Decision making and social neurocognition during adolescence

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Acknowledgments

I, Stephanie Burnett, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that these have been cited to the best of my knowledge.

Signed: ______________________________ Date: _________________

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Abstract

Adolescents show a tendency to engage in risky activities, such as dangerous driving and unsafe sex. This has led to the suggestion that adolescents are poor decision-makers, and are risk-seeking in general. The first two chapters of this thesis describe studies investigating adolescent decision-making using probabilistic decision-making tasks. In ***Chapter 2****, the tendency to seek risk, and the ability to integrate probability and reward information to make an optimal decision, is investigated in child, adolescent and adult participants. The emotional response to outcomes was also investigated. In* ***Chapter 3****, a computational approach is adopted to investigate the role of positive and negative performance feedback (wins and losses) in a probabilistic decision-making task in adolescents and in adults. The role of social-emotional factors in decision-making was also investigated.*

Adolescence is characterised by social and emotional development, as well as development in the functional brain correlates of social-emotional processing. Therefore, ***Chapters 4*** *to* ***6*** *focus on adolescent social-emotional processing using behavioural and functional neuroimaging methods. In* ***Chapter 4,*** *results are presented from a study of self-reported social and basic emotions across adolescence, where social emotions (e.g. embarrassment) are defined as emotions that require an awareness of others' mental states (e.g. emotions, opinions, desires). In* ***Chapter 5****, the neural correlates of social and basic emotion processing are investigated in adolescents and in adults, using functional magnetic resonance imaging (fMRI). Finally, in* ***Chapter 6****, these fMRI data are reanalysed using a technique known as psycho-physiological interaction (PPI) analysis, to look at age-associated changes in effective connectivity. Results are discussed in the context of social cognition and neuroanatomical development.*

Contents

List of figures

List of tables

Abbreviations

ACC	Anterior cingulate cortex
AI	Anterior insula
ANOVA	Analysis of variance
arMPFC	Anterior rostral medial prefrontal cortex
ATC	Anterior temporal cortex
BA	Brodmann area
BOLD	Blood oxygenation level-dependent
CCT	Columbia Card Task
CSF	Cerebro-spinal fluid
DLPFC	Dorso-lateral prefrontal cortex
DTI	Diffusion-tensor imaging
EV	Expected value
FA	Fractional anisotropy
fMRI	functional magnetic resonance imaging
FSH	Follicle-stimulating hormone
FSIQ	Full-scale intelligence quotient
GnRH	Gonadotropin-releasing hormone
IFG	Inferior frontal gyrus
IGT	Iowa Gambling Task
IPS	Intra-parietal sulcus
LH	Luteinising hormone
MA	Mid-adolescent
MNI	Montreal Neurological Institute
MPFC	Medial prefrontal cortex
MR	Magnetic resonance
MRI	Magnetic resonance imaging
MTR	Myelin transfer ratio
OFC	Orbitofrontal cortex
PDS	Petersen Development Scale
PFC	Prefrontal cortex
PPI	Psycho-physiological interaction

PSMD	Perceived self-mother difference
pSTS	Posterior superior temporal sulcus
RPI	Resistance to peer influence
SAD	Social anxiety disorder
STS	Superior temporal sulcus
SVC	Small volume correction
TPJ	Temporo-parietal junction
VBM	Voxel-based morphometry
VOI	Volume of interest
WASI	Wechsler Abbreviated Scale of Intelligence
WCST	Wisconsin Card Sort Task
YA	Young adolescent

Chapter 1

Introduction

Adolescence: behaviour, cognition and the brain

This chapter will first define adolescence, and will then summarise findings in adolescence research from a range of interconnected fields: endocrinology, including the effects of puberty hormones on adolescent development; adolescent psychology and behaviour, including social behaviour, emotional development and decision-making; structural brain development during adolescence, including histological findings and the volumetric changes shown in human MRI studies; adolescent functional neuroimaging, with a particular focus on the functional magnetic resonance imaging correlates of social cognition and decision-making; and adolescent cognitive development, including development within the domains of social cognition and decision-making. Finally, subsequent experimental chapters will be briefly introduced.

1.1 Adolescence: definition

Adolescence is the period of physical, cognitive and psychosocial maturation between childhood and adulthood (Lerner & Steinberg, 2004; Sisk & Foster, 2004). The beginning of adolescence occurs around the onset of puberty (mean age 11 in females, 12 in males). Therefore, adolescence is marked by dramatic changes in hormone levels and physical appearance. As a result, and in combination with environmental factors and hormonally-independent biological influences, an individual enters a profoundly altered social and interpersonal environment. Finally, adolescence is marked by protracted changes in the structure and function of the brain.

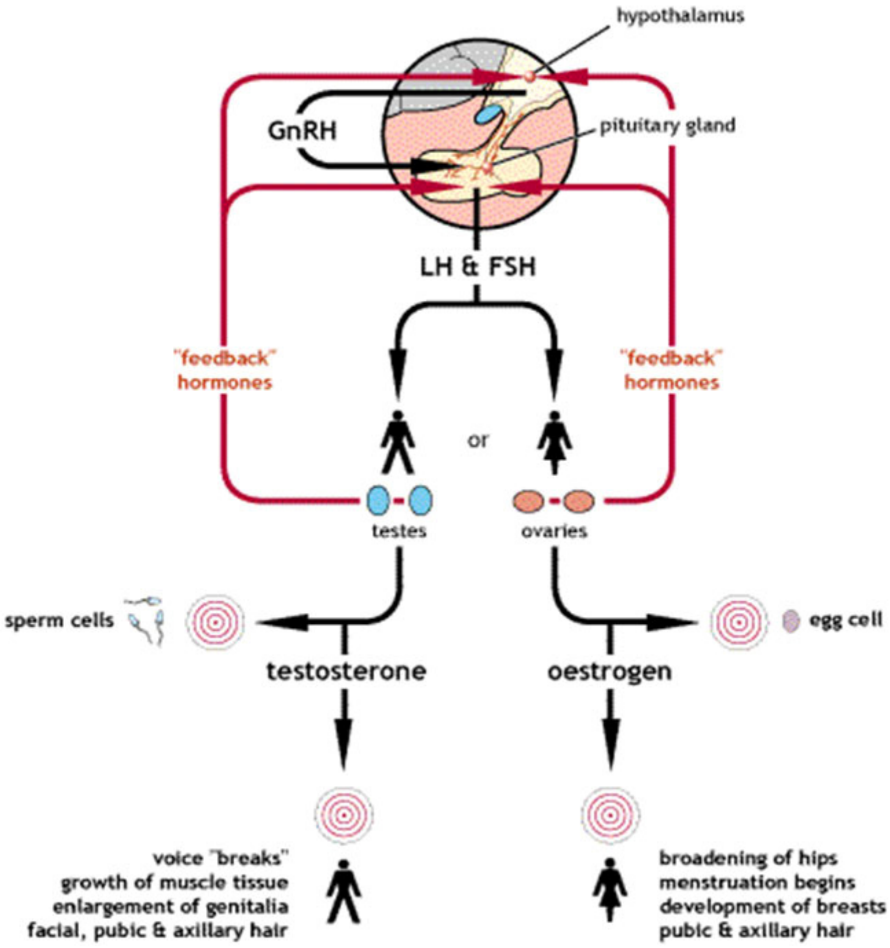
The end of adolescence is said to occur when an individual has attained a stable adult role (Lerner & Steinberg, 2004). Therefore, whereas the beginning of adolescence is loosely anchored to the biological events of puberty, the endpoint of adolescence is defined according culturally-variable psychosocial and economic criteria (Gluckman & Hanson, 2006). Many use the age of attainment of legal majority as a convenient marker for the endpoint of adolescence (Spear, 2000). Elsewhere, it has been argued that in developed nations and at the present point in history, a stable economic and psychosocial adult role is not attained until the early or mid-twenties (Baumrind, 1987). However in practice, this period of 'extended' adolescence tends to be referred to as young adulthood or youth (e.g. Gardner & Steinberg, 2005; Arnett, 2000). For the purposes of this thesis, adolescence is defined as the period between the mean age of puberty onset (11-12 years) and 18 years of age.

1.2 Puberty

Early adolescence is characterised by the transition through puberty, which is defined as the biological process resulting in the attainment of reproductive competence (Sisk & Foster, 2004). Puberty comprises three hormonally-driven events: gonadarche, adrenarche and activation of the growth axis (for a review, see Dorn et al. 2006). Gonadarche, or activation of the hypothalamic-pituitary-gonadal axis, is initiated between age 8-14 years in females, and 9-15 in males in response to increased release of gonadotropin-releasing hormone (GnRH) from the hypothalamus, which is detected by the pituitary gland (Susman & Rogol, 2004; Dorn et al., 2006; see **Figure 1.1**). The pituitary gland responds with the production of hormones that are detected by the gonads (ovaries, testes; Susman & Rogol, 2004; Spear, 2000). The gonads respond by producing eggs or sperm, as well as gonadal steroids or 'sex hormones': oestrogen in females, testosterone in males; progesterone is released by the corpus luteum following ovulation in females. The sex hormones trigger changes in the reproductive organs and stimulate the appearance of secondary sexual characteristics (Susman & Rogol, 2004).

Adrenache, or activation of the hypothalamic-pituitary-adrenal axis, is initiated earlier than gonadarche, from age 6-9 in females and a year later in males (Grumbach & Styne, 2003; Dorn et al., 2006). At the onset of adrenarche, adrenal androgens (weaker forms of gonadal testosterone) begin to rise, and this contributes to changes in pubic hair and body odour. The mechanism for the initiation of adrenarche is unknown, although there is evidence for a role of adrenocorticotropic hormone (Weber et al., 1997). Finally, activation of the growth axis occurs during puberty, resulting in a shift from night-time to constant 24-hour release of growth hormone (Dorn et al., 2006). This leads to a linear growth spurt at around age 12 in girls and age 14 in boys, as well as changes in body size and composition (Marshall & Tanner, 1969, 1970; Reiter & Rosenfeld, 2003).

Figure 1.1 Gonadarche, which is a component of puberty. Gonadotropin-releasing hormone (GnRH) release from the hypothalamus triggers the start of gonadarche. GnRH is detected by the pituitary gland, which responds by secreting luteinising hormone (LH) and follicle-stimulating hormone (FSH). LH and FSH are detected by the gonads (testes or ovaries), which respond by producing sperm and egg cells and the gonadal steroid hormones testosterone and oestrogen, which trigger the development of some secondary sexual characteristics. Figure from www.kallmans.org



1.2.1 Hormonal effects on brain and behaviour

Sex hormones influence the physical appearance of the body, but they also affect the brain and subsequent behaviour. These effects are hypothesised to occur via two mechanisms: organisation and activation (Phoenix et al., 1959; Sisk & Foster, 2004; Schulz et al., 2009). Organisational effects occur pre- and peri-natally, with waves of testosterone masculinising and defeminising neural circuits in males, and the absence of testosterone resulting in a female neural phenotype. Activational effects occur at puberty, with gonadal hormones including testosterone acting on dormant neural circuits to elicit adult reproductive behaviours in context. A recent modernisation of this dichotomy holds that the hormonal events of puberty exert organisational as well as activational effects (Schulz et al. 2009). It has recently been proposed that the pubertal wave of gonadal hormones gives rise to a second period of structural reorganisation in the brain (Sisk & Foster, 2004).

Animal studies indicate that gonadal steroid hormones exert three main effects on behaviour at puberty via specific brain structures. The first effect is the facilitation of directly reproductive behaviours, which occurs mainly via the hypothalamus (e.g. Putnam et al., 2005). The second effect of gonadal hormones on behaviour is via reorganisation of sensory and association regions of the brain, including the visual cortex (Nunez et al., 2002), amygdala and hippocampus (Romeo & Sisk, 2001; Hebbard et al., 2003). This is thought to influence behaviour by altering sensory associations, e.g. the smell or sight of an adult female, with consequences for an animal’s response to potential sexual partners or competitors (Sisk & Foster, 2004). The third effect of gonadal hormones occurs via reward-related brain structures, such as the nucleus accumbens and dopaminergic pathways to the prefrontal cortex. These effects are necessary if the animal is to seek out reproductive opportunities. For example, in the rodent nucleus accumbens, pubertal increases in testosterone remodel neural circuits to elicit an increase in pleasure-seeking behaviours including sexual behaviour (Sato et al., 2008). Researchers have begun to investigate the effects of puberty hormones on the human brain and behaviour (e.g. Vermeersch et al., 2008). This research draws on a wealth of human psychology research on adolescence, which will be summarized in the next section.

1.3 Behavioural and psychological characteristics of adolescence

1.3.1 Social behaviour and self-awareness

The onset of human adolescence marks a change in patterns of social behaviour. Individuals begin to spend less time with their families, and spend more time both with friends and by themselves (Larson & Richards, 1991). During the time spent with friends, adolescents share their worries, secrets and ambitions more than they did as children (Laible et al., 2004). This intimacy in friendships also has negative consequences, as it allows for a greater incidence and influence of psychological bullying, including social exclusion (Parker et al., 2006).

Peer relationships become more complex and hierarchical during adolescence (Brown, 2004). The transition from adolescence to adulthood sees a continuation in hierarchical relationships, but a decrease in the amount of time spent with friends and acquaintances and a resurgence in the amount of time spend with family (Cartensen, 1992).

The adolescent years mark a change in social and self-awareness. It has long been held that the onset of adolescence marks an increase in self-consciousness, and indeed the self-conscious emotion embarrassment has been labelled 'the adolescent emotion par excellence' (Harré, 1990). There is limited empirical evidence to corroborate this notion, at least with regards the frequency and intensity of self-conscious emotions *per se*. However, social psychology self- and other-report studies indicate that from early adolescence, individuals become more aware that other people are making judgments about them, and they place a higher value on these judgments (Harter, 1990; Vartanian, 2000). This is particularly true for judgments elicited from peers. Adolescents are more likely than children to compare themselves with others, especially peers (Simmons et al., 1973; Elkind, 1967; Elkind & Bower, 1979; Parker et al., 2006).

It has been suggested that the developmental increase in social and self-awareness is due to developing proficiency in social perspective-taking (Lapsley, 1993). Others have suggested that it may be a response to the interpersonal realities of adolescent life: adolescents have been estimated to spend almost a third of their day with peers

(Csikszentmihalyi et al., 1977), so peer acceptance and reputation are powerful determinants of self-esteem and happiness (O'Brien, & Bierman, 1988; Sebastian et al., 2009).

1.3.2 Emotional development

Adolescence is said to be a time of emotional turbulence, or 'storm and stress' (Hall, 1904). Empirical studies show some support for this notion, although the degree of turbulence appears to be modulated by cultural variables (Arnett, 1999). Self-report studies conducted in North America have shown that the average emotional state becomes less positive between late childhood and early adolescence, as well as more labile; these trajectories stabilise in middle and late adolescence (Larson & Richards, 1991, 1994; Larson et al., 2002). Elsewhere, it has been shown that inner turmoil, as represented by feelings of misery and self-depreciation, is frequent in 14-15 year olds (Rutter et al., 1976). However, these findings may be influenced by self-report bias, and not all studies report heightened emotional lability and negativity during adolescence (e.g. Silk et al., 2003).

Adolescence is an important period for the refinement of emotional self-regulation abilities. Poor emotion self-regulation during adolescence is associated with increased risk for depressive symptoms (Silk et al., 2003), and indeed, pathological emotional turmoil, such as occurs in clinical depression, increases in prevalence from adolescence onset (Davey et al., 2008). Emotion regulation in a social context in particular becomes more sophisticated during the adolescent years. Relative to children, adolescents show a heightened awareness of the interpersonal consequences of expressing certain emotions to parents and to peers (Zeman & Garber, 1996; Zeman et al. 2006).

1.3.3 Risk and decision-making

Another aspect of typical adolescent psychology and behaviour is the tendency to seek out and engage in risky activities (e.g. Eaton et al., 2007; Steinberg, 2008; Geier & Luna, 2009). These activities include dangerous driving, unsafe sex, tobacco and alcohol use, poor dietary habits and physical inactivity. The increase in risky activities between childhood and late adolescence partially accounts for the so-called 'health paradox' of adolescence, whereby a peak in lifetime physical health is nevertheless accompanied by high morbidity and mortality. In the United States, morbidity and mortality rates increase by 200% between mid-childhood and late adolescence (Resnick et al., 1997; Ozer et al., 2004), and a recent epidemiological survey in the United States found that 72% of all deaths among 10-24 year-olds were a result of accidents, homicides and suicides (Eaton et al. 2007).

The high percentage of adolescent harm resulting from risky activities is of course partially a result of low illness (e.g. heart disease, infant illness), and also because adolescence marks an increase in access to certain risky activities (e.g. driving). This increased access occurs at an age when risk-estimation abilities may still be immature (see Boyer, 2006). This may be due to cognitive-developmental factors, or to developing expertise and experience. Another contributing factor may be the increase in self-reported sensation-seeking that is seen at the onset of adolescence (Steinberg, Albert et al., 2008). It has been suggested that sensation-seeking is an important trait to possess in the transition to an adult role, as it will motivate exploration and independence from parents (Spear, 2000).

Social and emotional factors play a pivotal role in adolescent risky decisions. Heightened emotionality (reviewed in section **1.3.2**), in combination with sensation-seeking and an increase in the importance of peer reputation (section **1.3.1**) contribute to a distinctively social context for adolescent risk-taking (e.g. Steinberg, 2008). For example, whereas most adults who commit crimes do so alone, most adolescent crime occurs in the presence of peers (Zimring, 1998). Other potentially risky activities, such as alcohol and substance use and sex, are strongly influenced by perceived peer engagement in these activities (e.g. Chassin et al., 2004).

Engagement in risky activities is a key psycho-behavioural characteristic of the adolescent period, as are the social and emotional changes which occur during this time. In the next section, another defining characteristic of adolescence will be covered: The continuing development of the brain.

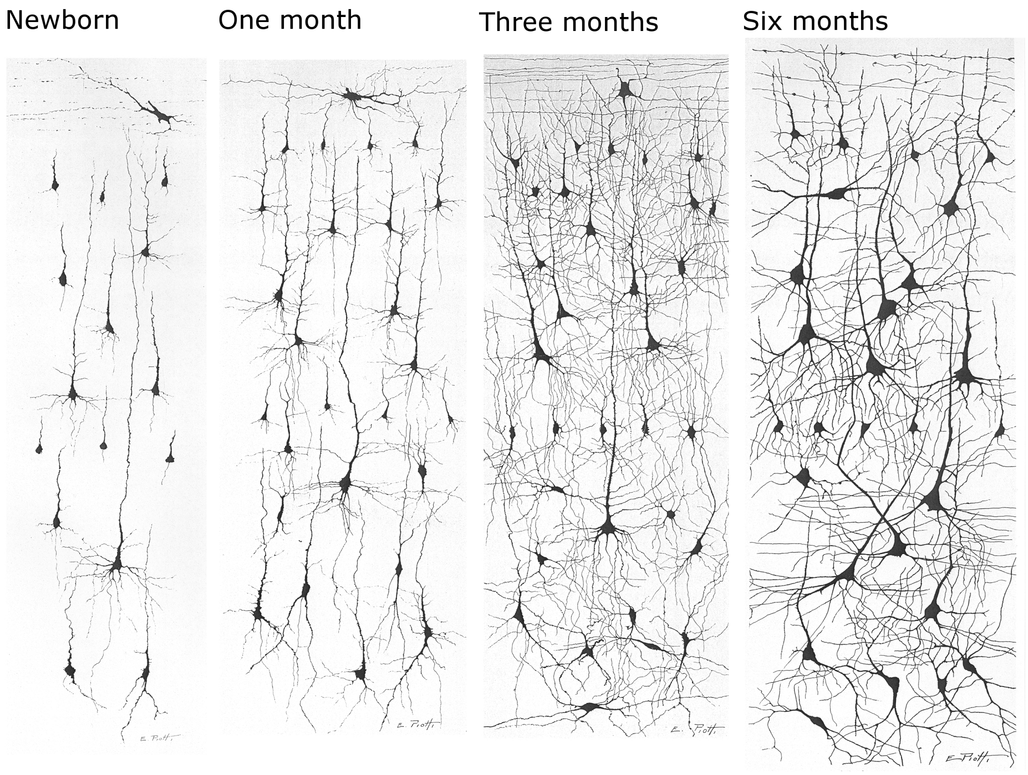
1.4 Adolescent structural brain development

In the first year of life, the brain undergoes rapid increases in volume, and changes in structure and composition. Until relatively recently, it was widely held that this brain development only occurred during early childhood. However, a small number of studies published in the 1960s and 70s using *post mortem* brain samples (Yakovlev & Lecours, 1967; Huttenlocher, 1979) suggested that parts of the brain continue to develop throughout childhood and into adolescence. More recently, the advent of magnetic resonance imaging (MRI) and techniques such as diffusion tensor imaging (DTI) has supported this notion, by showing continuing development of grey and white matter throughout the second decade of life (and beyond). The following sections will first describe early histological studies of the developing brain, then evidence from MRI studies showing continuing development of the brain during the adolescent years.

1.4.1 Early histological studies of the developing brain: non-human animal studies

Early histological experiments carried out using non-human animals (mainly rodents and primates) showed that early in development, during the equivalent of human infancy and early childhood, cortical neurons undergo substantial dendritic outgrowth (see **Figure 1.2**) and the formation of new synapses (synaptogenesis; Rakic et al. 1986; Bourgeois et al. 1994; Petanjek et al., 2008). This is followed by a period of synaptic pruning, in which many of the existing synaptic connections are eliminated. Thus, synaptic density shortly after birth greatly exceeds that in adulthood (for example, Rakic et al. (1986) showed a 2:1 ratio of synaptic density in young child vs. adult rhesus macques). Another process which has been shown to occur in the developing brain is the substantial increase in absolute and proportional myelin content, as axonal fibres become progressively ensheathed in layers of insulating myelin (Wells & Dittmer, 1967; Norton & Poduslo, 1973; Waxman, 2004).

Figure 1.2 Fast dendritic outgrowth shortly after birth, which is accompanied by synaptogenesis. The drawing below from Conel (1939-1967) shows pyramidal neurons and their dendrites, which participate in synaptic connections, in human frontal cortex from newborn to six months old. On the basis of this dendritic outgrowth, one would expect major synaptogenesis to occur postnatally, as indeed has been demonstrated (Huttenlocher et al., 1979, 1983, 1997; Petanjek et al., 2008).

