move would be the basketball, because in the Director Present condition (A) the female director is standing in front of the shelves and can see all the objects, and in the Director Absent condition (B), the two boxes below the "F" (for "female") indicate that all objects can be moved by the participant. If the voice is male, the correct object to move would be the football, because in the Director condition (A) the male director is standing behind the shelves and therefore cannot see the larger basketball in the occluded slot, whereas in the No-Director condition (B) the single clear box below the "M" (for "male") indicates that only objects in open shelves can be moved/that no objects in front of a grey background can be moved. C. Adolescents (14 to 17 years) old make more errors than adults in the Director condition, whereas in the No-Director condition no difference is found between these age groups. Adapted from Dumontheil et al. (2012, 2010a).

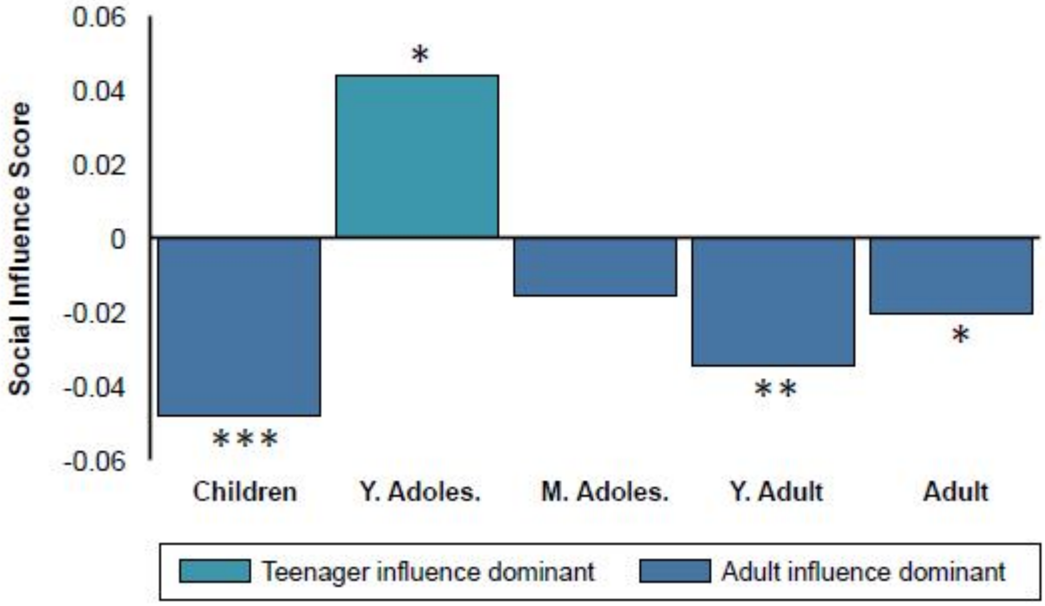

Figure 4: Effect of Social Influence on Risk Ratings. Participants (N= 563) rated the riskiness of everyday situations – before and after they were informed about the ratings of a social influence group (teenagers or adults). Social influence score, an index of conformity to other people's ratings,

is shown relative to the source of the social influence for five age groups: children (aged 8 to 11 years), young adolescents (Y. Adoles., aged 12 to 14 years), mid-adolescents (M. Adoles., aged 15 to 18 years), young adults (Y. Adult, aged 19 to 25 years), and adults (aged 26 to 59 years). Significant difference in social influence effect between social influence groups (adults vs. teenagers) is shown for each age group (***P < 0.001; **P < 0.01; *P < 0.05). Adapted from Fuhrmann et al. (2015); data published in Knoll et al. (2015).

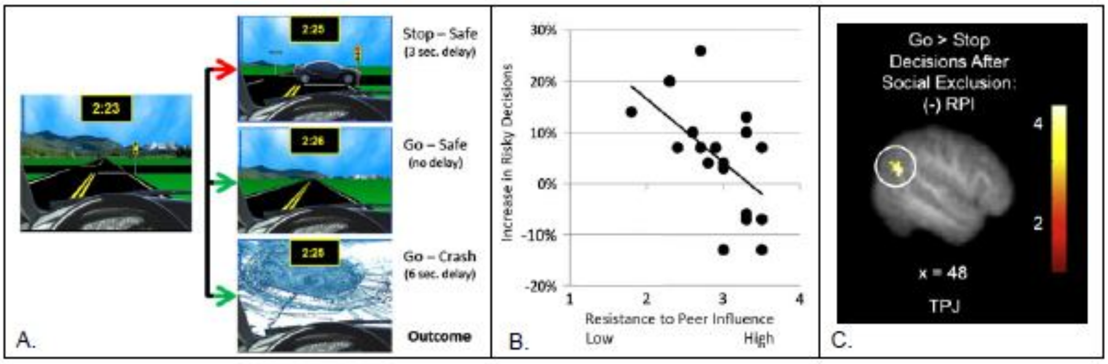

Figure 5: Participants played two rounds of the stoplight driving-game in the presence of two online peers, before and after being socially excluded by these peers. A. Possible decisions (Stop vs. Go) and outcomes (Safe vs. Crash) the stoplight game; Stop decisions resulted in a 3 second delay, Go decisions either resulted in either no delay (Safe outcome) or a 6 second delay (Crash outcome). B. Adolescents with low self-reported resistance to peer influence (RPI) showed a significantly greater increase in risky (Go) decisions after peer exclusion. C. Activity in right temporoparietal junction (TPJ) was negatively correlated with RPI between during risky decisions (Go > Stop) after social exclusion. X: left–right and superior–inferior dimensions in MNI space. Results thresholded at p<.005, k = 19, and displayed on an average group structural. Adapted from Peake et al. (2013).