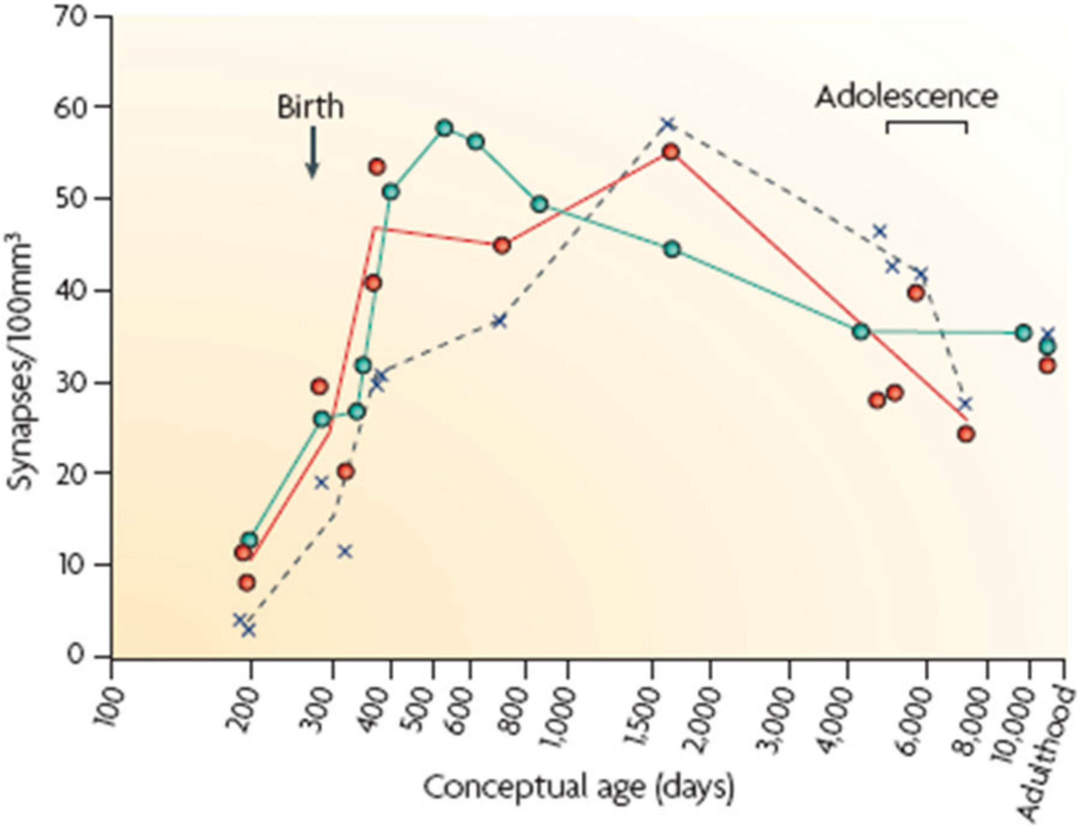


1.4.2 Early histological studies of the developing human brain

1.4.2.1 Synaptic development

In the 1970s, research on *post mortem* human samples revealed that some areas of the brain, in particular the frontal cortex, undergo cycles of synaptogenesis and pruning well beyond early childhood. Studies by Huttenlocher et al. compared synaptic density in visual cortex and the middle frontal gyrus in *post mortem* human brains between the ages of zero to 27 years (Huttenlocher et al. 1979, 1983, 1997). Results showed that the number of synapses in visual cortex peaked at around one year after birth, after which there was a gradual decline into middle childhood when synaptic density stabilised to adult levels. In contrast, in the frontal cortex, synaptic density reached a peak substantially later, increasing throughout early childhood and up to the age of five. Furthermore, synaptic density in the frontal lobe showed an extended profile of decline, stabilising to adult levels only towards the end of adolescence (see **Figure 1.3**). These observations were interpreted to suggest that certain regions of the brain, including parts of the frontal cortex, do not complete their cycle of synaptogenesis and pruning until well into adolescence.

Figure 1.3 Development of synaptic density in sensory and frontal brain regions. Graph shows mean synaptic density in the primary auditory cortex (red circles), the primary visual cortex (blue circles) and the prefrontal cortex (middle frontal gyrus; blue crosses) in *post mortem* human brains. The *x*-axis shows conceptual age in days, from 200 days post-conception to 10,000 days post-conception (approximately 27 years: the period of adolescence is indicated by a horizontal bar). Synaptic density increases in all three regions during early childhood, and is followed by a period of decreasing synaptic density. This sequence occurs later in the frontal cortex. From Blakemore (2008).



1.4.2.2 Axonal myelination

Another significant neurodevelopmental event that occurs in adolescence is axonal myelination. *In utero*, the human brain contains a small proportion of myelinated fibres. Within the first year of life, the proportion of cerebral myelin increases dramatically, which contributes to the rapid increase in total cerebral volume during the first year of life. It has been demonstrated that axons in certain brain regions continue to be myelinated throughout childhood and adolescence, albeit at a slower rate (Yakovlev & Lecours, 1967; Benes et al., 1989, 1994). Myelination increases axonal conduction speed (Waxman, 2004), which not only 'speeds up' neural processing but also allows for greater temporal precision in information encoding (Paus et al., 1999).

1.4.3 Structural MRI studies of the developing human brain

Until recently, the structure of the human brain could be studied only after death. The advent of non-invasive brain imaging techniques, in particular magnetic resonance imaging (MRI), has enabled investigation of the development of the living human brain.

1.4.3.1 Introduction to structural MRI

Structural MRI uses static and radiofrequency magnetic fields to visualise different tissue types in the brain (e.g. grey matter, white matter and cerebro-spinal fluid (CSF)), by measuring differences in proton content. Techniques such as voxel-based morphometry (VBM) are then used to quantify and compare the amount of each tissue type in MR-images from groups of experimental participants which differ on a variable of interest (e.g. age). These structural MRI measurement techniques generally proceed in the following manner:

First, the MR-images are registered to standard stereotaxic space, in order to remove gross differences in brain shape and to superimpose on the image a three-dimensional grid of voxels (Ashburner & Friston, 2000). Next, an automated computer algorithm segments the MR-images into grey matter, white matter, CSF and three other background tissue types, by classifying each voxel according to its predominant tissue type. The images are then smoothed to reduce the impact of noise from the normalisation and tissue classification steps.

At this point, grey and white matter 'density' (concentration) can be calculated across a brain region of interest: the whole brain, the cortex, a particular lobe or a circumscribed structure (e.g. the amygdala). The density of a tissue type in a smoothed MR-image is its relative proportion in normalised volume (Ashburner & Friston, 2000). Alternatively, absolute grey and white matter volumes can be calculated by multiplying the 'density' of each tissue by the relative voxel volume, that is, using the parameters that describe how the raw MR-image was deformed into standard space (Ashburner & Friston, 2000; Paus, 2005). Grey matter thickness can be calculated in a similar manner (Gogtay et al., 2004). Finally, the density, volume or thickness of brain tissues of interest, within brain structures of interest, can be statistically compared across participant groups (Friston et al., 1994a; Ashburner & Friston, 2000).

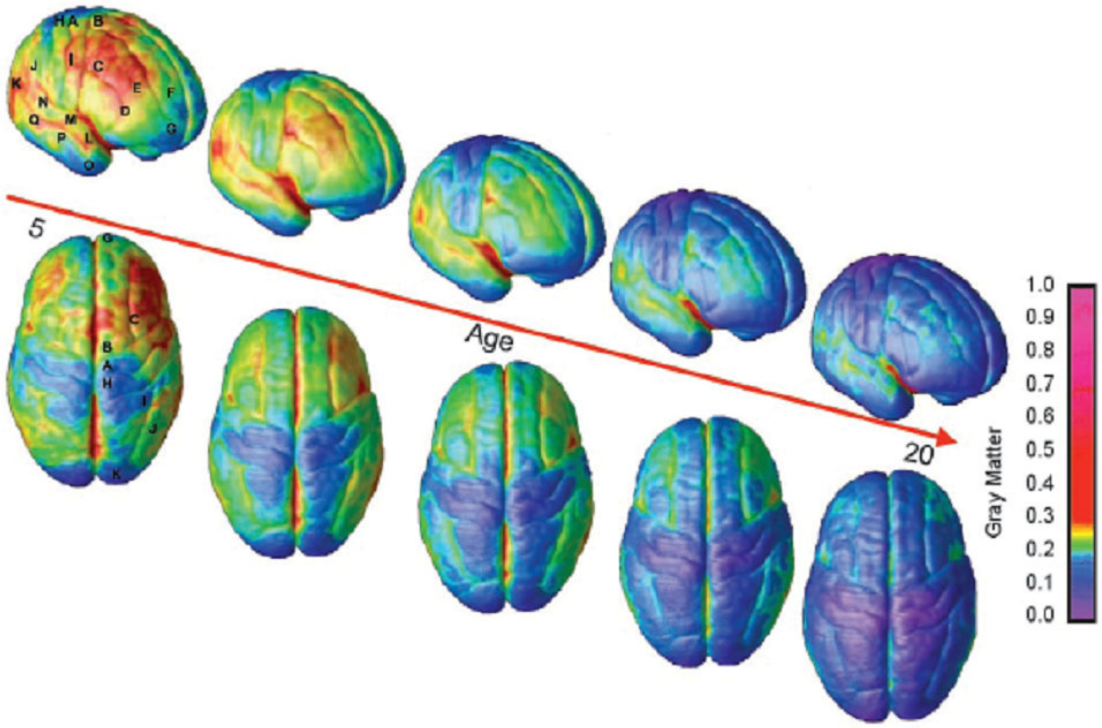
1.4.3.2 Adolescent structural MRI studies

In the past decade, a number of structural MRI studies have shown changes across adolescence in the tissue composition of the brain. These changes, which will be described in some detail the following sections, are hypothesised to reflect the histological changes described in section **1.4.2**. In brief, two main age-associated changes have been described: firstly, cortical grey matter volume and density change in a non-linear and region-specific manner; and secondly, white matter volume and density increase linearly across the brain. Evidence from additional MRI techniques suggests concurrent changes in white matter macromolecular structure and integrity; this evidence will be briefly described in the final part of this section.

1.4.3.2.1 Adolescent changes in grey matter

Structural MRI studies have shown that grey matter volume changes during childhood and adolescence in a region-specific and predominantly non-linear manner. One of the first studies to provide evidence for this finding was a partially longitudinal study, in which a large sample of participants at a range of ages were scanned on at least two time-points, approximately two years apart (Giedd et al. 1999a; see also Sowell et al. 1999; Gogtay et al. 2004; Shaw et al., 2008). These and subsequent structural MRI studies have shown that grey matter volume and density across much of the cortex follows an inverted U-shaped pattern of development, initially increasing during childhood before attaining a peak in volume and density (the age at peak volume and density differs between brain regions). This peak is followed by a gradual decrease in volume and density, before stabilising to an adult level. In general, peak volumes are attained at younger ages in primary sensorimotor regions as well as in polar cortex, and at older ages in secondary and association cortex: this pattern can be seen in **Figure 1.4**.

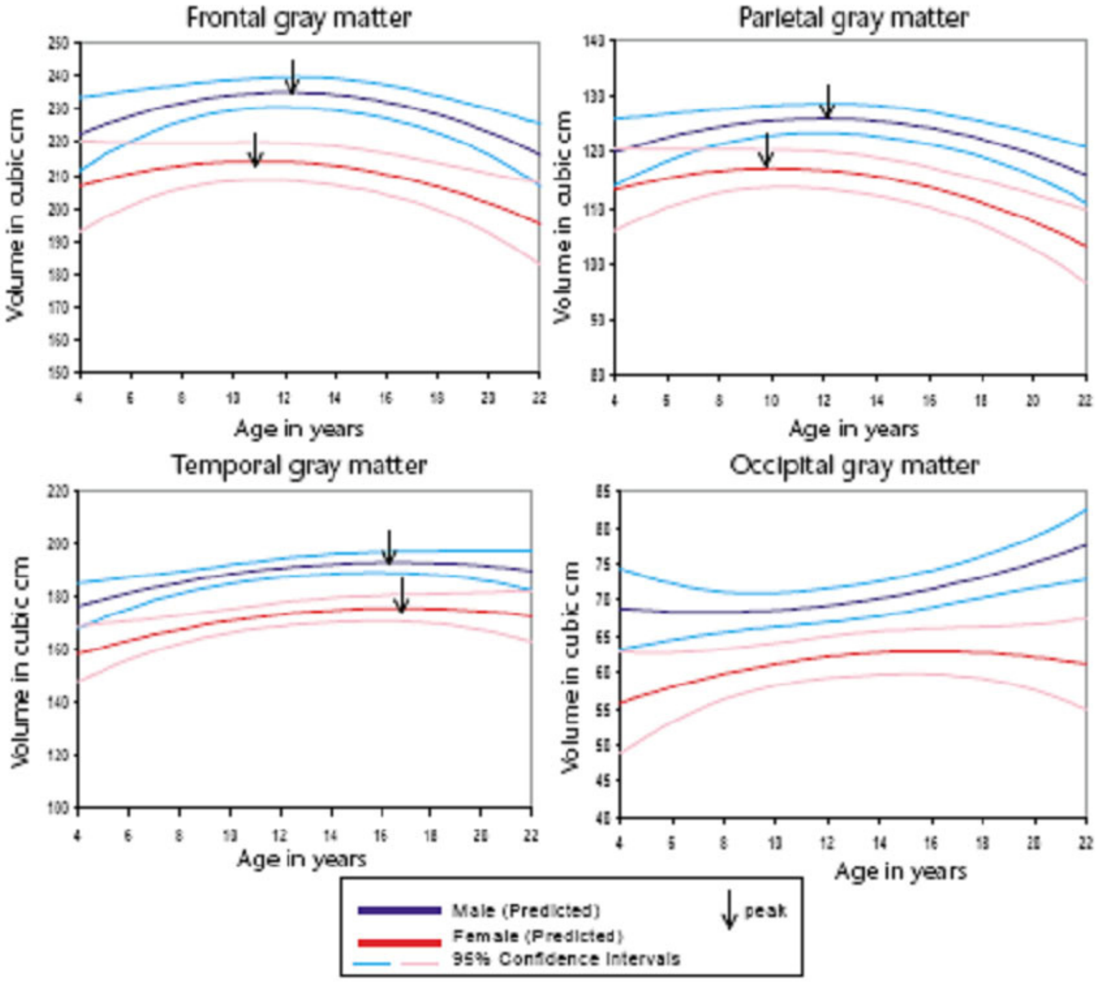
Figure 1.4 Development of grey matter density across the cortical surface, as revealed with MRI. Figure shows the dynamic sequence of grey matter maturation across the cortical surface, between the ages of five (left) and 20 (right). The side bar indicates grey matter density. It can be seen that regions including temporal and frontal association cortex undergo protracted changes in grey matter density up to the age of 20, whereas regions such as the occipital pole and somatosensory cortex stabilise early. From Gogtay et al. (2004).



The next figure (**Figure 1.5**) illustrates region-specific trajectories of grey matter change. In the frontal and parietal lobes, grey matter density follows an inverted-U shaped trajectory with its peak at around puberty onset (age 11 in girls and 12 in boys; **Figure 1.5,** top). In the temporal lobe, grey matter density peaks at on average 16-17 years of age (Giedd et al., 1999a; **Figure 1.5**, bottom left). In contrast, grey matter density in the occipital lobe does not show the same pubertal or adolescent peak (see **Figure 1.5,** bottom right; note that Shaw et al., (2008) reported peak occipital grey matter at around age eight).

Within each lobe, particular sub-regions have their own developmental patterns of grey matter change. For example in the frontal lobe, precentral grey matter peaks prior to adolescence, whereas dorsolateral prefrontal cortex (DLPFC) and parts of the medial prefrontal cortex (MPFC) attain peak grey matter volume later: at around puberty onset or later (Gogtay et al., 2004; Shaw et al. 2008). In the temporal lobe, middle and inferior regions attain peak grey matter density relatively earlier (age 11-12) than superior and insular temporal cortex (ages 14 and 18 respectively; Shaw et al., 2008). Therefore, adolescence is characterised by grey matter thinning across much of prefrontal cortex and parts of the temporal cortex; certain parts of the temporal cortex undergo extended grey matter thinning during late adolescence and into early adulthood.

Figure 1.5 Region-specific trajectories of grey matter change. Graphs show regional changes in cortical grey matter ‘volume’ (relative volume or density: see section **1.4.3.1**) in the frontal, parietal, temporal and occipital lobes (predicted size with 95% confidence intervals) in 243 MR scans acquired cross-sectionally and longitudinally from 89 males (blue) and 56 females (red) aged 4 to 22 years. Arrows indicate peaks of the curves. From Giedd et al. (1999a).



1.4.3.2.1.1 Implications of adolescent grey matter change

Grey matter is composed of the cell bodies, dendrites and axons of neurons, as well as glial cells and capillaries. In light of the histological findings of Huttenlocher et al. (described in section **1.4.2.1**), it has been suggested that the inverted-U shaped developmental trajectory of grey matter volume seen in MR scans is due to dendritic outgrowth and synaptogenesis, followed by synaptic pruning (e.g. Giedd et al., 1999a). This implies that puberty onset is marked by an exuberance of synaptic connections in prefrontal and parietal cortices, and that the period of adolescence is characterised by prefrontal and parietal synaptic pruning, with the same pattern occurring slightly later in parts of the temporal lobe.

Therefore, changes in grey matter shown in structural MRI studies are hypothesised to reflect cellular changes that impact on neural function. It has been suggested that synaptic proliferation in the prefrontal cortex around the onset of puberty leads to 'noisy' neural processing, and subsequent synaptic pruning results in more finely-tuned and efficient circuits (Durston et al., 2006).

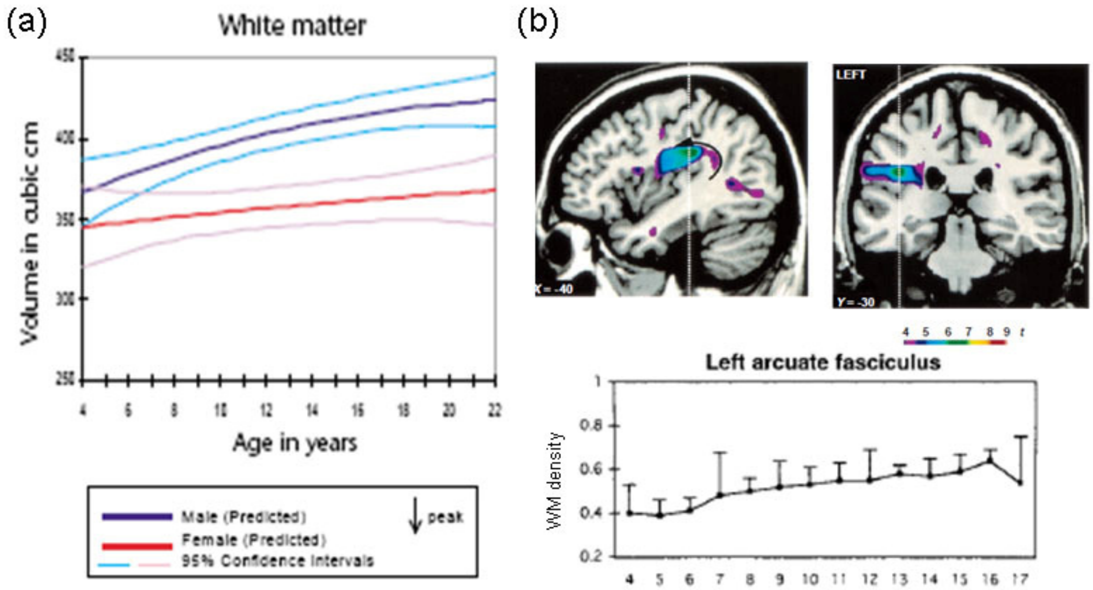
There is indirect evidence in support of this hypothesis. The time-course of synaptic pruning in frontal cortex appears to coincide with increases, up to age 12, in the coherence of event-related potentials between frontal and posterior brain regions, and between the frontal lobes (Thatcher, 1992). It has been suggested that the two are causally related (Kaiser & Gruzelier, 1996; Barry et al., 2004). A similar argument has been made for regional changes in the pattern of functional metabolic/vascular response, as measured in functional MRI ('diffuse-to-focal' pattern, cf. Durston et al., 2006; see Thomason et al., 2005). However, direct evidence using invasive methods in non-human animals has not supported the notion that adolescent changes in synaptic density necessarily lead to altered functionality of neural circuits. A recent primate electrophysiology study showed that the pruning of excitatory synapses in dorsolateral prefrontal cortex during adolescence has little functional impact, since the synapses which undergo pruning are functionally immature and make a minimal contribution to neural circuits (Gonzalez-Burgos et al., 2008). More research is needed to resolve this controversial and unresolved issue.

Recently, it has been argued that the loss of grey matter during adolescence might not be due to synaptic pruning. Instead, it has been suggested that the apparent grey matter loss is a result of intracortical myelination (Paus et al., 2008). Since grey matter contains both myelinated and unmyelinated axons, intracortical myelination could give rise to a progressive ‘whitening’ of grey matter tissue. Therefore it has been argued that with increasing age, there will be an increase in the amount of cortical ‘grey’ matter (i.e. cortical laminae I-VI) that is classified as white matter on MR scans. The following section will discuss MRI findings showing age-related increases in white matter volume.

1.4.3.2.2 Adolescent changes in white matter

Although the steepest increases in white matter volume occur shortly after birth, white matter volume and density continue to increase during childhood, adolescence and indeed into the twenties (Paus et al., 1999; Giedd et al., 1999b). In contrast to the regionally specific, inverted-U shaped trajectories of grey matter change, increases in white matter volume and density are reported to occur linearly across the brain during childhood and adolescence (e.g. Giedd et al., 1999b; **Figure 1.6a**). For example, a cross-sectional MRI study in 4-17 year olds showed linear age-related increases in white matter density within corticospinal and thalamocortical tracts, and in the left arcuate fasciculus, which links frontal and temporal cortical regions involved in speech (Paus et al., 1999; **Figure 1.6b**).

Figure 1.6 Age-related increases in white matter volume. Graph (**a**), left, shows linear increase in white matter density across the whole brain (from Giedd et al., 1999a). **(b)** Top right figure shows regions of the left arcuate fasciculus for which white matter density has been shown to increase linearly with age (graph, bottom right; from Paus et al., 1999).



1.4.3.2.4 Implications of adolescent white matter change

White matter is composed of neuronal axons, many of which are ensheathed in an insulating layer of myelin. In light of the histological findings showing an increase in axonal myelination across development (see section **1.4.2.2**), it has been suggested that age-related increases in white matter volume during childhood and adolescence correspond to progressive axonal myelination, and/or increases in axonal calibre (diameter). These changes would both be expected to result in increases in the speed and efficiency of neural processing (e.g. Waxman, 2004).

1.4.3.2.2.2 Other MRI measures of white matter change

Diffusion-tensor imaging (DTI) has been used to support findings from structural (volumetric) MRI studies showing age-related development in cortical white matter during adolescence. In DTI, a commonly-used measure is fractional anisotropy (FA), which is the extent to which the diffusion of water molecules in the brain is anisotropic (not equal in all directions). Higher FA values are thought to reflect increasing organization of white matter tracts (due to processes including myelination), since water molecules will tend to diffuse in parallel with the tracts. Increased FA during adolescence, followed by a levelling-off into adulthood, have been observed within several white matter tracts, including the body of the corpus callosum and descending motor pathways (Giorgio et al., 2008). Higher values of FA in the frontal lobes have also been observed in older versus younger adolescents (Barnea-Goraly et al., 2005).

Another technique which has been used is the myelin transfer ratio (MTR) in MRI. The MTR provides information on the macromolecular content (e.g. myelin content) of white matter tissue. Studies that have measured the MTR in structural MR-images have shown age-related decreases in MTR during childhood and adolescence (Paus, Keshavan & Giedd, 2008). This has been suggested to reflect increases in axonal calibre, since the larger the calibre, the fewer axons will fit into the same unit of imaged volume, resulting in a relative decrease in the amount of myelin.

Therefore, while some evidence suggests that age-related increases in white matter volume/density shown in structural MR-images may represent myelination, other evidence suggests that these changes are due to increasing axonal calibre. Both changes would be hypothesised to result in altered functionality of the neural circuitry, as do the changes that result in age differences in grey matter volume and density. The following section will describe evidence for functional brain development during adolescence.

1.5 Adolescent functional brain development

Adolescent neuroanatomical development is hypothesised to result in altered functionality of neural circuits, as are some of the hormonal changes of puberty. Alterations in behaviour and in the environment during adolescence are also hypothesised to be linked to changes in brain function. Therefore in the last decade, research has been conducted to investigate age-related changes in functional brain activity across adolescence. Techniques that have been used include electro-encephalography and functional MRI (fMRI). The following section will focus on fMRI studies only, in the interests of relevance and brevity.

1.5.1 Introduction to functional MRI

FMRI is an MRI technique in which images of the brain are acquired very rapidly (one volume every 1-4 seconds) while a participant is performing a series of cognitive tasks. The impact of local increases in blood flow on the measured proton alignment response to a radiofrequency magnetic field, known as the blood oxygenation level-dependent (BOLD) response, is then compared between cognitive tasks. Differences in BOLD response between cognitive tasks are thought to be a consequence of performing the cognitive tasks.

The BOLD response is thought to be generated by local increases in neuronal activity, resulting in a local energy demand. This energy demand is predominantly met by a local increase in blood flow (Attwell & Iadecola, 2002), which following an initial dip, causes a rise in the proportion of oxygenated vs. deoxygenated haemoglobin molecules present locally. This causes a change in the magnetic resonance of vascular protons, which is detected as the BOLD signal. Broadly, distinct cognitive tasks are accompanied by distinct spatial patterns of BOLD signal change. This finding is interpreted within the theoretical framework of functional specialisation: if a given cognitive task is accompanied by BOLD signal change (‘activation’) within a circumscribed set of brain regions, this set of brain regions is hypothesised to be causally or coincidentally (neuronally) active during the cognitive task (for discussion, see section **7.2.5**).

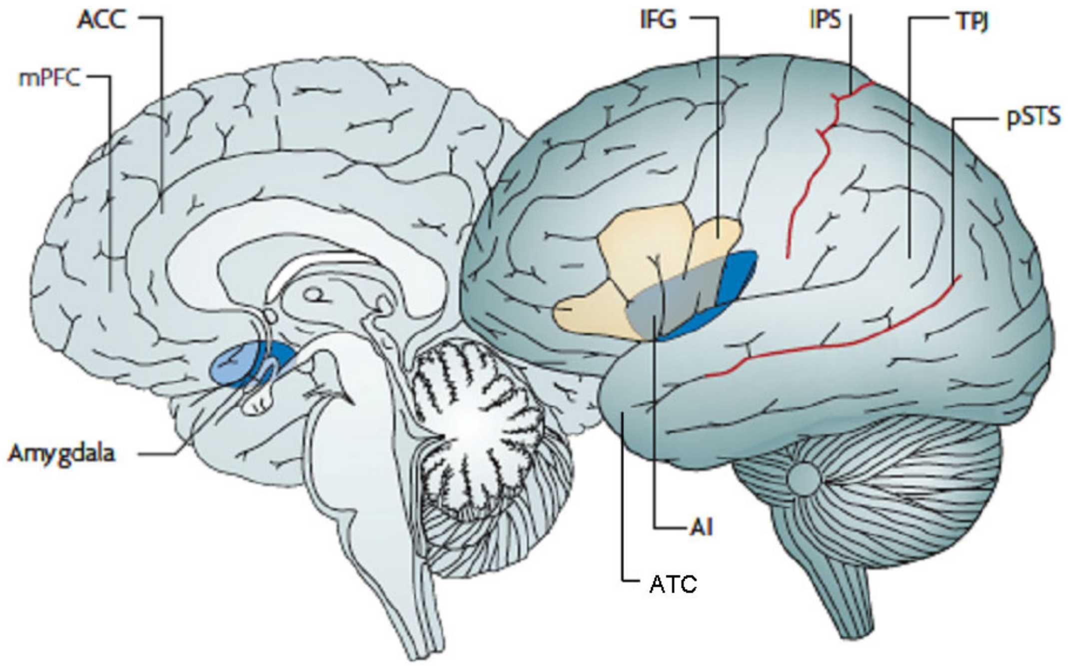
1.5.2 Adolescent functional MRI studies

Recent fMRI studies have been conducted comparing adolescents with adults, and sometimes younger children. These studies often use cognitive tasks that rely on anatomically late-maturing brain regions, such as the prefrontal and temporal cortex, as it is hypothesised that neuroanatomical development will result in altered neuronal processing and/or the metabolic/haemodynamic response (see sections **1.4**; **7.2.5**). Similarly, recent adolescent fMRI studies have investigated the fMRI correlates of cognitive tasks that are relevant to typically ‘adolescent’ behaviours and traits (e.g. social behaviours and risk; see section **1.3**), as altered proficiency or a change in the cognitive strategy taken to accomplish these tasks is hypothesised to be accompanied by changes in neuronal processing (e.g. the set of brain regions that are recruited; level of activity within the same set of brain regions), resulting in changes in regional BOLD response. In the following sections, findings from adolescent fMRI studies will be described, with a focus on studies that investigate **social cognition** and **decision-making**, as these are particularly relevant to adolescent behavioural characteristics (section **1.3**).

1.5.2.1 Social cognition and the social brain

Social cognition refers to the collection of mental processes required to interact with social agents. In humans, these processes include identifying social agents, evaluating their mental states (e.g. intentions, beliefs and desires), understanding and predicting their actions, and engaging with them (Frith & Frith, 2007). These mental processes are said to rely on a collection of brain regions known as the ‘social brain’ (Brothers, 1990; Frith, 2007; Frith & Frith, 2007; see **Figure 1.7**).

Figure 1.7 The social brain. Regions that are involved in social cognition include the anterior rostral medial prefrontal cortex (arMPFC) and temporo-parietal junction (TPJ), which are implicated in mental state processing; the posterior superior temporal sulcus (pSTS), active during observation of faces and biological motion; the anterior temporal cortex (ATC), which represents semantic social information; and the amygdala, which attaches value to social stimuli. Other regions of the social brain include the inferior frontal gyrus (IFG), the intraparietal sulcus (IPS), the anterior cingulate cortex (ACC) and the anterior insula (AI). Modified, from Blakemore (2008).



Over the past two decades, research has begun to shed light on how these social brain regions contribute to human social abilities. Briefly, and according to Frith (2007), the suggested roles of some of these brain regions in social cognition are as follows (the review is not exhaustive):

The amygdala is responsible for attaching value (positive/negative, approach/avoid) to objects, and this includes social objects. Thus, the amygdala plays a role in social cognition by attaching value to facial expressions (e.g. happy = positive, angry = negative; Le Doux, 2000), as well as to individual social agents and classes of social agents (Winston et al., 2002). Thus, the amygdala is thought to play a role in implicit social prejudices, or automatic social judgments (Winston et al., 2002; Frith & Frith, 2007).

Another component of the social brain is the anterior temporal cortex (ATC) or temporal poles. This brain region is thought to be a multimodal convergence zone, where highly processed information about complex social (and non-social) stimuli at the 'end' of the ventral visual stream is integrated with emotional signals from the orbitofrontal cortex and amygdala (see Olson et al., 2007). Zahn et al. (2007) have shown evidence that the ATC is active during the representation of abstract social semantic concepts (e.g. brave, stingy), and studies in individuals with fronto-temporal dementia have shown deficits in the knowledge of social scripts (e.g. 'what happens in a restaurant'). Thus, it has been suggested that the ATC represents semantic information relevant to specific social encounters.

The posterior superior temporal sulcus (pSTS) is often reported to be active in social tasks. This brain region is generally responsive to complex movements (Kawawaki et al., 2006), including biological movements of the eyes, face and hands (e.g. Perrett et al., 1982; Haxby et al., 2000). The pSTS is more active when predictions based on these movements are in error than when they are correct (Pelphrey et al., 2004a, 2004b). Therefore, this brain region may play a role in decoding social gestures and signals, and using these to form predictions of action or intent.

The temporo-parietal junction (TPJ),which is often active during the same tasks as the pSTS, has been shown to respond to spatial perspective information (Aichhorn et al., 2006). This is needed to understanding the epistemic states of social agents based on what they can and cannot see. This knowledge forms a part of theory of mind, or 'mentalising', which is the ability to attribute mental states to social agents. There is some debate over the role of the TPJ in social tasks. While some have suggested a central role for the TPJ in representing mental states, i.e. a role that is not limited to visual perspective information (Saxe & Wexler, 2005), others have suggested that the TPJ is generally responsive to attentional reorienting, whether this reorienting is between mental state information, or other non-social information (Mitchell, 2007).

Another region of the social brain is the medial prefrontal cortex (MPFC), specifically the anterior rostral MPFC (arMPFC, Brodmann area (BA) 10; also referred to as dorsomedial prefrontal cortex). This brain region is thought to track and represent mental states, including the emotional, motivational and epistemic mental states of self and other (Amodio & Frith, 2006; Gilbert et al., 2006). More specifically, it has been suggested (e.g. Frith, 2007) that the arMPFC is crucial in representing the sorts of mental states that are needed for communicative interactions, i.e. second-order mental representations. These are representations of another individual's mental representation of your mental representation. To clarify using two examples, second order mental representations are used when (i) a teacher attempts to judge whether a student has understood an instruction, or (ii) a liar tries to judge whether their victim realises they have been lied to. A number of studies have shown evidence for a role of arMPFC in this function: for example, Hampton et al. (2008) reported that activity within arMPFC tracks the expected actions of an opponent in response to one's own actions during the game of 'work or shirk'. In this game, a participant must decide on each trial whether or not to 'shirk' (a form of cheating) based on the likelihood that they will be discovered by an inspector who inspects infrequently.

Functional MRI studies of social cognition in adolescence have shown age group differences in activity within many of the brain regions noted above. Some of these studies will now be described, with a focus on **face processing**, **mentalising** and **peer influence,** as these are domains that have been the focus of developmental fMRI studies conducted to date.

1.5.2.2 Adolescent functional MRI studies of social cognition

1.5.2.2.1 Face processing

A number of developmental fMRI have investigated the neural correlates of face processing, and these have focused on facial emotion processing. Some of these studies have shown greater activity in parts of the prefrontal cortex during emotional face processing tasks, in adolescents relative to children and/or adults. For example, in a study conducted by Yurgelun-Todd and Killgore (2006) in which participants aged eight to 15 years old passively viewed fearful faces, it was found that activity within a number of lateral and superior prefrontal regions (bilaterally for girls, right sided for boys) showed a positive correlation with age. In Monk et al. (2003), children and adolescents (aged nine to 17 years), but not adults (aged 25-36), activated regions of the anterior cingulate cortex (ACC) and left orbitofrontal cortex (OFC) during the passive viewing of fearful relative to neutral faces.

1.5.2.2.2 Mentalising

A number of developmental fMRI studies have investigated age group differences in the neural correlates of mentalising. As defined above, mentalising is the ability to attribute mental states to social agents, and a large number of studies in adults have shown that mentalising relies upon a subset of social brain regions known as the 'mentalising network'[1], or mentalising system, comprising arMPFC, pSTS/TPJ and ATC (Frith & Frith, 2003). Recently, several fMRI studies have shown that functional activity within the mentalising system differs between adolescence and adulthood (see **Figure 1.8**). Specifically, these studies have shown greater activity in the arMPFC in adolescents than in adults during social cognition relative to control tasks. Conversely, activity within certain posterior components (e.g. in the temporal cortex) shows the opposite developmental pattern (Blakemore, 2008).

For example, in Blakemore et al. (2007), adolescents (aged 12-18) and adults (aged 22-38) were scanned with fMRI while they read sentences about causal intentions (e.g. "You want to go to the cinema. Do you look in the newspaper?"), relative to sentences featuring unintentional physical causality events (e.g. "It has been raining all night. Is the ground warm?"). Results showed that part of arMPFC was more active in adolescents than in adults during intentional vs. physical causality (**Figure 1.8**, blue dots), whereas the adult group showed more activity than did adolescents within a region of right STS in this comparison. A similar age-associated shift in brain activity was found in Wang et al. (2006). When children and adolescents (aged 9-14) and adults (aged 23-33) judged whether a series of communications were sincere or ironic (sarcastic), children and adolescents showed stronger activation of the arMPFC than did adults (**Figure 1.8**, green dots). Adults activated more posterior brain regions, including the superior temporal and fusiform gyri, more. The results from these and other studies

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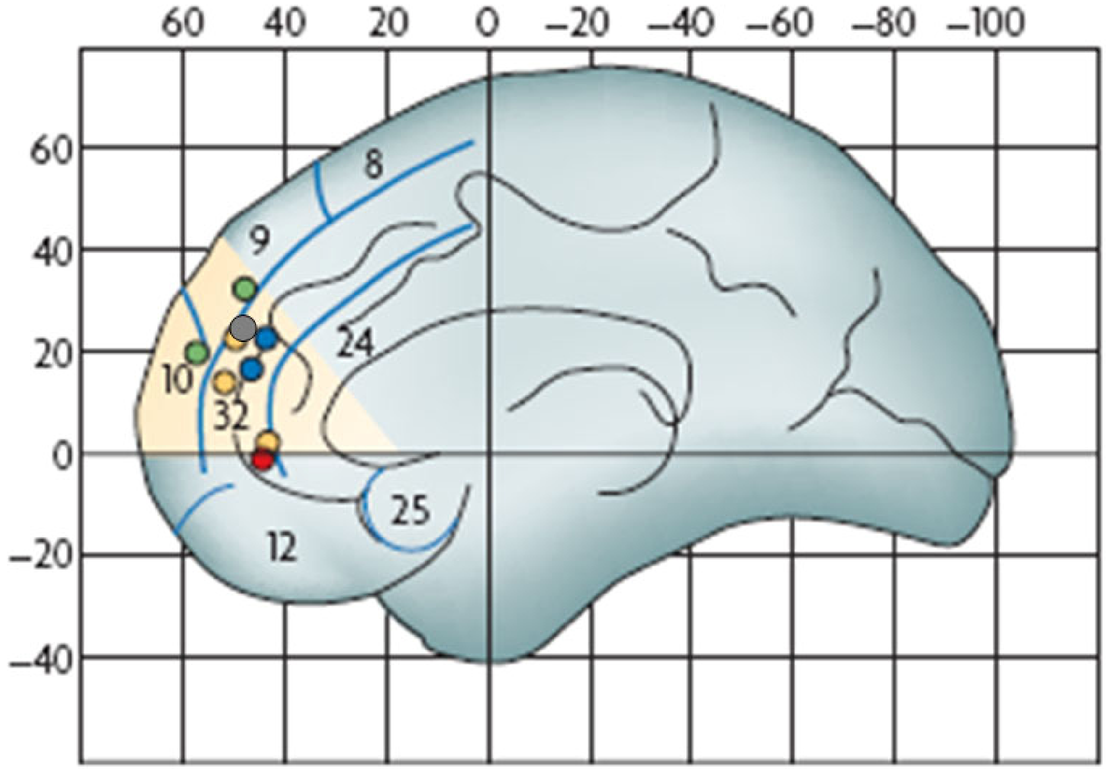
[1] A network is defined as a set of brain regions that demonstrate functional integration despite spatial separation. Due to the lack studies to date that have investigated functional integration (e.g. functional/ effective connectivity) between arMPFC, pSTS/TPJ and ATC during mentalising tasks (although see **Chapter 5**), they will here be collectively referred to as the 'mentalising system'.

(which will be described in more detail in **Chapter 5**) suggest that the neural strategy for mentalising shifts between adolescence and adulthood, with activity moving from anterior (arMPFC) to posterior (e.g. temporal) regions with age.

Figure 1.8 Adolescent fMRI studies of mentalising show an age-related decrease in activity within anterior rostral medial prefrontal cortex (arMPFC). The yellow shaded area indicates the anterior rostral section of MPFC that is activated in studies of mentalising (Amodio & Frith, 2006). The coloured dots indicate voxels in which altered activity is observed between late childhood and adulthood (green: Wang et al., 2006; blue: Blakemore et al., 2007; yellow: Pfeifer et al., 2007; grey: Pfeifer et al. 2009), or across adolescence (red: Moriguchi et al. 2007), during social-cognition tasks. See **Chapter 5** for details of studies.



1.5.2.2.3 Peer influence

A recent fMRI study investigated the neural correlates of resistance to peer influence. In this study, Grosbras et al. (2007) investigated the relationship between brain activity during passive viewing angry facial expressions and angry hand gestures, and a behavioural measure of the ability to resist peer influence (RPI), in ten-year old children. This social psychology measure of RPI has previously been shown to correlate with age across childhood and adolescence (Steinberg & Monahan, 2007).

Results from this fMRI study showed that children characterised by low RPI showed greater activity during observation of angry gestures within motor and decision/control-related brain regions (right dorsal premotor cortex, left dorsolateral prefrontal cortex). However, children characterised by high RPI showed stronger correlations in activity (functional connectivity) between brain regions underlying action perception (e.g. biological motion regions in STS) and decision making (e.g. lateral prefrontal cortex, premotor cortex). Given the reported susceptibility to peer influence of adolescents, it would be interesting if a follow-up fMRI study were conducted in children older than 10. The authors conducted a structural MRI study in 12-18-year olds, showing that inter-regional correlations in cortical thickness within lateral prefrontal and premotor cortex increased with RPI independently of age (Paus et al., 2008).

This review of the developmental fMRI literature on social cognition is clearly not exhaustive. A tentative generalization based on these studies is that across development, or with increasing proficiency, there is a decrease in task-relevant activity within prefrontal cortex.

1.5.2.3 Adolescent fMRI studies of decision-making and reward

A number of recent developmental fMRI studies have investigated brain activity during tasks in which decisions are made in order to gain a reward. These have included tasks in which decisions result in certain rewards (e.g. delayed-response tasks) and tasks in which decisions result in uncertain rewards (e.g. the Iowa Gambling Task, IGT). Functional brain activity during these tasks has been reported from decision, expectation and outcome phases of the tasks. Thus, it is a challenge to generalise across studies. All tasks, however, share a requirement for the integration and control of behaviour and emotion (i.e. reward-based emotions; Rolls, 2005), and recruit regions of the prefrontal cortex (PFC) involved in decision-making, cognitive control and emotion, as well as subcortical reward-responsive structures such as the ventral striatum (including the nucleus accumbens) and amygdala.

A commonly-reported finding in these studies is that adolescents show more ‘diffuse’ activity within task-related regions of PFC than do adults (e.g. Galvan et al., 2006; discussed in Durston et al., 2006). In this usage, the term ‘diffuse’ refers to a qualitatively-judged difference in the pattern of suprathreshold BOLD-signal change, comprising a larger volume of BOLD-signal change in adolescent groups, but smaller test statistic values at peak voxels within the activated PFC volume. As such, this does not constitute a statistical description of developmental differences in activity and is not considered to be a valid description in the current thesis.

Many studies report weaker adolescent relative to adult activity within task-related regions of PFC during decision-making tasks (e.g. Eshel et al. 2007; van Leijenhorst et al. 2006; Bjork et al., 2007). However, this finding is reported in very different regions of PFC, including orbito-frontal, anterior cingulate and dorso-lateral PFC, and therefore is a challenge to interpret.

Elsewhere, it has been reported that adolescents show weaker activity within the nucleus accumbens during decision and anticipation phases of reward-based decision-making tasks, and stronger activity in this structure relative to adults during outcome phases of the same tasks (e.g. Ernst et al., 2005; for reviews, see Geier & Luna, 2009 and Casey et al. 2008; although disparate findings are reported in Bjork et al., 2004). The amygdala has been reported to show weaker activity in adolescents relative to adults, during both anticipation and consummation phases of these tasks (Geier & Luna, 2009).

In summary, a number of developmental fMRI studies of reward-based decision-making have shown age-related increases in activity within various PFC sub-regions. Relative to adults, adolescents show weaker activity within the nucleus accumbens during decision-making and anticipation of risky or certain rewards, but a stronger response to reward outcome and consummation (Geier & Luna, 2009). It is suggested that these changes in functional brain activity might reflect, or be responsible for, adolescent real-life engagement in risky activities (e.g. Steinberg, 2008; Casey et al., 2008). This may be mediated via changes in the cognitive abilities that underlie decision-making. The next section will summarise adolescent cognitive development, in the domains of **decision-making** and **social cognition**.

1.6 Cognitive development

1.6.1 Social cognitive development during adolescence

1.6.1.1 Face processing

Some of the earliest empirical studies on adolescent social cognitive development focussed on face processing. For example, Carey et al. (1980) showed that, while performance in a facial identity recognition task improved steadily during the first decade of life, this was followed by a brief dip in performance at approximately age 12. It was later suggested that this decline was due to puberty, rather than age *per se*, as a study by Diamond et al. (1983) showed that females at mid-puberty performed worse those at pre- or post-puberty when the groups were matched for age.

More recently, evidence for a pubertal dip in facial emotion (rather than identity) processing was also shown (McGivern et al., 2002). In this study, male and female participants aged 10 to 17 performed a match-to-sample task, in which the task was to match faces showing emotional expressions to emotion words. An increase in reaction time of around 10–20% was shown at age 10-11 years in females, and 11-12 in males, which then declined during adolescence to reach pre-puberty levels only at age 16-17. Since the age of the male and female performance dip coincides with the sexually dimorphic age of puberty onset, these results were interpreted to suggest that the dip in performance was related to puberty. Future studies are needed to provide evidence for this suggestion.

Further studies should also investigate whether the results of Carey et al., Diamond et al. and McGivern et al. are specific to face processing, or due to a domain-general effect of adolescent cognitive development. For example, a study by Itier and Taylor (2004) showed evidence that continuing development during adolescence of facial identity recognition in an N-back task may be due to improved working memory processing capacity. In this task, faces were presented sequentially on a computer screen, and participants were asked to press a button when they saw a face that had previously been shown (either with an intervening face, i.e. 1-back, or with no intervening face, i.e. 0-back). Faces were presented either in an upright configuration (thought to recruit specialist neuro-cognitive face-processing systems), or in an inverted or reverse contrast configuration (thought to recruit domain-general systems for object recognition). Improvements were seen across the age range (from age 8 to 16) in recognition accuracy for all face configurations, and not just for the upright, true-contrast face configuration, and therefore this could be explained by a general improvement in working memory processing capacity. Whether similar domain-general explanations underlie developmental findings on facial emotion recognition, however, remains to be investigated.

In summary, studies of face processing show continuing development during adolescence in both facial emotion processing and facial identity recognition. This development may be at least in part due to developing executive functions, and some have suggested a link with puberty.

1.6.1.2 Mentalising

Mentalising, the ability to attribute mental states to agents, is a key social cognitive ability. The development of mentalising up to age five has been studied extensively and is well characterised (e.g. Frith & Frith, 2003), but until recently, very little was known about the development of mentalising beyond early childhood. This can be attributed to a lack of suitable paradigms: generally, in order to create a mentalising task that does not elicit ceiling performance in children aged five and older, the linguistic and executive demands of the task must be increased. This renders any age-associated improvement in performance difficult to attribute solely to improved mentalising ability.

However, based on recent fMRI findings showing age differences across adolescence in functional brain activity during mentalising tasks, and in view of the increasing complexity and importance to the self of social relationships during adolescence, it has recently been hypothesised that aspects of mentalising will show continuing development during adolescence (e.g. Blakemore & Choudhury, 2006). Tecent mentalising studies have supported this hypothesis.

A study by Choudhury et al. (2006) investigated the development during adolescence of emotional perspective-taking, which is the ability to infer the feelings of others or ‘step into their shoes’, and is a component of mentalising. In this study, 107 participants, divided into child (mean age 9 years), adolescent (mean age 13 years) and adult (mean age 24 years) groups, were tested using an emotional perspective-taking task. In this task, the participant imagined either how s/he, or how a third person, would feel in various situations, and reaction times were measured. The results showed that the difference in reaction time for taking one’s own compared with another person’s perspective decreased with age. This was interpreted as indicating an age-related increase in the efficiency of emotional perspective-taking across adolescence.

More recently, a novel online mentalising task (Keysar et al., 2003) has been used to show continuing development during adolescence of the ability to take another person’s visual perspective (Dumontheil et al., 2009). In this study, 177 female participants aged seven to 28 years performed a task in which they were instructed to sequentially move objects between a set of shelves arranged in a grid, as instructed by a ‘Director’ (see **Figure 1.9a**). The Director could see the contents of only some of the shelves (those which were not occluded on the side nearest to the Director). Therefore, correct interpretation of the Director’s instructions required participants to take into account what the director could and could not see – his visual perspective. In a control condition, participants were instructed to ignore objects in shelves that had a grey background. Thus this condition was similar to the Director condition in terms of the goal of the task, except that it relied on following a rule that was not couched in terms of an agent’s visual perspective. However, the Director condition also involves the need to work out someone else’s intentions (which object the Director wants the participant to move) and take their perspective in an online communicative situation. Results showed that performance in both visual perspective and rule-based trials increased throughout childhood and adolescence. However, there was continuing development between late adolescence and adulthood only on performance in visual perspective (Director) trials (see **Figure 1.9b**). These results indicate that the online use of mental state (visual perspective) information continues to develop during adolescence in females[2]. Whether

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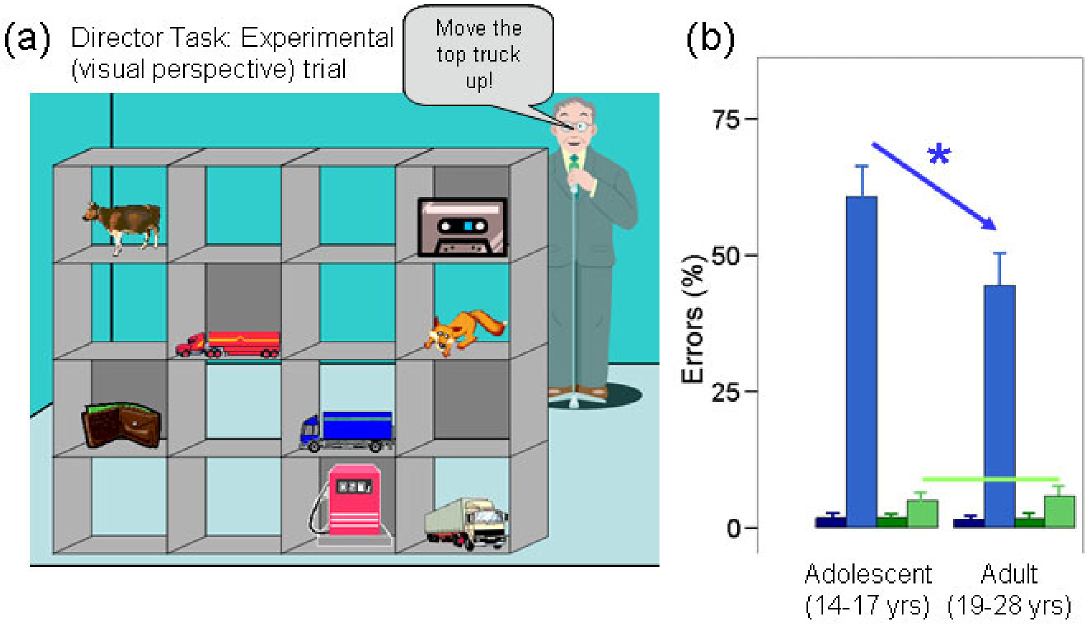
[2] This result has now been replicated in a large cohort of male participants (I. Dumontheil, personal communication).

this development is due to the development of specifically social cognitive abilities requires further investigation; the authors suggest that age-associated improvements task performance are due to a developmental interaction between improving executive and social abilities.

Figure 1.9 Adolescent development of online mentalising. Development during adolescence of the use of visual perspective information: **(a)** In the Director task, participants are instructed to move objects between shelves. A trial is shown from the Experimental (visual perspective) condition, in which participants must take into account the visual perspective of a Director who cannot see objects in occluded shelves. In the trial shown here, the correct response is to move the blue (target) truck and ignore the red (distracter) truck. **(b)** Results from the Director task show continuing development between the late adolescent and adult groups in performance on visual perspective trials (light blue), but no further developments in performance on rule-based trials (light green) or in other control trials (dark blue, light green). For more details, see Dumontheil et al. 2009.



1.6.1.3 Social concepts

Another important aspect of social cognition is the understanding of social concepts or principles, including fairness and reciprocity. Behavioural economic studies in children show an emerging awareness of social principles during early and middle childhood (Fehr et al., 2008), and during adolescence, a refinement in their use in social interactions. For example, in a recent study by Güroğlu et al. (2009a), child and adolescent participants played an economic game known as the Ultimatum Game. This game assesses the tendency of participants to act on the principle of fairness (moral outrage). In this game, participants can make decisions to forego money, in order to punish unfair behaviour (low offers of money from the other player). Results in Güroğlu et al. showed that, between the ages of nine and 18 years, there was an increase in the tendency for fair offers to be strategically modulated by the perceived ability of a social partner to reject the offer. A similarly protracted development in the social context-dependent tendency to reciprocate (a specific form of fairness) has been demonstrated during adolescence in the Trust Game, which assesses the degree to which participants respond fairly to fair offers of money (Güroğlu et al., 2009b).

Further studies should investigate the role of domain-general abilities in age-associated development in performance on these tasks. For example, the ability to understand abstract concepts (Inhelder & Piaget, 1958) may underlie the ability to act on social principles of trust and fairness. Development in the ability to respond to feedback (e.g. Byrnes et al., 1999; Crone & van der Molen, 2004), whether this feedback is social or non-social, may underlie age-related improvements in performance in economic games.

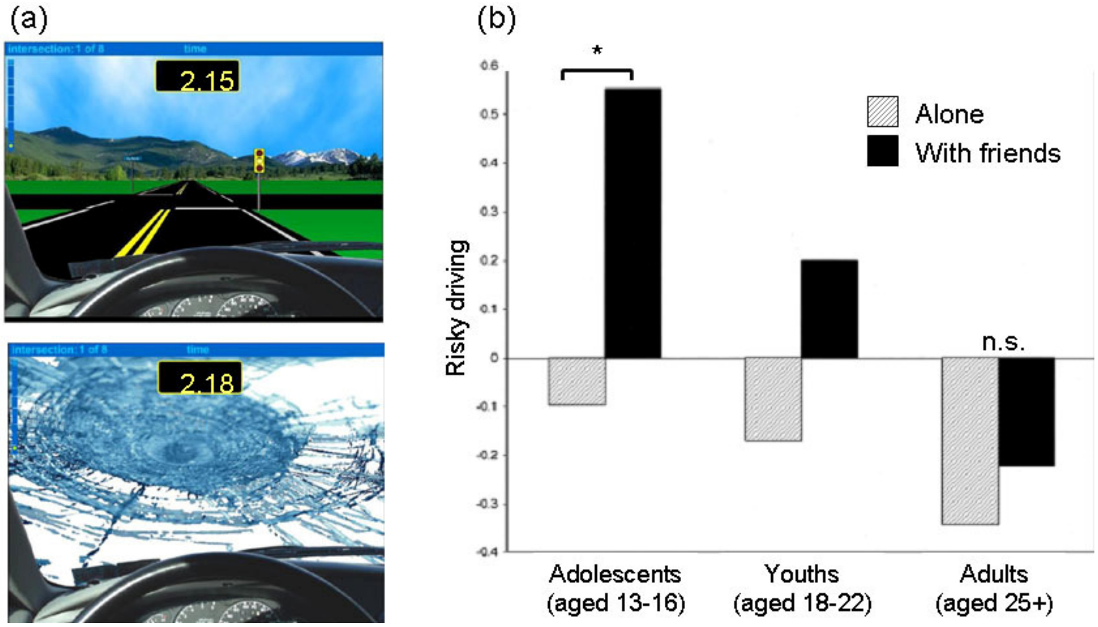
1.6.1.4 Peer influence

The ability to act in accordance with social principles is important for social interactions, as is the ability to infer the mental states of others. However, sometimes it is appropriate to ignore or discount the opinions and perspectives of others (e.g. Brass & Heyes, 2005). One aspect of this social ability, and one that has been studied with particular interest in the context of adolescent development (see section **1.5.2.2.3**) is the ability to resist peer influence. As described in section **1.5.2.2.3**, a recent self-report study showed a linear increase between childhood and adolescence in the ability to resist peer influence in a variety of negative and neutral domains (e.g. peer influence to commit crime, peer influence on personal taste; Steinberg & Monahan, 2007). A recent experimental study was carried out to investigate a behavioural correlate of this change in social psychological tendency:

In this study, conducted by Gardner and Steinberg (2005), the influence of peers on the number of risks taken in a car driving game was investigated in 306 participants aged 13-16 (adolescent age group), 18-22 (youth age group) and 24+ (adult age group).

Participants played a car driving simulation game, in which there were opportunities to act in a cautious or risky manner, for example stopping vs. continuing at a yellow traffic light. Crucially, the game was played alone or in the presence of two silent peers (friends). The results showed that in the presence of peers, adolescents took many more risks when driving, compared to when they were alone (see **Figure 1.10**). In contrast, levels of risk-taking in adults did not differ between peer and alone conditions. The youths showed an intermediate effect. In summary, this study shows continuing development of the influence of a social context (presence of peers) on risk-taking during adolescence. Further studies should investigate the mechanism by which peers influence risk-taking in the task.

Figure 1.10 Adolescent development of the influence of peers on risk-taking. In a car driving simulation game, **(a)**, in which opportunities arise to choose a risky or cautious action, for example stopping or continuing to drive through an amber traffic light, **(b)** adolescents but not adults take more risks in the presence of peers than when alone, and youths show an intermediate pattern (Gardner & Steinberg, 2005).



Although continuing development during adolescence has been shown in a number of social cognition tasks, behaviour in these tasks and in ecological social contexts relies on many component processes that are not specifically social. These include the executive functions, which allow an individual to optimise and regulate their behaviour. There is evidence that some executive functions continue to develop during adolescence: For example, planning, prospective memory and inhibition (Romine & Reynolds, 2005; Davidson et al., 2006; Dumontheil et al., 2008). Further work is needed to elucidate developmental interactions between executive functions and social cognition in adolescence (see Dumontheil et al., 2009).

1.6.2 Adolescent development of reward-based decision-making

Evidence reviewed above (section **1.3.2**) suggests that the real-life tendency in adolescence to engage in risky behaviours is partly attributable to social factors, such as peer pressure. Recent studies using laboratory-based decision-making tasks suggest that, in addition to these social factors, there is continuing development during adolescence of a number of non-social cognitive components that underlie the ability to make optimal decisions. These studies will be reviewed below. In general, it appears to be the case that sub-optimal decision-making in adolescence is particularly evident when decisions are made in an emotional context.

1.6.2.1 Performance in probabilistic decision-making tasks

A number of recent studies have shown continuing development during adolescence in performance on laboratory-based decision-making tasks. Often in these tasks, participants must take into account the rewards and reward probabilities associated with a selection of choices, and then choose so as to maximize their total rewards (e.g. money, fictitious money, or points).

For example, in the Iowa Gambling Task (IGT; Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004; Huizinga et al., 2007), participants repeatedly select cards from an array of four decks with unknown reward distributions. Two of the decks yield low-magnitude, constant rewards and modest probabilistic losses, resulting in net gain across the task. The remaining two decks yield high-magnitude, constant rewards but substantial probabilistic losses, resulting in a net loss. Several studies have shown that the tendency to adopt the advantageous strategy of selecting from the former two decks continues to increase with age during adolescence (between 11 and 18+ years: Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004), although contradictory findings have been reported. In a study by van Leijenhorst et al. (2008), no differences were found between age 8-30 years in the ability to make advantageous selections in a version of the IGT.

In a study by Harbaugh et al., participants aged 5-64 made a series of decisions between a certain reward, and a gamble with equivalent expected value (EV: the sum of potential outcomes weighted by their respective probabilities; Harbaugh et al., 2002). Unlike in the many versions of the IGT, in this task participants are explicitly informed about the reward probabilities associated with each decision[3]. However, children and adolescents showed evidence of biased decisions in the task, relative to adults. Specifically, children and adolescents showed a lesser degree of indifference in their choice between the pairs of options with equivalent EV, relative to adults. A similar study by Levin et al. (2007), in which children (aged 5-11) and adults made a choice between gambles that differed in EV showed age-related increases in the tendency to make choices that maximised EV. The results from these two studies show that, even in relatively simple decision-making tasks in which participants are provided with all the necessary information to make optimal choices, the tendency to do so continues to develop up to (Levin et al.) and during (Harbaugh et al.) adolescence.

Several suggestions have been put forward to account for the age-related improvements in performance on these decision-making tasks. One suggestion is that, with age, adolescents become better able to take into account performance feedback (wins and losses) and use this to maintain or modify subsequent behaviour (Byrnes et al., 1999; Crone & van der Molen, 2004). This might be expected to impact on performance in tasks including the IGT, but not in the tasks used by Levin et al. and Harbaugh et al. (see preceding paragraph).

Another suggestion for the age-related improvements in performance on decision-making tasks is that the use of behavioural rules or strategies shifts during adolescence. For example, Huizinga et al. (2007) show evidence for an age-related improvement in

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[3] i.e. in Harbaugh et al., decisions are made under risk (probabilities of reward are known, but are less than unity), not uncertainty (probabilities of reward are unknown).

the sophistication of strategies employed during the IGT. At younger ages (e.g. 6-9 years), participants behaved in a way that was consistent with sensitivity to the frequency of loss and an insensitivity to loss magnitude, while up to and during adolescence (10-15 years), participants were increasingly likely to take into account both the frequency and magnitude of losses. This study will be discussed in more detail in **Chapter 3**. The suggestion that the development of decision-making proceeds via the adoption of increasingly sophisticated or unbiased strategies is in agreement with Harbaugh et al. (2002), and is also in broad agreement with some influential theories of the development of decision-making (e.g. Brainerd & Reyna, 1990).

1.6.2.2 Emotional influences on decision-making

A number of recent studies have investigated emotional influences on decision-making in adolescence. Depending on one's conceptualisation of emotion, it could be argued that any reward-based decision-making task is, strictly, emotional (in that reward receipt, omission or termination gives rise to 'reward-based emotions'; Rolls, 2005). However, it is possible to manipulate the level of emotional salience or emotional intensity in decision-making tasks.

In a study by Figner et al. (2009), adolescent participants aged 13-19 years and adult participants aged 20+ years played the Columbia Card Task (CCT), in which cards shown face down are sequentially turned over to win points. On a given trial, cards can be turned over as long as gains are encountered, but the game terminates as soon as the participant turns over a loss card and the amount specified on the loss card is subtracted from the total payoff. In this particular study, two versions of the game were played: an emotional or 'hot' version of the task, and an unemotional or 'cold' version of the task. In the cold version, participants decided at the start of each trial how many cards they would turn over (a single number, e.g. 15). In the hot CCT, this decision was made incrementally: After each card was turned over, the participant made a decision either to quit with their current payoff, or turn over another card. Therefore, the hot CCT provides reward feedback at each decision point. The results showed that, regardless of age, participants turned over a greater number of cards in the hot than in the cold CCT. However, the difference between the number of cards turned over in the hot version and the number of cards turned over in the cold version of the task was greater in adolescents than in adults. The authors suggest that this effect arises due to a greater tendency for emotional factors to produce risk-seeking behaviour in adolescents, relative to adults.

In summary, a number of experimental studies have shown evidence that some basic cognitive components of decision-making continue to develop during adolescence. In addition, the impact of emotion on decision-making may be particularly high in adolescence. **Chapter 2** of this thesis describes an experiment that was carried out to investigate decision-making and emotion across adolescence. In the following sections, this and subsequent experimental chapters will be summarised.

1.7 Summary of experimental chapters

Evidence reviewed in the preceding sections indicates that reward-based decision-making continues to develop during adolescence. It has been suggested that this may underlie the developmental peak in real-life risky decision-making that occurs during adolescence, the so-called 'inverted-U shaped trajectory' of risk-taking (e.g. Steinberg, 2008; Casey et al., 2008). However, real life risky behaviour could arise due to a number of factors. Few studies have shown convincing evidence either that (a) adolescents show a true preference for risk-taking *per se* (rather than deficient probability and outcome judgment), or that (b) adolescents take more risks relative to both children and adults (cognitive studies conducted so far have compared adolescents with adults). In addition, the role of emotion in adolescent risk-taking is not well understood, but it is hypothesised to be important. **Chapter 2** describes a study that was carried out to explore these outstanding issues. Eighty-three male participants aged nine to 35 years old performed a probabilistic decision-making task in which paired gambles differed in EV, risk (measured as outcome variance) and the potential to generate counterfactual emotions (Camille et al., 2004). Participants indicated their emotional responses to the outcome of each gamble using a linear rating scale. A panel logit regression procedure was used to test the contribution of EV and risk to participant behaviour across age, and it was predicted that whereas the former would show a linear age-related improvement, risk-seeking would peak in adolescence. The emotional response to counterfactual outcomes was compared between groups, and developmental differences were predicted.

Chapter 3 describes a study carried out to investigate social and utilitarian influences on decision-making, in adolescents and in adults. Twenty-two adolescents (aged 12-13) and 14 adults (aged 21-43) completed a novel decision-making task in which happy and angry face stimuli were stochastically associated with reward (Averbeck & Duchaine, 2009). Decisions were analysed by first creating a computational model of the 'ideal observer' who optimally integrates outcomes over trials. Participant decisions were compared with the decisions of this model on a trial-by-trial basis, and performance was compared between age groups. It was hypothesised that adults would outperform adolescents. As a next step in the analysis, an 'ecological observer' model was created that more closely emulated participant decisions, as it contained parameters that encapsulated distinct behavioural biases that participants were hypothesised to exhibit. These included biases arising from the social nature of the stimuli (the emotion expressions), and differential sensitivity to positive and negative performance feedback (wins and losses). The influence of these behavioural biases was compared between adult and adolescent groups. In line with previous studies (e.g. Huizinga et al., 2007; Gardner & Steinberg, 2005; Steinberg & Monahan, 2007), it was hypothesised that the response to performance feedback and social cues would develop across age.

Adolescence is a time of profound socio-emotional development, and there is evidence that the hormonal and psycho-social changes of puberty contribute to changes in social awareness and emotion processing. In **Chapter 4,** a study is described that investigated pubertal changes in self-reported social emotions. Eighty-three female participants aged 9-16 years were divided into three puberty groups on the basis of a physical development questionnaire, and completed an emotional self-report task. Patterns of emotional responding were investigated to evaluate the hypothesis that the onset of puberty marks an increase in the awareness of complex, or 'mixed,' emotions. The emotional self-report task consisted of a series of scenarios that were designed to evoke either predominantly social emotions (embarrassment or guilt) or predominantly basic emotions (anger or fear), where social emotions are defined as those which require the representation of others' mental states. It was hypothesised that mixed emotion responding would develop across puberty, and that this development would be particular to social emotion.

In **Chapter 5**, emotional scenarios from the study described **Chapter 4** were adapted to investigate the neural processing of social and basic emotions. Nineteen female adolescents (aged 10-18) and 10 female adults (aged 22–32) underwent fMRI scanning while processing social or basic emotion scenarios. Participants were instructed to read and imagine each scenario, and to rate their imagined emotional response. Social emotions were defined as emotions that require mental state processing, and therefore it was predicted that activity would be observed within the mentalising system (arMPFC, pSTS/TPJ, ATC) during social relative to basic emotion conditions. Previous studies have reported differences in activity within the mentalising system between adolescence and adulthood (specifically, age-related decreases in arMPFC activity), during mentalising relative to control tasks. Therefore, it was predicted that a similar developmental pattern of activity between age groups during social relative to basic emotion processing would be observed in the current study.

The mentalising system (arMPFC, pSTS/TPJ, ATC) is often collectively referred to as the mentalising ‘network’. However, a network is defined as a set of brain regions that demonstrate functional integration, and no study to date has investigated functional integration within the mentalising system. Therefore in **Chapter 6**, fMRI data from **Chapter 5** were reanalysed to investigate connectivity between arMPFC and other mentalising system components, using psycho-physiological interaction (PPI) analysis. Connectivity was investigated across age (11-35 years), and was then compared between the adult and adolescent groups. It was hypothesised that regions of the mentalising system would show evidence of connectivity during the mentalising condition (social emotions) relative to the control condition (basic emotions), and that this connectivity would differ between age groups.

Chapter 2

The development of expected value maximising, risk-seeking and counterfactual emotion in a probabilistic gambling task

Human adolescents are prone to engage in risky behaviours such as dangerous driving and unsafe sex. In this chapter, a study is described that was conducted to investigate adolescent risk-seeking in a behavioural economic task. Male participants aged nine to 35 completed a probabilistic gambling task assessing decision-making under risk, and the emotional response to decision outcomes (e.g. counterfactual emotions, relief and regret). Results show an inverted U-shaped developmental trajectory for risk-seeking, but the ability to maximize expected value improved gradually across age. In addition, there was an increase between childhood and young adolescence in the strength of counterfactual emotions (relief and regret) reported after receiving feedback about the gamble outcome.

2.1 Introduction

2.1.1 Adolescent development of risk-seeking

Adolescents show a tendency to engage in risky behaviours, such as dangerous driving and unsafe sex (Steinberg, 2008; Eaton et al. 2006). It has been suggested that adolescents are risk-taking in general, relative to children and adults (Steinberg, 2008; Casey et al., 2008). However, engagement in risky behaviour in real life is likely to have a variety of social, emotional and cognitive causes, and few empirical studies have directly compared risk-seeking in children, adolescents and adults using laboratory-based behavioural tasks (Harbaugh et al., 2002; Crone et al. 2008; van Leijenhorst et al., 2008; see Boyer, 2006, for review). The current study investigated the development of risk-seeking between late childhood (age 9) and adulthood (age 35), using a behavioural economic task in which gambling decisions were made in an emotional context. Heightened risk-seeking was predicted in adolescents relative to adults, in line with previous empirical data (Eshel et al. 2007; Figner et al. 2009). In line with theoretical suggestions (Steinberg, 2008; Casey et al., 2008) and recent empirical findings (O'Brien & Steinberg, 2009), adolescents were also hypothesised to show heightened risk-seeking relative to children.

2.1.2 Adolescent development of emotion

Also of interest in the current study were age differences in the emotional response to gamble outcomes. When faced with gamble outcomes, participant choices are influenced by the rewards that they hope to gain, the economist's "expected value" (EV), but are also influenced by they think they will *feel* afterwards. The emotional component of decisions is thought to be the reason why, once an individual is committed to a course of action, s/he may prefer to ignore what would have happened if the alternative decision had been made – especially if the chosen decision results in an unfavourable outcome. In this situation, counterfactual comparison between *what is* with *what might have been* shows that the alternative decision would have been better, and this can result in the feeling of regret (a 'cognitively-mediated emotion'; Camille et al. 2004). Alternatively, a better outcome than the alternative may result in the feeling of relief. These cognitively-mediated emotions influence decision-making in adults (Camille et al., 2004; Coricelli et al., 2007).

It has been suggested that ability to think counterfactually about the outcomes of decisions develops during adolescence (Baird & Fugelsang 2004). This may impact on adolescent decision-making. For example, immature counterfactual emotional responses during decision-making might contribute to risky decision-making in adolescents (Steinberg, 2008). In general, it has been suggested that adolescents show exaggerated or more labile emotional responses to outcomes relative to children and adults (Ernst & Mueller, 2007; Casey et al. 2008; Ernst et al., 2005; Eshel et al., 2007), which may also impact on decision-making. However, no previous study has investigated the development of risk-seeking and the experience of counterfactual emotions within the same paradigm.

2.1.3 Probabilistic gambling task

In the current study, participants aged nine to 35 years played a probabilistic gambling task (Camille et al., 2004; Coricelli et al., 2005) in which paired gambles differed in EV (the sum of potential outcomes weighted by their probabilities) and risk, as well as the potential to generate counterfactual emotions (relief and regret). On each trial, the participant chose between two gambles presented in the form of 'wheels of fortune' (see **Figure 2.1**). The two possible outcomes of each gamble (wins or losses of points), and their probabilities, were indicated on each wheel. When the participant had indicated which of the two gambles he wished to play, an arrow spuns round on the appropriate wheel, coming to rest on the number of points won or lost on that trial. In this type of task, a rational decision-maker should choose gambles with greater EV, since this will maximise winnings. However, gambles with the same EV can differ in their level of risk, where risk is measured as the outcome variance of a gamble (Bossaerts & Hsu, 2008; see **Methods, 2.2**). The contribution to choice of risk (outcome variance) and the EV of a set of gambles was used to evaluate the participants' utility function (Bossaerts & Hsu, 2008).

2.1.3.1 Predicted development in the ability to maximize expected value

The first goal in using this gambling task was to investigate the impact of EV on choice across age. It was predicted that, even at the youngest ages, participants would tend to choose gambles with higher EV, since it has been shown previously that children as young as five years old show a rudimentary sensitivity to EV (Schlottmann, 2001): When five-year olds view probabilistic events associated with different prizes won by a puppet, the level of happiness children judge the puppet will feel is proportional to the value of a prize multiplied by its approximate probability. It was expected, however, that the ability to maximise EV would continue to develop during childhood and adolescence. Although probability and value judgment may be mature by mid-adolescence (Boyer, 2006), the use of this information to guide behaviour in emotional contexts, as in the current paradigm, is still developing. For example, in a behavioural economic study by Harbaugh et al. (2002) in which participants aged five to 64 years made a series of choices between a certain outcome and a gamble with equivalent EV, an age-related increase was shown throughout adolescence in the tendency towards rational (indifferent) decisions. Children and adolescents showed evidence of a biased treatment of the probability information relative to adults. Indeed, up to the age of 21 years, participants behaved in a way that was consistent with a bias to over-weight the probability of rewards and under-weight the probability of losses. A study by Levin et al. (2007) in which children (aged 5-11) and adults made a choice between gambles that differed in EV also showed age-related increases in rational (EV-maximising) decisions. This evidence suggests that the ability to maximise EV, even when the rewards and probabilities are known, continues to develop during adolescence. The current study set out to fill in this developmental picture, by testing the ability of children, adolescents and adults to maximize EV when choosing between pairs of gambles that differed in EV.

2.1.3.2 Predicted development in the influence of risk on choice

The second goal of the current study was to investigate age differences in the impact of risk on choice. Participants' preference for risk was evaluated by testing the contribution of the outcome variance of gambles to behaviour, where a risk-seeking participant is one who shows a tendency to choose gambles with high variance. Because the probabilities and outcomes of gambles were shown to participants, risk-seeking in the current study refers to a preference for risk proper. In contrast, seemingly risky behaviour in real-life could arise due to a number of factors, including incomplete knowledge of the range of possible outcomes, or a reduced ability to detect their probabilities. The hypothesis was tested that there would be an inverted U-shaped trajectory of risk-seeking with age between childhood and adulthood, with its peak in adolescence, as has been suggested in a number of recent studies (Figner et al. 2009; O'Brien & Steinberg, 2009).

For example in Figner et al. (2009), adolescent participants aged 13-19 years, and adult participants aged 20 years and older played the Columbia Card Task (CCT), in which cards shown face down are sequentially turned over to win points. On a given trial, cards can be turned over as long as gains are encountered, but the trial terminates as soon as the participant turns over a loss card and the amount specified on the loss card is subtracted from the total payoff. In this particular study, two versions of the game were played: an emotional or 'hot' version of the task, and an unemotional or 'cold' version of the task. In the cold version of the task, participants decided how many cards they would turn over at the start of each trial (a single number, e.g. 15). In the hot CCT version, this decision was made incrementally: after each card was turned over, the participant then made a decision either to quit with their current payoff, or turn over another card. Therefore, the hot CCT provides reward feedback at each decision point, presumably encouraging risky decisions because participant feel they are 'on a roll', or because they might 'miss out' if they quit. Indeed, the results showed that across age, participants turned over a greater number of cards in the hot than in the cold CCT version. However, the difference between the number of cards turned over in the hot version and the number of cards turned over in the cold version of the task was greater in adolescents than in adults. The authors suggest that this effect arises due to a greater tendency for emotional factors to produce risk-seeking behaviour in adolescents, relative to adults.

Similar findings were elicited in a study in which adolescents and adults made risky or safe decisions in a car driving game: adolescents took more risks than adults in a hot, social-emotional condition in which their friends were present relative to a cold condition in which they played alone (Steinberg, 2008; O'Brien & Steinberg, 2009).

In light of this previous evidence, adolescents were predicted to take more risks than adults in the emotional decision-making task used in the current **Chapter**. Few (if any) empirical studies show increased adolescent relative to child risk-taking in emotional contexts; however, it is said that risk-taking follows an inverted U-shaped developmental trajectory between childhood and adulthood (Figner et al. 2009; O'Brien & Steinberg, 2009). This pattern was therefore was predicted in the current study.

2.1.3.3 Predicted development of counterfactual emotion

The third goal of the current study was to investigate age differences in counterfactual emotion (relief and regret). During the gambling task, participants indicated their emotional to the outcome of each gamble on a linear rating scale. On half of the trials (gambles in the *complete feedback* condition), the outcome of the unselected wheel was revealed alongside the outcome of the selected wheel, whereas on the other half of trials (*partial feedback* condition) only the outcome of the selected wheel only was revealed.

Previous work in adults has shown that, in the complete feedback condition, viewing the outcome of the unselected wheel gives rise to a counterfactual comparison between the outcome of a choice (reality) and the outcome of a foregone alternative (what might have been), and that this comparison modulates emotional responses (Camille et al. 2004, Coricelli et al. 2005). In this study as in previous studies, the emotional response to the outcome of a decision that is better than its rejected alternative is defined as relief, and worse than its alternative as regret. Based on suggestions that the ability to think counterfactually about the outcomes of decisions continues to develop during childhood and adolescence, it was hypothesised that there would be age group differences in the modulation of the emotional response to counterfactual outcomes in the complete feedback condition, and that this might be related to risk-taking.

2.2 Methods

2.2.1 Participants

20 pre-adolescent male participants (aged 9 to 11) were recruited from a selective primary school in London. 52 adolescent male participants (aged 12 to 18) were recruited from a selective secondary school in the same area of London and at which a proportion of school leavers from the primary school enrol each year. 17 adult male participants (aged 25 to 35) were recruited from a database of former students of the secondary school. Therefore, child, adolescent and adult participant groups were well matched for educational background and socio-economic status.

The 89 participants were divided into four Age Groups of approximately equal size based on school year group: child (*N* = 20, age range 9.83-11.83 years: mean (sd) = 10.83 (.641)), young adolescent (YA) (*N* = 26, aged 12.25-15.83: mean (sd) = 13.77 (1.10)), mid-adolescent (MA) (*N* = 26, aged 15.5-18.08: mean (sd) = 16.74 (.880)) and adult (*N* = 17, aged 25.67-35.0: mean (sd) = 30.32 (3.08)).

Participants had no history of psychiatric or neurological disorder, and none had received a diagnosis of attention-deficit/hyperactivity disorder, autism or dyscalculia.

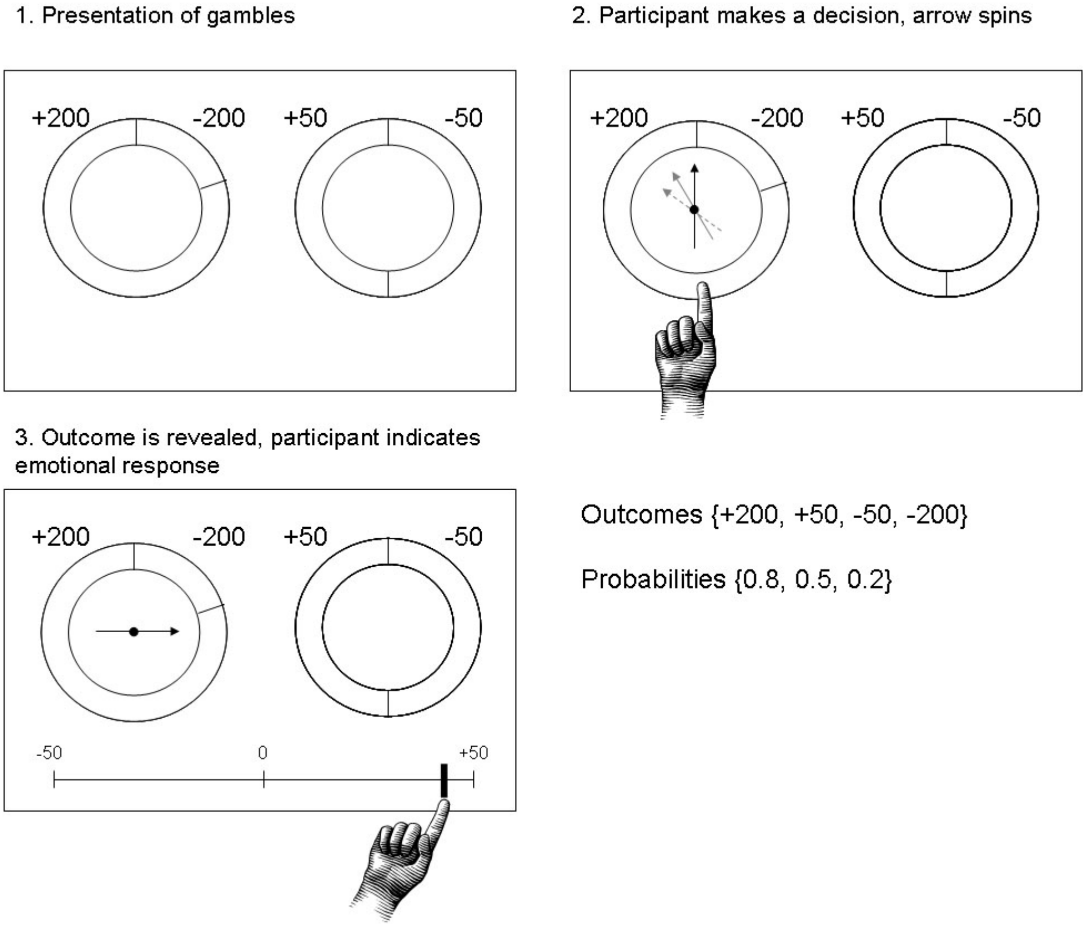
To reduce variance attributable to developmental sex differences in traits such as sensation-seeking, which might influence risk preferences (Steinberg et al. 2008), this study was restricted to male participants only. The selection of males rather than females was related to the particular focus on risk-seeking in the current study: previous studies have shown higher risk-seeking in males than in females (e.g. van Leijenhorst et al., 2008).

Prior to the study, written informed consent was obtained from adult participants, and from a parent or guardian of adolescent participants. The study was approved by the local Ethics Committee. Participants were not paid.

2.2.2 Procedure

Each participant completed the probabilistic decision-making task described in Camille et al. (2004). On each trial of the task, the participant is presented with two ‘wheels of fortune’ on a computer screen (**Figure 2.1**). The participant must choose one of the wheels, with the aim of maximising the number of points won. Possible wins and losses on each wheel are indicated by positive or negative numbers next to the wheels, and their associated probabilities are indicated by the relative size of adjacent sectors on the wheel. When the participant has pressed a button indicating his choice, an arrow spins round on the wheel and comes to rest showing the number of points that have been won or lost on that trial. The participant is then asked to indicate how he feels using a linear rating scale at the bottom of the screen: from -50 (extremely negative) to +50 (extremely positive).

Figure 2.1 The probabilistic gambling task: Partial feedback condition (example). On each trial, the participant is presented with two gambles (**screen 1**). In this example, the participant rejects the right hand gamble 2 (**screen 2**), which would incur a 0.5 chance of winning 50 points and a 0.5 chance of losing 50 points, and chooses to play left hand gamble 1 which incurs a 0.8 chance of winning 200 points and a 0.2 chance of losing 200 points. Probabilities and wins can occur in any combination, with the exception of combinations that result in identical EV between wheels. Once the participant has chosen, the arrow spins round on the selected gamble until it comes to rest on the obtained outcome (**screen 3**). Finally, the participant indicates his emotional response to the outcome on a continuous scale from -50 (I feel very negative) to +50 (I feel very positive).



The game is played under two conditions, lasting approximately 10 minutes each. Each condition contains 30 self-paced trials, separated by an inter-trial interval of 1 sec. In the *partial feedback* condition (**Figure 2.1**) which is played first, the participant is shown the outcome of the chosen wheel, but not the outcome of the unchosen wheel. In the subsequent *complete feedback* condition, the participant is shown the outcomes on both wheels, but only gains the number of points indicated by the arrow on the wheel which he has chosen. The task was run using Cogent software running in Matlab, which logged behavioural responses. Prior to the decision-making task, participants completed a five-trial practice task.

Possible gamble outcomes took the discrete values of +200, +50, -50 or -200 points. Outcome probabilities for each wheel could be 0.2/0.8 or 0.5/0.5. The two gambles always differed in EV (see **Equation 2.2**) and in the value of their actual outcomes. Otherwise, pairs of gambles and the combination of probabilities and outcomes on each gamble were split approximately evenly among possible combinations. Thus, the EV of all 120 gambles ranged from -170 to +170, with a mean and median close to or at zero (mean EV = -8, median EV = 0), and a range of differences in EV between the paired gambles across the 30 trials in each condition from -195 to +195 (pairings of extreme good EV gambles with extreme bad EV gambles were avoided as this sort of trial is experienced as an 'obvious' choice), with a mean and median close to zero (mean dEV = 3, median dEV = 12). The set of pairs of gambles and the order in which they were presented was the same in each condition (see **Appendix 2.1** for full parameter structure of the task).

The task was administered individually to child and adolescent participants in a quiet room in school, and at the home or workplace of adult participants. The total duration of the experiment was between 15 and 25 mins, depending on participant reaction times.

2.2.3 Data analysis

Data points lying >3 s.d. from the grand mean of the dependent variable in each analysis were considered outliers and were excluded from that analysis.

2.2.3.1 Logit regression analysis: the effects of expected value and risk on choice

Decision-making was analysed by conducting regression analysis with a panel logit procedure (Camille et al. 2004; Coricelli et al. 2005). This procedure treats each participant as a unit and each subsequent trial as time, and calculates the maximum likelihood of a model of the data that takes into account decision variables, in this case the difference in EV and risk (variance) between gambles.

In the current model, x_1 and y_1 represent the highest and the lowest outcome of gamble 1 (g_1, the left hand wheel), and x_2 and y_2 represent the highest and the lowest outcome of gamble 2 (g_2, the right hand wheel). The probability of x_1 is p and the probability of y_1 is $1 - p$; the probability of x_2 is q and the probability of y_2 is $1 - q$. The probability of choosing gamble 1 is estimated as:

(2.1) $$\Pr(g_{1it}) = 1 - \Pr(g_{2it}) = \mathrm{F}[\, dEV_{it}, dSD_{it}]$$

where i = individual, t = time and the function $F[\theta]$ denotes the function $e^{\theta}/(1 + e^{\theta})$. The effect on choice of the difference in EV and risk between paired gambles was investigated, with the variables dEV and dSD defined as:

(2.2) $$dEV = \mathrm{EV}(g_1) - \mathrm{EV}(g_2) = [(px_1 + (1 - p)y_1) - (qx_2 + (1 - q)y_2)]$$

(2.3) $$dSD = \mathrm{stdev}(g_1) - \mathrm{stdev}(g_2)$$

where:

(2.4) $$\mathrm{stdev}(g_1) = \sqrt{}[p(x_1 - \mathrm{EV}(g_1))^2 + q(y_1 - \mathrm{EV}(g_1))^2]$$

A participant who maximizes EV and risk will choose g_1 if $[\mathrm{EV}(g_1) > \mathrm{EV}(g_2)]$ (**Equation 2.2**), and if $[\mathrm{stdev}(g_1) > \mathrm{stdev}(g_2)]$ (**Equation 2.3**).

To ascertain whether the impacts of EV and risk on behaviour were dependent on participant age, the two variables *dEV* and *dSD* were first orthogonalised (with all common variance attributed to *dEV*) and then interactions between age and each of the orthogonalised parameters *dEV* and *dSD* were modelled. The hypothesis that risk-seeking would show an inverted U-shaped trajectory with age was tested by modelling the interaction between a quadratic function of age (age^2) and the impact of risk (*dSD*) on behaviour; a quadratic relationship between age and EV was also tested. In order to compare directly the models testing for linear and quadratic effects of age on the variables *dEV* and *dSD*, a likelihood ratio test was carried out.

The outputs of the logit regressions show the coefficients of model parameters (*dEV*, *dSD*) and their associated significance levels. A coefficient that is not significantly different from zero indicates that participant behaviour is neutral with respect to that coefficient. For example, participants could be risk-neutral, or insensitive to EV. A coefficient that is significantly different from zero indicates that participants tend to maximise or minimise the decision variable. The sign of the coefficient indicates whether the decision variable increases (+) or decreases (-) the probability of choice. For example, a high, positive coefficient for risk (*dSD*) indicates that a more risky choice (one with higher outcome variance) has a higher probability of being chosen. Significance of the variables *dEV* and *dSD* was tested across participants and within each Age Group separately, with the threshold for significance set at $p < 0.05$.

First, a simple model is reported, in which the utility function is estimated using the decision variables *dEV* and *dSD* (**Table 2.1a**). Subsequently the age variable is added, and its interaction with *dEV* and *dSD*, and then quadratic effects of the variables are tested by including interactions between age^2 and the variables *dEV* and *dSD*. We tested whether the addition of each variable improved the model, and report a reduced model including only the variables that significantly explain choice (**Table 2.1b**).

2.2.3.2 Proportion of EV and risk-maximising choices by Age Group

To complement results from the logit regression analyses, which treat age as a continuous variable and therefore may be influenced by the distribution of age, the proportion of trials for which each of the four Age Groups selected the gamble that maximized EV or risk was calculated. One-way ANOVA was used in each case to test for Age Group differences, with a threshold for significance at $p < 0.05$ and Bonferroni corrections applied to *post hoc* tests. The curve resulting from a regression between age^2 and the proportion of risky choices was interrogated to locate the point of inflection, which is the age at which the proportion of risky choices is maximal.

2.2.3.3 Other indices of performance

Mean winnings closely follow the proportion of EV-maximising choices, since a participant who maximizes EV will win more points. However to add detail to the current pattern of results, the relationship between participant age and mean winnings was investigated, by conducting linear regression analysis. Two regressions were performed, the first across the entire age range, and the second on the child and adolescent age range, in order to rule out the possibility that this effect was driven by two discrete clusters in age, and since it was hypothesised that the major changes in performance would occur during this age range.

To ascertain whether any effects of age and Age Group on performance (mean winnings; tendency to maximise EV) were simply due to slower learning of the task at younger ages (Crone & van der Molen, 2007), rather than to stable age differences in strategy, linear regression was conducted between age and the difference in mean winnings between the first and second 15 out of the 30 trials per condition, as well as one-way ANOVA on the mean difference in winnings between the first and second half of both conditions, with Age Group as a between-subjects factor.

2.2.3.4 Strength of counterfactual emotions by Age Group

It was hypothesised that the modulation of emotion evaluations by counterfactual comparison would differ according to Age Group. To test this hypothesis, trials were selected for which a counterfactual comparison could either enhance or diminish the degree of satisfaction a participant would feel for a given outcome. That is, trials were selected from the complete feedback condition for which the obtained outcome was either +50 or -50, and the unchosen alternative was either +200 or -200. To clarify, consider the obverse situation in which a participant wins +200 points. In this case, any unobtained outcome (+50, -50 or -200) would have been worse; the counterfactual comparison will always be in the downward direction and will always be confounded with outcome magnitude. In contrast, a win of -50 may appear satisfactory if the unobtained outcome is revealed to be -200, but unsatisfactory if the unobtained outcome is revealed to be +200. Emotion evaluations from the latter trial types were therefore used to calculate Age Group differences in the strength (magnitude) of counterfactual emotions defined according to the counterfactual and reward context in which they were elicited, which was previously described as the ‘regret effect’ in Coricelli et al. (2005).

Counterfactual emotions were compared between the four Age Groups using one-way ANOVA with a threshold for significance at $p < 0.05$, and Bonferroni-corrected *post hoc t*-tests.

2.2.3.5 Overall emotional response between Age Groups

Overall differences in emotion intensity between Age Groups and conditions were investigated by conducting mixed model repeated measures 2x2x4 ANOVA on emotion evaluations in response to positive and negative absolute outcomes (within-subjects factor 1: Valence; two levels: win, loss) and in the partial and complete feedback condition (within-subjects factor 2: Feedback; two levels: partial feedback, complete feedback), between age groups (between-subjects factor: Age Group; four levels: child, YA, MA, adult). Bonferroni-corrected *post hoc t*-tests were used to investigate simple effects. Because order effects (the partial condition was always played first) may contribute to a main effect of Feedback or interactions thereof, only those age-independent effects that replicate previous results are reported (Camille et al. 2004; Coricelli et al. 2005; Bault et al. 2008).

2.3 Results

2.3.1 Performance

2.3.1.1 Behavioural sensitivity to the difference in EV between gambles

Logit regression analysis showed that during both the partial and the complete conditions, across participants as well as within each Age Group separately, the difference in EV (see **Equation 2.2**, **Methods, 2.2**) between gambles affected choice. Overall, participants exhibited a behavioural preference for gambles with higher EV. Since the behaviour of participants with regards EV was similar in the partial and the complete conditions, and in order to increase power, we collapsed across conditions. Thus, for all 89 participants, EV coefficient $dEV > 0$, with $p < 0.05$ (see **Table 2.1a**) and for the Child, YA, MA and adult groups separately, $dEV > 0$, $p < 0.05$. However, participant age modulated the extent to which the difference in EV between gambles affected choice (interaction between age and dEV coefficient, $dEV*Age > 0$, $p < 0.05$; see **Table 2.1b**) such that the impact of the difference in EV between gambles on choice behaviour increased with increasing age. That is, older participants exhibited a stronger behavioural preference for gambles with higher EV than did younger participants. The interaction between age² and *dEV* was not significant, and was therefore removed from the model.

In order to assess statistically whether the relationship between age and the impact of EV on choice was better described as linear or quadratic, a likelihood ratio test was conducted. This showed that adding a quadratic component for the interaction between age and *dEV* (age²**dEV*) did not significantly improve the model (Likelihood-ratio test: LR $\chi^2(1) = 1.47$; $p = 0.226$). Therefore, the effect of age on *dEV* is concluded to be linear.

2.3.1.2 Proportion of EV-maximising choices by Age Group

One-way ANOVA on the proportion of trials for which participants in each of the four Age Groups chose the gamble with higher EV was not significant ($F_{3,85} = 2.354$, $p = 0.078$).

2.3.1.3 Correlation between age and mean winnings

Linear regression analysis showed that mean winnings across the task were positively correlated with age (mean winnings: $\beta = 0.280$, $r^2 = 0.078$, $p < 0.05$; two outliers were excluded: one YA, one MA[4]; see **Figure 2.2**). This result is consistent with the logit regression result showing an age-related increase in EV-maximising behaviour. In order to rule out the possibility that this effect was driven by two discrete clusters in age, a second linear regression analysis was carried out on mean winnings against age for the Child and Adolescent groups only. This showed that mean winnings across the task were also positively correlated with age across this age range ($\beta = 0.340$, $r^2 = 0.115$, $p < 0.05$).

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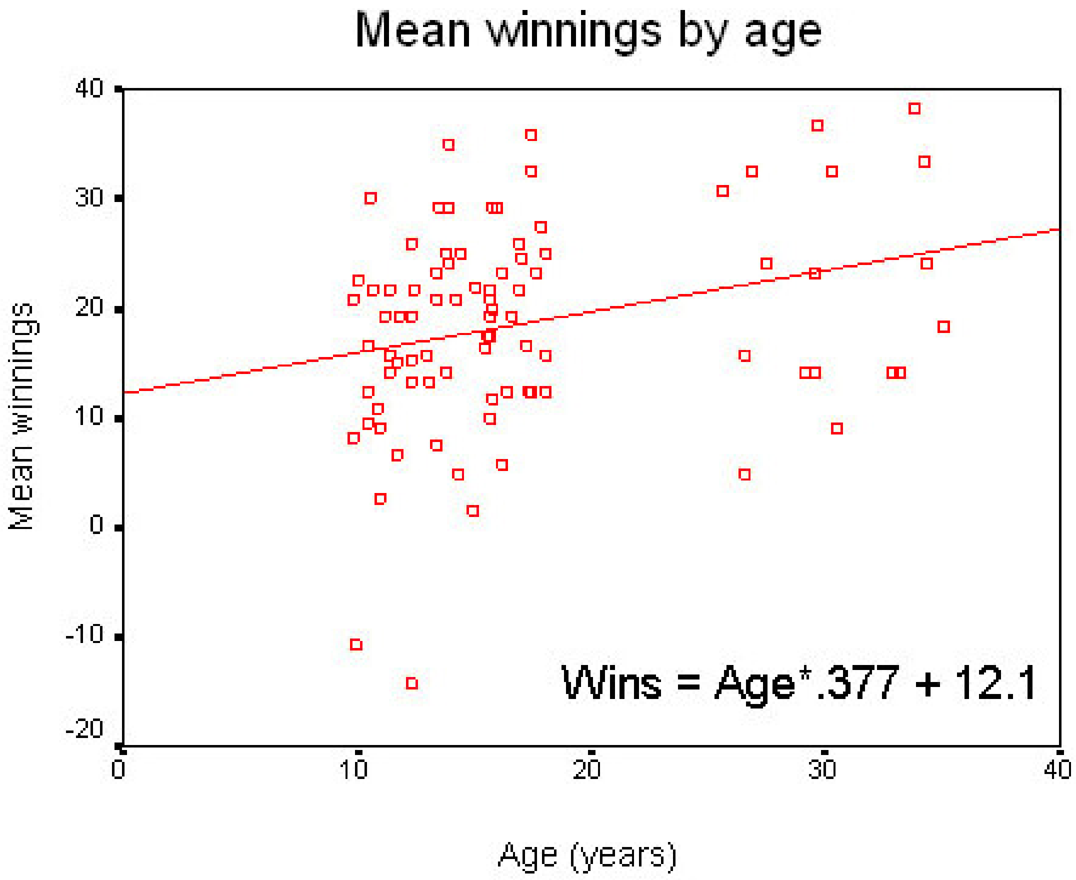
[4] Note that the two lower data points shown in **Figure 2.2** lie within 3 s.d. of the mean and are therefore not defined as outliers in this study. However, the linear relationship remains significant when these data points are excluded ($\beta = 0.265$, $r^2=0.070$, $p < 0.05$).

Figure 2.2 Mean winnings across the task show a positive correlation with age, ($\beta = 0.280$, $r^2 = 0.078$, $p < 0.05$). Two outliers >3 s.d. away from the mean were excluded.



2.3.1.4 Effect of age on learning

Linear regression between age and the difference in mean winnings between the first and second 15 out of the 30 trials per condition, as well as one-way ANOVA on the mean difference in winnings between the first and second half of both conditions, with Age Group as a between-subjects factor, revealed no significant effect of age (regression: $p = 0.879$; no outliers) or Age Group ($F_{3,84} = 0.204$, $p = 0.894$; one YA excluded due to incomplete partial condition) on the difference in mean winnings between the first and second half of each condition. This suggests that the effects of age and Age Group on performance are due to stable age differences in strategy, and are not simply due to slower learning of the task at younger ages.

2.3.2 Risk-seeking

2.3.2.1 Behavioural sensitivity to the difference in risk between gambles

Logit regression analysis showed that across Age Groups, the difference in risk between gambles (see **Equation 2.3**, **Methods, 2.2**) affected choice. Overall, participants exhibited a behavioural preference for more risky gambles, that is, gambles with higher outcome variance (risk coefficient $dSD > 0$; $p < 0.05$; see **Table 2.1a**). The difference in risk between gambles also predicted choice in the Child, YA and MA groups alone (risk coefficient for Child, YA and MA groups separately, $dSD > 0$, $p < 0.05$), but not in the Adult group alone ($p > 0.7$). That is, children and adolescents show a preference for more risky gambles, but adult behaviour is insensitive to risk.

2.3.2.2 Nonlinear relationship between age and the impact of risk on behaviour

A significant quadratic interaction between age and *dSD* showed that participant age modulated the extent to which the difference in risk between gambles affected choice (coefficient $dSD*Age^2 > 0$, $p < 0.05$; see **Table 2.1b**), but choice was not predicted by a linear function of risk*age (coefficient $dSD*Age < 1$, $p = 0.064$; see **Table 2.1b**). In order to directly compare linear vs. quadratic effects of *dSD*, a likelihood ratio test was conducted. This showed that adding a quadratic component for the interaction between age and the risk coefficient ($dSD*Age^2$) to a model containing the linear component only ($dSD*Age$) significantly improved this model (likelihood-ratio test: LR $\chi^2(1) = 5.31$; $p < 0.05$). Therefore, it is concluded that there is a quadratic relationship between age and the propensity to seek risk.

Table 2.1

(a) Participant choice behaviour as a function of the difference in expected value (dEV) between gambles and the difference in risk (dSD) between gambles.

Variable name	Coefficient	Standard error	Z	P	[95% Conf. Interval]	
Difference in expected value: dEV	0.02275	0.00061	37.58	<0.001	0.02156	0.02393
Difference in risk: dSD	0.00514	0.00051	10.09	<0.001	0.00414	0.00613
Constant	0.17911	0.03833	4.67	<0.001	0.10398	0.25423

Number of subjects = 89; number of observations = 5289. Data from all trials.

Log likelihood = -2151.0887, Wald chi^2(3) =1453.61, Prob > chi^2 = 0.000

(b) Participant choice behaviour as a function of the variables listed in column 1.

Variable name	Coefficient	Standard erro	Z	P	[95% Conf. Interval]	
Difference in expected value: dEV	0.01598	0.00179	8.92	<0.001	0.01247	0.01949
Difference in risk: dSD	-0.00224	0.00464	-0.48	0.629	-0.01133	0.00685
Interaction between EV and Age: $dEV*Age$	0.00043	0.00011	3.93	<0.001	0.00021	0.00064
Interaction between risk and Age: $dSD*Age$	0.00099	0.00049	2.03	0.042	0.00003	0.00194
Interaction between risk and Age^2: $dSD*Age^2$	-0.00003	0.00001	-2.5	0.012	-0.00005	-0.00001
Constant	0.18100	0.03890	4.65	<0.001	0.10475	0.25725

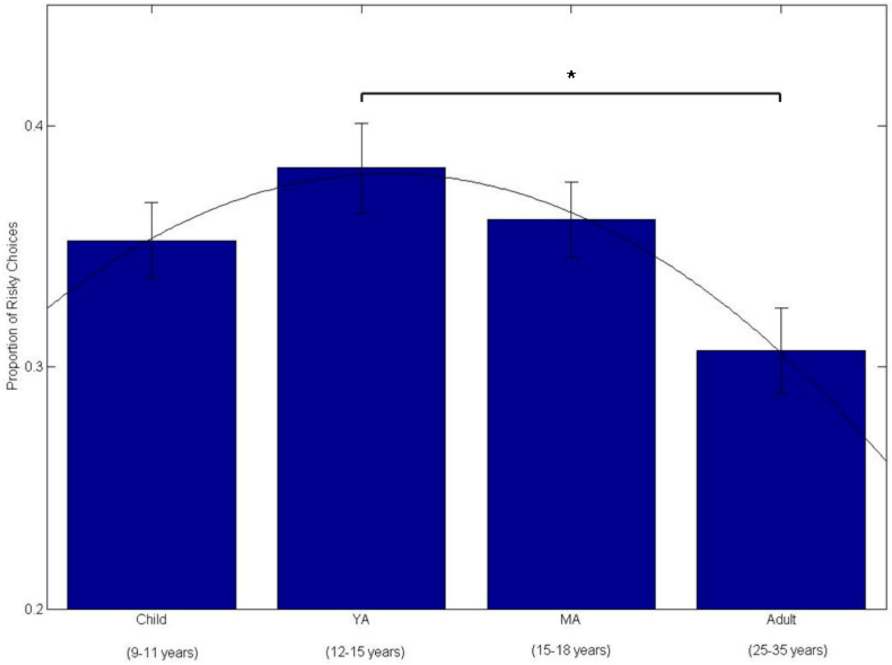
Number of subjects = 89; number of observations = 5289. Data from all trials.

Log likelihood = -2127.8668, Wald chi^2(3) =1414.01, Prob > chi^2 = 0.000

2.3.2.3 Proportion of risk-maximising choices by Age Group

One-way ANOVA on the proportion of trials for which participants in each of the four Age Groups chose the gamble with higher risk was significant ($F_{3,85} = 3.077$, $p < 0.05$). **Figure 2.3** shows the proportion of risky choices in each Age Group. For the purposes of illustration, a quadratic function has been fit to the group data. Paired *post hoc* Bonferroni corrected comparisons showed that the YA group made a significantly greater proportion of risk-maximising choices than did the Adult group ($p < 0.05$; all other comparisons $p > 0.2$). Interrogation of the curve resulting from a regression between age^2 as a continuous variable and the proportion of risky choices revealed that the point of inflection was located at 14.38 years. That is, 14.38 is the age at which participants made the greatest proportion of risky choices.

Figure 2.3 Proportion of risky choices made by each Age Group. Logit regression revealed an inverted U-shape relationship between age and the influence of risk on choice. The graph is fit with a quadratic function for the purposes of illustration; a quadratic fit between age as a continuous variable and the proportion of risky choices showed that the point of inflection was at age 14.38 years, and logit regression showed a quadratic relationship between age and the impact of risk on choice.

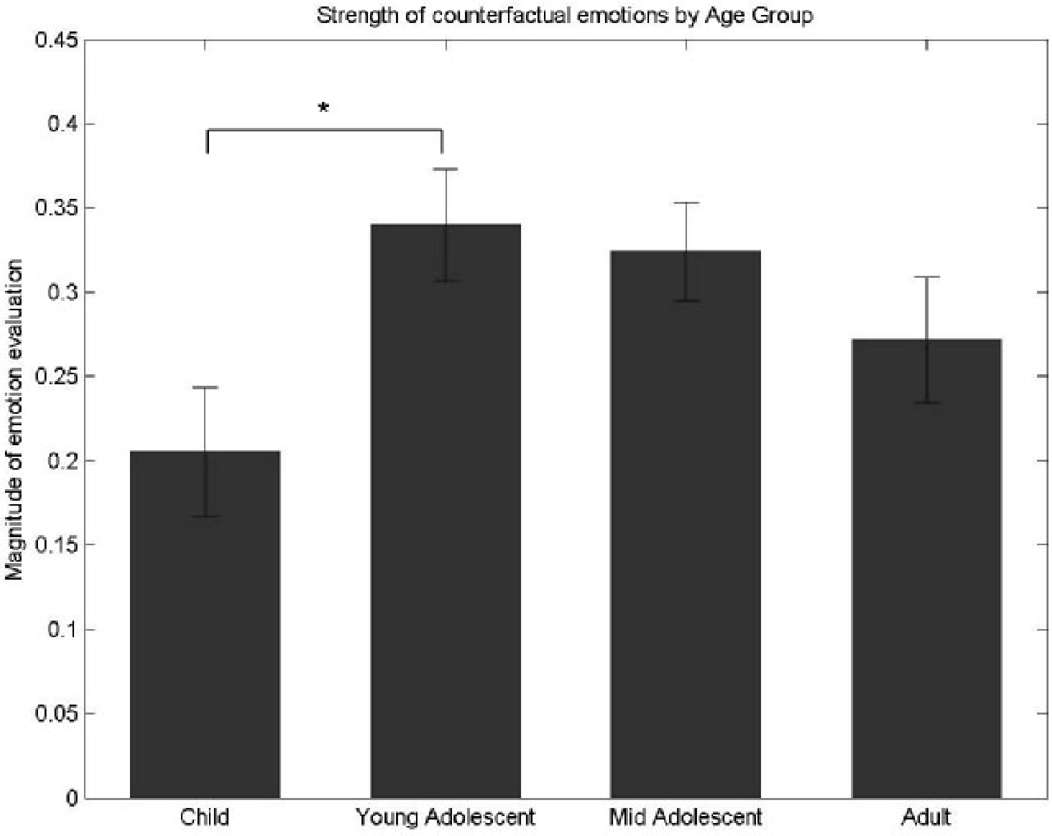


2.3.3 Emotional response to outcomes

2.3.3.1 Strength of counterfactual emotion by Age Group

One-way ANOVA showed a significant effect of Age Group ($F_{3,83} = 3.155$, $p < 0.05$; two outliers were excluded[5]) on the strength (magnitude) of counterfactual emotions, that is the emotional response to wins of ±50 when the unobtained outcome was ±200. Paired *post hoc* Bonferroni-corrected comparisons revealed significantly weaker counterfactual emotion evaluations in the Child than in the YA group (mean difference 6.74, $p < 0.05$), while no other comparisons reached significance (all comparisons $p > 0.5$, except Child vs. MA: mean difference 5.96, $p = 0.085$; see **Figure 2.4**). That is, the strength of counterfactual emotions increases between childhood and early adolescence, and thereafter shows no significant change.

Figure 2.4 Counterfactual emotion. The strength of the emotional response to counterfactual outcomes is greater in the Young Adolescent than in the Child group.



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[5] Outliers were one Child whose data lay +3.21 s.d. away from the mean, and one Adult whose data lay +4.31 away from the mean.

In contrast to the results regarding counterfactual emotions, on investigating overall differences in emotion intensity between Groups and conditions, no evidence was found for a generally heightened emotional response in adolescence. Repeated measures 2x2x4 ANOVA showed no two- or three-way interactions between Age Group and the within-groups factors: Valence x Age Group ($F_{3,83} = 0.50$, $p = 0.68$); Feedback x Age Group ($F_{3,83} = 1.05$, $p = 0.38$); Valence x Feedback x Group ($F_{3,83} = 0.32$, $p = 0.81$; three Child outliers excluded). This suggests that the Age Group difference in emotion evaluations reported above is specific to emotions that are counterfactually-modulated.

However, results from previous studies showing an influence of counterfactual and reward condition on the emotion evaluations were replicated. Specifically, emotion ratings were influenced by outcome Valence (positive vs. negative: $F_{1,83} = 400.45$, $p < 0.05$) and the nature of the Feedback (partial vs. complete: $F_{1,83} = 9.84$, $p < 0.05$), and by an interaction between the factors Valence and Feedback ($F_{1,83} = 39.82$, $p < 0.05$). These findings have been described previously in adults, using the same task (Coricelli et al. 2005; Bault et al. 2008). The current study therefore extends these observations to children and adolescents.

2.3.3.2 Post hoc tests on counterfactual emotion and risk-seeking

2.3.3.2.1 Relief vs. regret

Post hoc t-tests were conducted on Child vs. YA differences in counterfactual emotion evaluations separately for positive and negative outcomes, in order to investigate whether the stronger counterfactual emotion evaluations in YA relative to the Child group was driven by a hyper-responsiveness to positive rather than negative outcomes, as has previously been reported (Casey et al. 2008; Ernst et al., 2005; Eshel et al., 2007). Independent samples *t*-tests revealed higher YA than Child emotion evaluations on relief (or, ‘lucky escape’) trials ($t_{43} = -2.22$, $p < 0.05$ ($p = 0.02$ 1-tailed)) whereas the same comparison for regret trials was not significant ($t_{43} = .73$, $p = 0.24$ 1-tailed). This *post hoc* result provides evidence that the YA group showed an enhanced emotional response to relief or ‘lucky escape’ outcomes, relative to the Child group.

2.3.3.2.2 Relationship between relief and risk-seeking

Finally, it was of interest to investigate whether the developmental enhancement in the emotional response to relief or 'lucky escape' trials between childhood and young adolescence predicted risk-taking in these participants. Linear regression analyses were therefore conducted between the emotional response on relief trials and the proportion of risky choices across age, as well as within selected Age Groups. This showed no evidence for a relationship between the emotional response on relief trials and the proportion of risky choices across age across the entire age range participants ($\beta = 0.176$, $r^2 = 0.031$, $p = 0.103$). However, this relationship was significant within Child and YA groups together ($\beta = 0.305$, $r^2 = 0.093$, $p < 0.05$), and was marginally significant within Child, YA and MA groups together ($\beta = 0.228$, $r^2 = 0.052$, $p = 0.056$), but not in the Adult group alone ($\beta = 0.067$, $r^2 = 0.005$, $p = 0.804$). These regressions do not survive Bonferroni correction, and thus should be interpreted with caution.

2.4 Discussion

The current study was conducted to investigate the development between childhood and adulthood of the tendency to maximise expected value (EV) and seek risk, using a task that assessed decision-making under risk. Age differences in the emotional response to gamble outcomes were also investigated. Male participants aged nine to 35 years played a probabilistic decision-making task in which paired gambles differed in EV, risk and the potential to generate counterfactual emotions (relief and regret). Results show that the ability to maximise EV increased linearly with age, whereas risk-seeking showed a quadratic relationship with age. The proportion of risky choices peaked in mid-adolescence. This is one of the first behavioural studies to provide evidence for an inverted-U shaped relationship between age and risky decision-making. In addition, results show an increase between childhood and adolescence in the strength of counterfactual emotions, although individual emotion scores did not predict risky decision-making across the age range. This is the first study to investigate the development of risk-seeking and counterfactual emotions between childhood and adulthood using a behavioural economic task.

2.4.1 Development of rational decision-making: sensitivity to EV

Participants made a series of decisions between paired gambles that differed in EV, which is the sum of possible outcomes of a gamble weighted by their probabilities. Each of the four age groups showed evidence of taking EV into account when making decisions. At all ages, decisions were predicted by a model in which gambles with high EV were preferentially chosen over gambles with low EV. This result concurs with previous studies (see Boyer, 2006, for review), which have shown that even children as young as five have a rudimentary sensitivity to EV (Schlottmann 2001).

While all age groups showed evidence of taking EV into account when making decisions, the extent to which participants maximised EV differed according to age (see **Table 2.1b**). With increasing age, participants were more likely to make decisions that maximised EV. Since mean winnings closely follow the proportion of EV-maximising choices (a participant who maximizes EV will win more points) it was not surprising that there was also a positive correlation between age and mean winnings across the task. Therefore, it can be concluded that performance on the task improved across age (see **Figure 2.2**). This suggests that the ability rationally to integrate reward and probability information across gambles in order to maximise winnings shows continuing improvement between late childhood and adulthood.

This result is in agreement with previous findings. In a behavioural economic study conducted by Harbaugh et al. (2002) in which participants aged five to 64 years chose between a certain outcome and a gamble with equivalent EV, it was shown that the proportion of rational choices increased with age throughout childhood and adolescence. A study by Levin et al. (2007) showed age-related increases in the tendency to maximise EV between groups of young children (aged 5-7), pre-adolescents (aged 8-11) and adults in the Cups Task, which involves a choice between gambles that differ in EV. The current study extends this developmental picture, by showing that the ability to maximize EV when choosing between two gambles (rather than a gamble and a sure thing) shows linear development between late childhood, adolescence and adulthood.

2.4.2 Developmental profile of risk-taking

In the current gambling task, paired gambles differed in risk, measured as outcome variance (Bossaerts & Hsu, 2008). Analysis of behavioural decisions revealed that the child group, and both adolescent groups, showed evidence of taking risk into account when making decisions. In these age groups, decisions were predicted by a model in which gambles with high risk were preferentially chosen over gambles with low risk. In contrast, the adult group showed no evidence of taking risk into account when making decisions; adults were risk-neutral.

The extent to which participants maximized risk differed according to participant age. There was an inverted U-shaped relationship between age and the influence of risk on choice. Logit regression showed that the impact of the difference in risk between gambles on choice increased with increasing age at the younger end of the age range. Towards the middle of the age range, the increase in the impact of risk began to decrease with increasing age. By adulthood, the effect was reversed. That is, adolescents showed the strongest tendency to select high-risk gambles. In addition, there was a significant effect of age group on the proportion of trials for which participants selected the gamble with higher risk. Young adolescents (aged 12-15) made a significantly greater proportion of risky choices than did adults, and the age at which risky choices peaked was 14.38 years (see **Figure 2.3**).

These results extend those from previous studies that have shown that the tendency to make risky decisions in emotional gambling tasks decreases between adolescence and adulthood (age 11-15 vs. age 21-31, Eshel et al. 2007; age 13-19 vs. age 20+, Figner et al. 2009). However, it has been suggested that the tendency to make risky decisions shows an inverted-U shaped relationship with age, from childhood through adolescence and into adulthood. The current study is one of the first empirical studies to demonstrate an inverted U-shaped relationship between age and risky decisions (O'Brien & Steinberg, 2009). This result complements much theoretical and observational work. Epidemiological studies show a peak during adolescence in 'risky' activities such as dangerous driving (Eaton et al. 2006), which has led to the suggestion of an inverted U-shaped relationship between age and the tendency to engage in risky behaviours, peaking at adolescence (Steinberg et al. 2008; Casey et al., 2008). However, choosing to engage in these real life activities is likely to have a variety of underlying causes, and as such does not constitute a preference for risk in a behavioural economic sense. The current study showed that risk-taking in an emotional gambling task peaks during adolescence. This is an important first step towards clarifying the conditions under which adolescents are risk-taking, both in laboratory-based tasks and in naturalistic circumstances.

2.4.3 Development of counterfactual emotions

In this study, participants rated their emotional response to the outcome of each gamble. On half of the trials (*complete feedback* condition) participants were shown the outcome of the unchosen wheel as well as the outcome of the chosen wheel. Previous work in adults has shown that this gives rise to a counterfactual comparison between the outcome of a choice (reality) and its foregone alternative (what might have been), and that this comparison modulates emotional responses and behaviour (Coricelli et al. 2007). The current study investigated age differences in the emotional response to counterfactual outcomes (relief and regret). Results showed that the strength of counterfactual emotions differed across age groups, such that young adolescents (aged 12-15) responded with stronger emotion evaluations on counterfactual trials than did children (aged 9-11). That is, the strength of emotional responses to counterfactual outcomes increases between childhood and adolescence. This result is consistent with the suggestion that the ability to think counterfactually about the outcomes of decisions is still developing during adolescence (Baird and Fugelsang, 2004).

Post hoc tests indicated that the increased strength of counterfactual emotions in young adolescents relative to children was driven by a more strongly positive response to relief outcomes, or ‘lucky escapes’. On these trials, participants learned that they had won a number of points on choosing to play a gamble which could instead have resulted in a large loss. This result is compatible with a developmental picture showing heightened sensation-seeking and reward sensitivity in adolescents (aged around 15) relative to children (aged around 10) (Steinberg et al., 2008). Further studies are needed to replicate and extend this developmental finding showing an increase in the emotional response to ‘lucky escapes’. A tentative suggestion based on the (uncorrected) correlation between child and adolescent emotional responses on relief or ‘lucky escape’ trials, is that children and adolescents may become less cautious in their decisions after surprisingly lucky (relieving) wins. However, this conclusion is preliminary because the correlations between risk-taking and emotion did not survive Bonferroni correction.

2.4.4 Relationship between risk and other variables

The current study used an emotional gambling task to show that risk-seeking followed a non-linear relationship with age, peaking in adolescence, whereas the tendency to maximize EV increased linearly with age. These findings lend weight to the suggestion that risk-taking in adolescence cannot solely be explained by an inability to gauge the most advantageous course of action, for if this were the case then children would take more risks than adolescents in the current task. Results from the current study are compatible with the notion, which has been suggested elsewhere (Casey et al. 2008, Steinberg 2008), that adolescent risk-taking arises due to an interaction between two separate developmental processes: a gradual improvement in outcome judgment, and perhaps cognitive control-related abilities (here contributing to improvements in the ability to maximize EV), superimposed upon a non-linear trajectory of sensation-seeking and other socio-emotional factors. In the current study, it was found that the increase in risk-taking coincided with an increased strength of counterfactual emotions (in particular, relief). However, individual emotion scores did not strongly predict risk-taking. This may reflect a lack of power in the current study, or alternatively, either some other measure of emotional responding, or a cognitive variable (cf. Galvan et al. 2007) may be a more proximal predictor of individual risk-taking. Future studies could usefully test the relationship between risk-taking and the emotional response to a 'lucky escape'.

2.5 Conclusion

This study was conducted to investigate the development between late childhood (age 9) and adulthood (age 35) of decision-making under risk, and of the emotional response to the outcomes of decisions. Results show that the ability to maximize EV in order to win points increases linearly with age. In contrast, risk-seeking showed an inverted U-shaped developmental trajectory. The peak age for making risky decisions was 14.38 years. This is one of the first empirical studies to provide evidence for a peak in risky decisions during mid-adolescence, and the distinct developmental trajectories for EV-maximising versus risk-taking suggest that adolescents did not make risky decisions simply because they were unable to estimate the consequences of their decisions.

In addition, young adolescents (age 12-15) showed an enhanced emotional response to counterfactual outcomes (in particular, relief or a ‘lucky escape’) relative to children (age 9-11), although they did not differ from mid-adolescents (age 15-18) or adults (age 25-35) on this measure. Further studies should investigate whether child and adolescent relief responses predict risky choices, and should establish more generally which social-emotional and cognitive factors most strongly contribute to adolescent risk-taking.

Finally, the current study included only male participants, as we wished to reduce variance attributable to developmental sex differences in traits such as sensation-seeking, which might influence risk preferences, and in light of evidence for higher risk-seeking in males than in females. While a previous version of this task produced no sex differences in adults (Bault et al., 2008), it remains possible that there might be developmental sex differences. Therefore, it would be interesting to investigate whether the developmental trajectories of risk taking and counterfactual emotion found here in males are also seen in females.

2.5.1 The next chapter

In **Chapter 3**, a study is described that was carried out to investigate in more detail the influence of socio-emotional factors on adolescent decision-making. In this study, adult and adolescent participants completed a task in which paired happy and angry face stimuli were associated with differing probabilities of reward. Behaviour was analysed computationally, which enabled investigation of the mechanism by which social-emotional factors influence decision-making across age. The computational approach was also used to investigate age group differences in the ability to integrate positive and negative performance feedback (wins and losses), in order to perform optimally on the task.

Chapter 3

Development of the integration of social and utilitarian factors in a probabilistic decision-making task

Adolescence is characterized by continuing development in aspects of decision-making. In particular, adolescence is thought to be characterized by a tendency for emotional and social factors (e.g. reward feedback, presence of peers) to cause 'risky' or irrational decisions, and in ***Chapter 2*** *a study was descried in which adolescents showed a tendency to make risky decisions in an emotional gambling task. Across age, there was a linear improvement in the ability to take into account probability and reward information, in order to maximize expected value. The current chapter describes a study that was carried out to extend this developmental picture. Adolescent and adult participants completed a probabilistic decision-making task in which rewards were associated with happy and angry face stimuli. The results showed that decisions of both age groups were influenced both by the utilitarian feedback (wins and losses), and by reward-irrelevant social-emotional cues (happy and angry faces). There were age group differences in performance such that adults outperformed adolescents, and a computational analysis of adolescent and adult behaviour suggests that this difference was due to developmental asymmetry in the response to positive and negative performance feedback.*

3.1 Introduction

3.1.1 Developmental studies of decision-making

The development of decision-making during adolescence has previously been studied using a number of laboratory-based decision-making tasks (see

Introduction, 1.6.2). Often in these tasks, participants must take into account the rewards and reward probabilities associated with a selection of choices, and then make a choice so as to maximize their total rewards. For example, in the Iowa Gambling Task (IGT; Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004; Huizinga et al., 2007), participants repeatedly select cards from an array of four decks with unknown reward distributions. Two of the decks yield low-magnitude, constant rewards and modest probabilistic losses, resulting in net gain across the task. The remaining two decks yield high-magnitude, constant rewards but substantial probabilistic losses, resulting in a net loss. Several studies using the IGT have shown that the ability to adopt an advantageous decision strategy that takes into account both the magnitude and probability of wins and losses continues to develop during adolescence (between 11 and 18+ years: Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004; although see van Leijenhorst et al., 2008).

In a task devised by Harbaugh et al. (2002), participants make a series of decisions between a certain reward, and a gamble with equivalent expected value (EV: the sum of potential outcomes weighted by their respective probabilities). Unlike in the IGT, in this task participants are explicitly informed about the reward probabilities associated with each decision. When participants aged between five and 64 years completed the task, children and adolescents showed evidence of biased decisions relative to adults, that is, children and adolescents failed to show indifferent choices between the two options with equivalent EV. A similar study by Levin et al. (2007), in which children (aged 5-11) and adults made a choice between gambles that differed in EV also showed age-related increases in rational, or EV-maximising decisions.

Several suggestions have been put forward to account for the age-related improvements in decision-making tasks including these. One suggestion is that, with age, adolescents become more proficient at taking into account performance feedback, i.e. information regarding wins/losses from a given trial, in order to maintain or modify subsequent behaviour (Byrnes et al., 1999; Crone & van der Molen, 2004). An observation from studies that have used rule switching tasks, such as the Wisconsin Card Sort Task (WCST), is that there is an improvement between childhood (age 8-9), adolescence (age 11–18) and young adulthood (age 18-25) in the ability to take into account performance feedback. At all ages, individuals perform better in response to positive vs. negative feedback (i.e. instructions to maintain vs. switch strategy). Furthermore, the degree of asymmetry in the response to positive vs. negative feedback is greater at younger ages (Crone et al., 2004, 2008; Huizinga et al., 2006; van Duijenvoorde et al., 2008). Therefore, the ability to respond to positive and negative performance feedback in a rule-switching task continues to develop between childhood and adulthood. However, whether a similar developmental asymmetry in the response to performance feedback is elicited during probabilistic decision-making tasks such as the IGT, or whether this finding is specific to rule switching tasks, is not known. In the current chapter, age group differences in the response to positive and negative feedback in a simple probabilistic decision-making task were analysed using a computational modeling approach.

3.1.2 Developmental changes in strategy

Another explanation that has been put forward to explain age-related improvements in performance on decision-making tasks is that the use of behavioural rules or strategies shifts with age. By analysing IGT performance using a multivariate technique, Huizinga et al. (2007) demonstrated that pre-adolescents (aged 6-9 years) behave in a way that is consistent with sensitivity to the frequency of loss and an insensitivity to loss magnitude, while up to and during adolescence (10-15 years), participants were increasingly likely to take into account both the frequency and magnitude of losses. Between mid-adolescence (13-15 years) and young adulthood (18-25 years), there were further improvements in strategy, as seen by an increase in the tendency to take into account both sources of information, as well as increasingly unbiased choosing between the two equally beneficial decks (participants did not persist in choosing from their 'favourite' deck). These results suggest that developmentally immature decision-making may be characterized by simplistic strategies comprising a particular set of biases, and focus on a subset of stimulus attributes. This suggestion was investigated in the current study.

3.1.3 Influence of social and emotional cues

Across age, a particular source of bias in the decision-making process arises from social and emotional cues. It has been shown that adults drink more of a beverage when it has been subliminally paired with a smiling face (Winkielman et al., 2005).

Adults are also reported to be more likely to co-operate in economic exchange games with a partner who is smiling or attractive (Scharlemann et al., 2001; Wilson & Eckel, 2006).

Recently, a novel probabilistic Face Decision Task paradigm in which participant behaviour is modelled computationally, was used to investigate the nature of social influences on decision-making and to characterise how social cues are integrated with utilitarian information to perform the task (Averbeck & Duchaine, 2009). This study showed that adult participants show a bias to select stimuli that depict happy vs. angry faces. Bayesian modeling of the data showed evidence that this social bias acted on behaviour via two distinct mechanisms: (1) a prior expectation that happy faces will be rewarded ('prior bias'), (2) faster learning to associate happy faces with reward than with non-reward, and vice versa for angry faces ('likelihood bias').

There is evidence that adolescent decisions are also influenced by social and emotional cues. Two studies to date have shown a heightened effect of social and emotional cues on adolescent decision-making (e.g. Gardner & Steinberg, 2005; Steinberg, 2008). For example, in Gardner & Steinberg (2005)'s car driving game, adolescent (age 13-16) decisions to apply the brakes in response to a stop cue were modulated by the social presence of peers, whereas this was not the case in adults (age 24+). In a different study, an increase in reaction times to associate faces with emotional words was shown around puberty onset (age 11-12), relative to both pre-puberty (age 10-11) and late adolescence/adulthood (age 16+; McGivern et al., 2002). This effect was attributed to a greater interference by emotion on the decision-making process in early adolescence.

It is unknown whether adolescent decisions in simple decision-making tasks show influence of bias by social and emotional cues. Therefore, in the current study, the Face Decision Task from Averbeck and Duchaine (2009) was adopted to investigate social-emotional influences on adolescent decision-making.

3.1.4 The Face Decision Task

In the current study, groups of adults and adolescents were tested using the Face Decision Task (Averbeck & Duchaine, 2009; see **Figure 3.1**). In this task, participants made a series of selections between paired happy and angry face stimuli, which were associated with differing probabilities of reward. A decision to choose one stimulus over the other either resulted in a win (fictitious gain of 10 p) or a loss (fictitious gain of 0 p), and participants were instructed to win as much as possible.

Rewards were stochastically associated with each stimulus, and the reward probabilities of the two stimuli were constant across trials but are not highly dissimilar (0.6, 0.4). Therefore, it was not obvious to participants which stimulus should be selected on each trial. Reward feedback was stochastic, in the sense that choosing the more highly rewarded face (the face for which p[win] = 0.6) did not result in a win on every trial. Therefore, participants had to keep track of the history of positive and negative feedback across trials and integrate this to gain a best estimate of the more highly rewarded stimulus.

Patterns of decision-making in the task were analysed computationally, in order to model the effects on behaviour of a biased preference for happy over angry face stimuli, and to model separately the contribution of negative and positive performance feedback (wins and losses) to behaviour. This enabled a quantitative assessment of the extent to which distinct behavioural tendencies were responsible for any age-related improvements in performance on the task.

3.1.4.1 Ideal and ecological observer models

Behaviour in the task was analysed computationally. First, a model of the ‘ideal observer’ was created, and participant decisions were referenced to the ‘decisions’ of this model. The ideal observer model did not have access to the underlying reward probabilities of the two faces, but optimally integrated outcomes over all the trials that had elapsed at a given point in the experiment to gain a best estimate of the most highly rewarded face. This enabled quantification of the extent to which adult and adolescent participants acted like the ideal observer, optimally integrating performance feedback to make the best choice on a given trial. In line with the developmental decision-making literature, which has shown deficits in adolescent relative to adult decision-making (Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004; Huizinga et al., 2007; Harbaugh et al., 2002; for review, see Boyer et al., 2006), it was predicted that the behaviour of adolescents would deviate from that of the ideal observer to a greater extent than would the behaviour of adults.

After fitting the ideal observer model, parameters were added to the model that each encapsulated a distinct behavioural tendency that participants were expected to exhibit, and which might contribute to the observed deviations from ideal behaviour. These parameters encapsulated responsiveness to negative and positive performance feedback, and a biased social preference for one face stimulus (happy) over the other (angry). The parameters were fit to each participant's dataset, and then collated and statistically tested across groups to assess significant effects on behaviour. In line with findings from rule-switch tasks (Crone et al., 2004, 2008; Huizinga et al., 2006; van Duijenvoorde et al., 2008), differential effects on behaviour in the Face Decision Task of the positive and negative feedback parameters were predicted. In addition, it was predicted that the previously-reported effect of a prior bias to select the happy face, as well as an over-weighting of positive outcomes (wins) associated with happy vs. angry faces, would be elicited in adults (Averbeck & Duchaine, 2009). It was predicted that this finding would be extended to adolescents.

Finally, the behavioural influence of each parameter was compared between adult and adolescent groups. It was predicted that in general, adult participants would take into account performance feedback to a greater extent than would adolescents (Byrnes et al., 1999; Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004; Crone et al., 2004, 2008; van Duijenvoorde et al., 2008). In addition, it was predicted that a differential response to positive and negative feedback across age (Crone et al., 2004, 2008; van Duijenvoorde et al., 2008) might contribute to this tendency, such that adolescents would exhibit greater bias relative to adults in their treatment of positive and negative performance feedback.

3.2 Methods

3.2.1 Participants

Twenty-two adolescent participants (12 female; age range = 12.83-13.75 years; mean (s.d.) age = 13.28 (0.31) years) were recruited from a comprehensive secondary school in Greater London. Fourteen adult participants (9 female; age range = 21.33-43.0 years; mean (s.d.) age = 30.46 (5.59) years) were recruited from the local community, including the UCL Psychology Department volunteer database and an email distributed to all employees of Camden council.

Participants had no history of psychiatric or neurological disorder, and none had received a diagnosis of attention-deficit/hyperactivity disorder, autism or dyscalculia.

Participants' general ability was assessed by administering the 2-subtest form of the Wechsler Abbreviated Scale of Intelligence (WASI; Harcourt, 1999), after completion of the experimental task. Adult and adolescent groups did not differ in WASI score (adult: mean (s.d.) WASI score = 104.2 (6.47); range = 89-112; adolescent: mean (s.d.) WASI score = 102.3 (5.29); range = 90-114; independent samples *t*-test: $t_{34} = 0.96$, $p = 0.343$).

Information was obtained regarding the educational background of adult participants, and the projected educational background of adolescent participants based on the educational destinations of the previous year's cohort of school leavers. This was used to calculate the percentage of each age group for whom the highest obtained qualification was GCSE (0% adults and 6% adolescents), post-16 vocational qualifications such as NVQ (14% adults and 21% adolescents), A-level or equivalent (43% adults and 73% adolescents) or a university degree (43% adults; data not available for adolescents). Adult and adolescent groups were satisfactorily-matched for educational background: Although a greater proportion of the adolescent group is expected to obtain A-levels, this increase is in line with demographic trends (Data Service, 2009).

Prior to the study, written informed consent was obtained from adult participants, and from a parent or guardian of adolescent participants. The study was approved by the local Ethics Committee. Adult participants received a modest financial compensation for their time. As advised by the school, adolescent participants were not paid.

3.2.2 Procedure

Participants performed the Face Decision Task, which is a two-alternative forced-choice decision-making task, on a laptop computer (**Figure 3.1**; Averbeck &

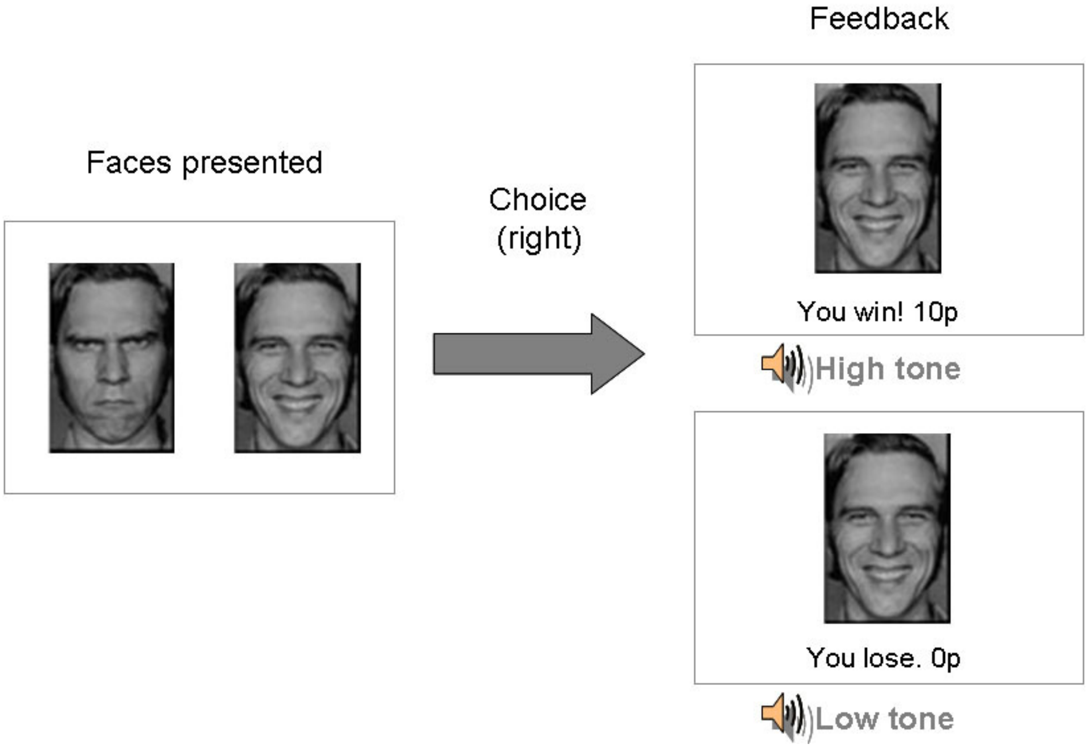
Duchaine, 2009). Each participant completed four blocks of the task, consisting of 26 trials per block. On each trial, the participant made a choice between two faces presented side by side on the screen. One of the faces always had a happy expression, and the other face always had an angry expression, and the happy and angry faces appeared pseudo-randomly on the left or right of the screen.

When the participant had selected one of the faces, they were told either that they had won (a fictitious gain of 10 pence) or that they had lost (a fictitious a gain of 0 pence). The game was arranged such that within a given block, one of the faces (either happy or angry) won 40% of the time, while the other won 60% of the time. Participants were instructed that within a block, both faces would win some of the time, but that one face would win more often than the other. Participants were told to try and pick the face that won more.

Participants were instructed that the winning face could change between blocks. Across the entire experiment, the happy face had a higher probability of winning on two out of four blocks, as did the angry face; participants were not informed of this. The order of presentation of happy-win and angry-win blocks was randomized across participants within each age group. Both the happy and the angry face had the same identity within a block. Two male facial identities were used across the experiment: identity A was used for two out of the four blocks (one happy-win and one angry-win) and identity B was used in the other two blocks (one happy-win and one angry-win). Facial identity alternated between blocks.

The task was self-paced: participants were given an unconstrained duration to make a key press response on each trial, and the faces remained on the screen until a response was made. After a response had been made, the chosen face was presented at the centre of the screen along with text indicating whether the participant had won (10 p) or not won (0 p) that trial. A 5 kHz tone accompanied a win, and a 2.5 kHz tone accompanied a no-win (loss).

Figure 3.1 The Face Decision Task. On each trial, a happy face and an angry face were presented on the screen. Participants were instructed that they could win (10 p) or lose (0 p) by choosing one or other of the faces, and that within a block, both faces would win some of the time, but one face would win more often than the other. Participants were instructed to try and pick the face that won more. Within a given block, one of the faces (either happy or angry) won 40% of the time while the other won 60% of the time.



All participants were tested individually. Adult participants completed the experimental session in a quiet room at their home or place of work, or in a testing room at the laboratory. Adolescent participants completed the experimental session in a quiet room in school. Prior to completing the experimental task, participants completed a one-block practice task in which the stimuli were pictures of fruits rather than faces, and in order to facilitate participant familiarisation with the task, the practice task was easier than the experimental task: Each stimulus won 30% or 70% of the time. The total duration of the test session (Face Decision Task and WASI) was approximately 30 minutes per participant, depending on response times.

3.2.3 Data analysis

Data analysis was carried out using Matlab and SPSS. Analyses were based on those described in detail in Averbeck and Duchaine (2009). Specifically, because actual outcomes (a win of 10p or 0p) in the experiment were stochastic, it was possible for the face with a lower probability of winning in an individual block (40%) actually to be rewarded more often, especially over a short run of trials. Therefore in the first series of analyses, participant decisions were referenced to those of an 'ideal observer,' which optimally integrated outcomes across trials. In the second series of analyses, parameters representing hypothesized behavioural tendencies were added to the ideal observer model, resulting in an 'ecological observer model,' which more closely emulated participant behaviour.

3.2.3.1 Ideal observer model

Since the outcome in each trial of the Face Decision Task was either a win or a loss, the ideal observer was based upon a binomial model. The likelihood that the rewards were being generated probabilistically by an underlying probability θ_i was given by:

(3.1) $$p(D \mid \theta_i) = \theta_i^{r_i}(1-\theta_i)^{N_i - r_i}$$

Here, D is the observed series of outcomes, θ_i is the probability that face i (happy or angry) is rewarded, r_i is the number of times face i was rewarded, and N_i is the number of times face i was selected. This equation therefore provides the distributions over reward probabilities for each face. Specifically, as participants did not know the underlying probabilities, they would infer a distribution of possible probabilities, given the reward outcomes. For example, if one observed 7 heads in 10 coin tosses, it would be possible that the coin was fair (i.e. $p = 0.5$), but it would also be possible that the coin was unfair and had a probability of heads equal to 0.7. **Equation 3.1** would give the complete distribution over the probabilities for some set of outcomes.

To make a decision, participants had to decide which face would win more often. This decision step was operationalised by assuming that participants would compute the probability that face i was more often rewarded than face j. This was given by:

(3.2) $$p(\theta_i > \theta_j) = \int_0^1 p(\theta_i \mid D) \int_0^{\theta_i} p(\theta_j \mid D)\, d\theta_j\, d\theta_i \, .$$

The integral is over the posterior. For the ideal observer the prior was flat and, as such, the posterior is simply the normalized likelihood. As a decision rule, this probability was thresholded at chance. This gives the 'ideal choice' ($\hat{f}$).

(3.3) $$\begin{cases} p(\theta_i > \theta_j) > 0.5 & \hat{f} = i \\ p(\theta_i > \theta_j) < 0.5 & \hat{f} = j \end{cases}.$$

For the analyses that compared the decision of the participant to the 'choice' of the ideal observer, the case of $p(\theta_i > \theta_j) = 0.5$ was handled by incrementing both the happy and the angry choice of the ideal observer by 0.5. The extent to which adult and adolescent groups showed evidence of selecting the correct face as determined by the ideal observer was assessed by first accumulating contingency tables comparing the actual choices of adult and adolescent participants to those predicted by the ideal observer on a trial by trial basis, then by conducting one-sample *t*-tests on the percentage correct selections with reference to the ideal observer (test criterion: 50%, i.e. at-chance agreement with the ideal observer model). An independent samples *t*-test was used to investigate whether there was an age group difference in percentage correct choices. It was expected that adults would outperform adolescents on the task (Harbaugh et al., 2002; Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004).

3.2.3.2 Ecological observer model

The ideal observer gives equal weight to negative and positive feedback, and ignores the emotional expressions displayed in the stimuli. Human participants, however, may be differentially influenced by the valence of the feedback (Crone et al., 2008; van Duijenvoorde et al., 2008), and may be influenced by the socio-emotional content of the stimuli (Averbeck & Duchaine, 2009). Therefore, extra parameters were added to the ideal observer model to account for these potential biases, and this new 'biased' model was named the 'ecological observer'. This model contained four extra parameters which modelled (1) the impact of positive performance feedback on choice (see **Equation 3.4, parameter *a***), (2) the impact of negative performance feedback on choice (see **Equation 3.5, parameter *b***), (3) differential weighting of feedback based upon the emotional content of the face that was chosen (likelihood, or 'evidence bias'; see **Equations 3.4 and 3.5, parameter *c***) and (4) and a prior bias towards one of the faces (see **Equation 3.7, 3.8, parameter *d***)..

For rewarded trials (positive performance feedback), the reward value in the ecological observer was calculated as:

(3.4)
$$r^e_{happy}(t) = 0.5 + a + c$$
$$r^e_{angry}(t) = 0.5 + a - c$$

Whereas for unrewarded trials (negative performance feedback) it was calculated as:

(3.5)
$$r^e_{happy}(t) = 0.5 - b - c$$
$$r^e_{angry}(t) = 0.5 - b + c$$

The variables *a, b,* and *c* were fit as free parameters in the model. The superscript *e* indicates the reward calculated under the ecological model. The parameter *a* measures the amount that positive rewards are weighted. For the ideal observer, positive rewards are valued at 1, so $a = 0.5$. The parameter *b* measures the amount that negative feedback is weighted. For the ideal observer, negative feedback is valued at 0, so again $b = 0.5$ for the ideal observer model. Therefore, values of *a* and *b* below (above) 0.5 measure the amount that feedback is under (over) weighted, and values of *a* and *b* near zero indicate that positive or negative feedback are ignored. The variable *c* controls the bias introduced by the expression. If *c* is positive, positive feedback is given increased weight for the happy face and decreased weight for the angry face, and negative feedback is given decreased weight for the happy face and increased weight for the angry face. Therefore, positive values of *c* indicate that the participant is more willing to pick the happy face than would be expected based on the feedback alone.

The total reward in the block under the ecological observer for face *i* was then calculated as:

(3.6) $$r_i = \sum_{t=1}^{T} r_i^e(t) .$$

Thus, the total reward for each face, up to trial *T* in the current block was the sum of the biased reward values.

The prior bias was modeled using a Beta distribution to model the prior disposition towards each face as:

(3.7) $$p(\theta_i \mid \alpha_i, \beta_i) = \theta_i^{\alpha_i - 1}(1-\theta_i)^{\beta_i - 1}.$$

To get a good model fit, α_i and β_i were constrained by reducing them to one degree of freedom. This was done by estimating a single parameter, *d*, and then computing α_i and β_i as:

(3.8) $$\begin{aligned} \alpha_{happy} &= N_{prior}(0.5+d) \\ \alpha_{angry} &= N_{prior}(0.5-d) \\ \beta_{happy} &= N_{prior}(0.5-d) \\ \beta_{angry} &= N_{prior}(0.5+d) \end{aligned}$$

N_{prior} was set to 4. Allowing it to float freely resulted in unrealistic values for *d* (i.e. values which were outside +/- 0.5), and a Hessian that was not invertible, which indicated that the optimization algorithm was not finding the maximum likelihood estimates. Effectively, N_{prior} and *d* were correlated in the model, so one of these was fixed to eliminate this problem. The specific value of N_{prior} had minimal effect on the likelihood of the model.

The parameters of the model were fit to individual participants by maximizing the likelihood of the parameters, given the data. Thus, the following was calculated

(3.9) $$p(\theta_i \mid D, a, b, c, d) = \frac{p(D \mid \theta_i, a, b, c)\, p(\theta_i \mid d)}{p(D \mid a, b, c, d)}$$

And then the belief estimate under the ecological observer was calculated using

(3.10) $$p(\theta_i > \theta_j) = \int_0^1 p(\theta_i \mid D, a, b, c, d) \int_0^{\theta_i} p(\theta_j \mid D, a, b, c, d)\, d\theta_j\, d\theta_i .$$

There were no prior distributions placed over the parameters, in order for these terms to be completely data driven. The ideal observer can be recovered by setting *a* and *b* to 0.5, *c* to 0 and assuming a flat prior on θ_i, which could be achieved by setting N_{prior} to 0. Next, the likelihood of predicting the individual participant's sequence of decisions was maximized by adjusting the parameters *a, b, c* and *d*. The likelihood was given by:

$$\textbf{(3.11)} \qquad p(D^* \mid a,b,c,d) = \prod_{k=1}^{N} \left(p_k(\theta_i > \theta_j) l_k + (1 - p_k(\theta_i > \theta_j))(1 - l_k) \right).$$

Where $l = 0$ if the participant selected face *i* (e.g. the happy face) and $l = 1$ if the participant selected face *j* (e.g. the angry face). Here, D^* is the series of decisions of the participant, as opposed to the series of outcomes, which is collected in D in the previous equations. The likelihood was maximized using *fminsearch* in Matlab. The initial starting point for all parameters was generally zero, to minimize the probability of finding false positives when significance testing was carried out.

Initially, all four parameters (positive feedback, negative feedback, evidence bias, prior bias) were fit to the data. However, the evidence bias was not significant in either age group (one sample *t*-test (test criterion = 0): adult: $t_{13} = 0.99$, $p = 0.342$; adolescent: $t_{21} = 0.302$, $p = 0.765$), so a reduced model containing the three remaining parameters was subsequently fit. One-sample *t*-tests were used to assess significance within each age group of each of the three parameters, using a threshold for significance at $p < 0.05$.

3.2.3.3 Group differences in ecological observer model parameters

Of interest in the current study was the extent to which adolescent decisions in the Face Decision Task differed from those of adults, and what were the mechanisms underlying these differences. Therefore, age group differences in the three parameters of the final ecological observer model were assessed using independent-samples *t*-tests with a significance threshold of $p < 0.05$[6].

3.2.3.4 Gender differences

Finally, gender differences were investigated by conducting independent-samples *t*-tests with Bonferroni correction on all parameters of interest between male and female participants, irrespective of age group.

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[6] Note that it was not valid to assess the parameters within a single mixed design ANOVA, as they do not take values along a common scale.

Statistical thresholds were set at $p < 0.05$, two-tailed unless otherwise specified.

3.3 Results

3.3.1 Performance referenced to the ideal observer model

Participant decisions were initially referenced to those of a fictitious ideal observer who optimally integrated outcomes across trials. Contingency tables were created comparing the actual choices of adult and adolescent participants to those predicted by the ideal observer, on a trial by trial basis (**Table 3.1**). Results show that both age groups selected the correct face as determined by the ideal observer significantly above chance (adult group: 63.5%, *t*-test on percentage correct (test criterion 50%): $t_{13} = 3.76$, $p < 0.05$; adolescent group: 57.9%, *t*-test on percentage correct (test criterion 50%): $t_{21} = 5.92$, $p < 0.05$). As predicted, there was a significant difference between age groups in the percentage correct choices, with adults selecting a higher percentage of correct choices with reference to the ideal observer model (independent samples *t*-test: $t_{34} = 1.70$, $p < 0.05$, one-tailed)[7].

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[7] Note that this difference between groups is not due to slower learning of the task in adolescents relative to adults, as the pattern of percentage correct across blocks was similar between age groups. See **Appendix 3.1** for graph.

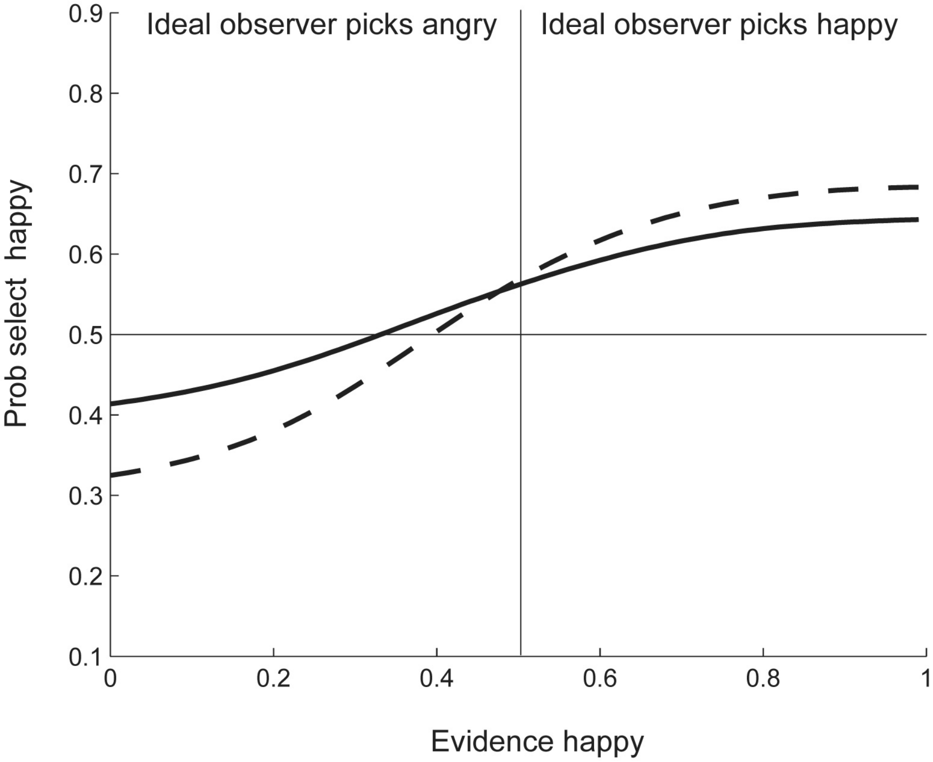
Table 3.1 Contingency table showing the choices made by the adult (left) and adolescent (right) age groups, referenced to the choices of the ideal observer. The top left cell in each age group table shows the number of trials on which participants picked the angry face when the model evidence indicated that the angry face was correct, from which we ascertain $p(a,a)$; top right shows the number of trials on which participants picked the angry face when the model evidence indicated that the happy face was correct, from which we ascertain $p(a,h)$; and so on for the bottom left and right cells. These probabilities were used to calculate, using Bayes' rule, the conditional probabilities that participants picked the 'wrong' face as determined by the ideal observer model, e.g. $p(h|a) = p(a,h)/p(a)$. Note that in cases where the ideal observer model had accumulated equal evidence for angry and happy (a tie), a value of 0.5 was added to each cell.

		Ideal observer choice				**Ideal observer choice**	
		Angry	Happy			Angry	Happy
Participant choice: ***Adult*** ***(N=14)***	Angry	431	248	**Participant choice:** ***Adolescent*** ***(N = 22)***	Angry	580.5	444.5
	Happy	284.5	492.5		Happy	519.5	743.5

In a previous study using the Face Decision Task, it was shown that although typical adults were able to choose the correct face as determined by the ideal observer significantly above chance, they also exhibited deviations from ideal behaviour. A specific deviation in behaviour shown by adult participants was that they were more likely to select the happy face when the ideal observer selected the angry face, than they were to select the angry face when the ideal observer selected the happy face (that is, $p(h|a) > p(a|h)$; Averbeck & Duchaine, 2009). The current study replicated this finding in adults, and extended it to a sample of adolescents: A comparison between the probability that participants chose the happy face when they should have chosen the angry face (adult mean $p(h|a) = 0.\ 419$; adolescent mean $p(h|a) = 0.483$) and the probability that participants chose the angry face when they should have chosen the happy face (adult mean $p(a|h) = 0.320$; adolescent mean $p(a|h) = 0.380$) was significant for each age group (paired t-tests, adult: $t_{13} = 6.22$, $p < 0.05$; adolescent: $t_{21} = 3.21$, $p < 0.05$). There was no group difference in mean bias (independent samples t-test: $t_{34} = 0.104$, $p = 0.918$).

These results indicate that both age groups showed a bias towards the happy face, such that they picked it more often than they should have, given the feedback about rewards captured by the ideal observer as the evidence in favor of one face or another. **Figure 3.2** illustrates this information, showing the fraction of times the adult (broken line) and adolescent (solid line) groups picked the happy vs. angry face (*y*-axis), as a function of the evidence given by the ideal observer in favor of the happy vs. angry face (*x*-axis). The choice function of both age groups intersects the line $y = 0.5$ at an *x*-value of less than 0.5, indicating that both age groups show a bias towards choosing the happy face.

Figure 3.2 Graph depicting the probabilities that the adult (broken line) **and adolescent** (solid line) **participants picked the happy vs. angry face** (y-axis) **as a function of the evidence given by the ideal observer in favour of each face** (x-axis)**.** The choice function of both age groups intersects the line y = 0.5 at an x-value of less than 0.5, indicating that both age groups show a bias towards choosing the happy face.



3.3.2 Ecological observer model of behaviour

The next analysis was carried out to test hypotheses regarding the nature and extent of specific deviations from ideal behaviour. In other words, this additional analysis was carried out to investigate the mechanisms that contributed to the (suboptimal) choices made by each group. This analysis was carried out via the following steps:

For each participant dataset, an ecological observer model was fit that consisted of the ideal observer model plus parameters representing hypothesized influences on behaviour. These comprised (1) the impact of positive performance feedback on choice (see **Equation 3.4, parameter *a***), (2) the impact of negative performance feedback on choice (**Equation 3.5, parameter *b***), (3) differential weighting of feedback based upon the emotional content of the face that was chosen (**Equations 3.4 and 3.5, parameter *c*:** subsequently dropped from the analysis due to non-significant effects in both groups; see **Methods, 3.2**) and (4) a prior bias to select one of the faces (**Equation 3.7, 3.8, parameter *d***). After extracting the value of each parameter for each participant, significance testing was conducted to evaluate the effect of each parameter on the behaviour of adolescent and adult groups.

Results showed a significant impact of negative feedback on choice, in both the adult and the adolescent groups (1-sample t-test: adult: $t_{13} = 3.05$, $p < 0.05$; adolescent: $t_{21} = 2.99$, $p < 0.05$; see **Figure 3.3**). There was no group difference in the impact of this variable ($t_{34} = 1.50$, $p = 0.144$). Therefore, both adults and adolescents were less likely to select a face once it had been associated with a non-reward, and there was no groups difference in the extent of this tendency.

However, the impact of positive feedback on choice differed between age groups. The adult group was more sensitive to positive feedback than was the adolescent group ($t_{34} = 2.23$, $p < 0.05$; see **Figure 3.3**); that is, the adult group showed a stronger tendency than did the adolescent group to select a face once it had been associated with a reward. One-sample t-tests showed that the adult group showed a marginally significant sensitivity to positive feedback, but the adolescent group was insensitive to positive feedback (adult: mean (s.d.) = .378 (.682); $t_{13} = 2.07$, $p = 0.059$; adolescent: mean = .028 (.229); $t_{21} = 0.57$, $p = 0.577$).

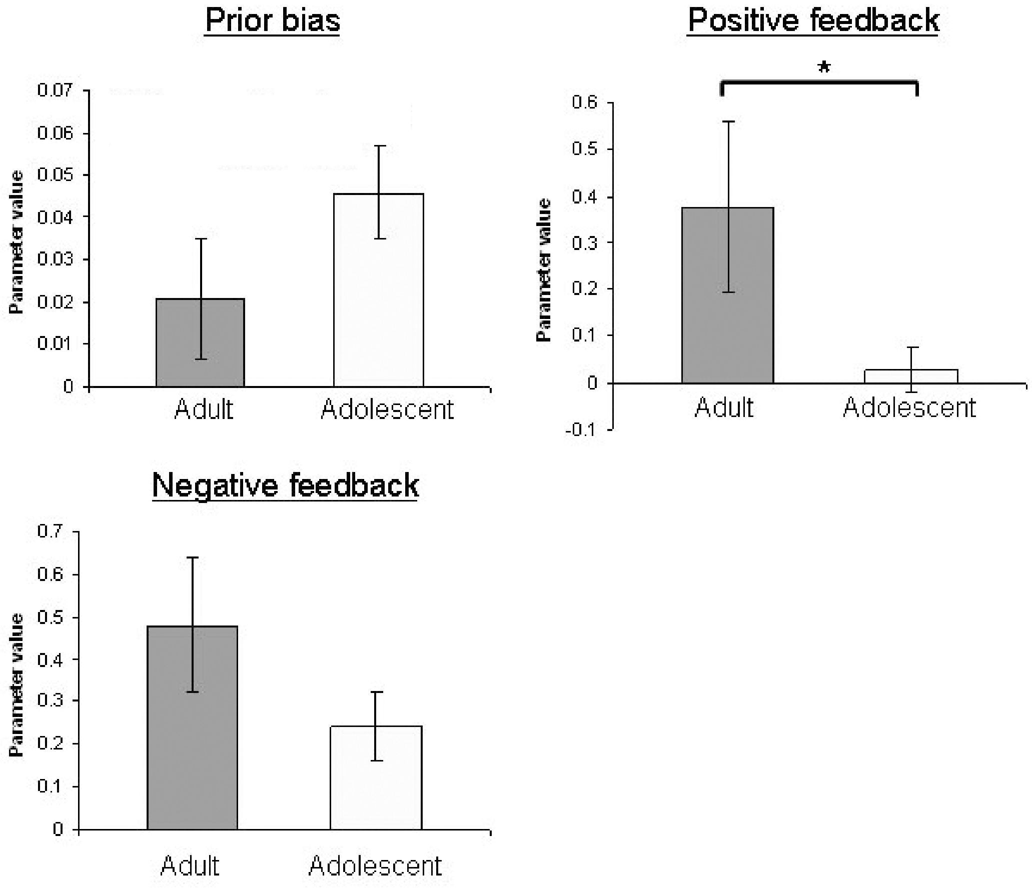
Contingency **table 3.1** indicates that participant choice was biased by the emotion shown in the face stimuli. Therefore, ecological observer model parameters encapsulating the effects of facial emotion on choice were evaluated. This indicated that the adolescent group showed a prior bias to select the happy over the angry face ($t_{21} = 3.42$, $p < 0.05$), whereas the adult group did not ($t_{13} = 1.50$, $p = 0.158$). There was no group difference in the strength of the prior bias parameter ($t_{34} = 1.21$, $p =$

0.236; see **Figure 3.3**), and as indicated in **Methods** section **3.2.3.2**, there were no likelihood bias effects. These results indicate that the pattern of behaviour shown in **Table 3.1,** whereby adolescents are more likely to select a happy face when the ideal observer selects the angry than vice versa, arises in part due to a prior belief that happy faces will be rewarded and angry faces will not be rewarded. This result extends findings from a previous study in adults using the Face Decision Task to a group of adolescent participants (Averbeck & Duchaine, 2009). The current study did not replicate the previous finding that adults show a prior bias to select the happy face (Averbeck & Duchaine, 2009). This issue will be addressed in the **Discussion**.

3.3.3 Gender differences

There was no evidence of gender differences in parameters of the ecological observer model.

Figure 3.3 Parameters of the ecological observer model in adults (dark bars) **and in adolescents** (pale bars). A parameter that is significantly different from zero can be said to influence participant behaviour. The top left graph shows the impact on decision-making behaviour of a prior bias to select the happy face. Adult behaviour results from a tendency to select a face which has previously been rewarded (top right graph), and a tendency to avoid a face that has previously been unrewarded (bottom left graph). Adolescent behaviour results from a biased expectation that happy faces will be rewarded (top left graph), and a tendency to avoid faces that have previously been unrewarded (bottom left graph). Adolescents are significantly less likely than are adults to persist in choosing a face that has resulted in a probabilistic win.



3.4 Discussion

The current study investigated adult and adolescent decision-making using a novel probabilistic decision-making paradigm in which rewards were associated with paired happy and angry faces. Decisions were analysed computationally. The results show that both adult and adolescent decisions showed evidence of bias by social cues, such that decisions were best described as a composite of both social (facial emotion) and utilitarian (win/loss feedback) factors. In adolescents, there was evidence that this social bias arose due to a prior expectation that happy faces would be rewarded, but the model failed to capture the mechanism of social bias in adults. However, adults outperformed adolescents in the task, and the results suggest that this is because the adolescents showed a relative and absolute lack of sensitivity to probabilistic wins. In the following discussion, it is suggested that the adolescent pattern of behaviour is consistent with a simple strategy of switching choices after incurring a loss.

3.4.1 Performance referenced to the ideal observer model

Participant decisions were referenced to those of a fictitious ideal observer who optimally integrated outcomes across trials, in order to gain a best estimate of the most highly rewarded (or ‘correct’) stimulus. The results of this referencing to the ideal observer showed that both adult and adolescent participants picked the correct stimulus at a rate significantly above chance. Therefore to an extent, both age groups were able to take into account utilitarian feedback information in order to choose the more highly rewarded face.

Although participants selected the correct face stimulus significantly above chance levels, the percentage of correct selections was not particularly high: adults selected the correct face stimulus on 63.5% of trials, and adolescents selected the correct face stimulus on 57.9% of trials. These figures are comparable to that reported in a previous study with adults using the Face Decision Task (66% correct; Averbeck & Duchaine, 2009), and indicate that the task was challenging for both adult and adolescent participants. Indeed, it is the relative difficulty of the Face Decision Task that enables subtle biases in behaviour to exert detectable effects (Averbeck & Duchaine, 2009).

The percentage of correct choices was significantly higher in the adult than in the adolescent group. This result was predicted, on the basis of evidence from previous decision-making studies showing that adults show superior performance on gambling tasks relative to adolescents (Harbaugh et al., 2002; Overman et al., 2004; Crone & van der Molen, 2004; Hooper et al., 2004). Many of these previous developmental studies have used the IGT. Unlike the current task, the IGT uses non-stochastic feedback i.e. win or loss feedback on each trial indicates whether the participant should maintain or switch strategy. In the Face Decision Task, feedback is stochastic in that choosing the more highly rewarded stimulus on a given trial may in fact result in a loss (in fact, it will result in a loss on two out of five trials). Therefore, the current study presents novel evidence that the ability to integrate stochastic feedback over multiple trials improves between adolescence (age 12-13 years) and adulthood (age 21-43). Furthermore, by creating a model of the ecological observer, we were able to investigate possible mechanisms driving this age group difference in performance (see section **3.4.4**, later).

3.4.2 Performance referenced to the ideal observer model: social bias

In the current task, a purely utilitarian or 'ideal' observer should ignore the expressions shown in the face stimuli and make decisions purely on the basis of the history of wins and losses associated with each stimulus. However, in the current study and previously (Averbeck & Duchaine, 2009), this was not the case. Instead, in both groups, decisions showed evidence of a social bias, such that participants were more likely to choose the happy face when the ideal observer model specified that they should choose the angry face, than they were to choose the angry face when the ideal observer model specified that they should choose the happy face. The current result replicates this previous finding in adults, and extends it to a group of adolescents.

It has been suggested that the social bias arises in this task arises because the face stimuli act as primary reinforcers (Averbeck & Duchaine, 2009; Matthews & Wells, 1999). Participants are willing to trade fictitious financial rewards in order to view a happy face, and to avoid viewing an angry face. An alternative suggestion is that the faces act as communicative stimuli: Viewing an angry face acts as a signal that behaviour should be suppressed or altered (Averbeck & Duchaine, 2009; Blair & Cipolotti, 2000).

Previous studies have suggested that, under some circumstances, adolescents may be more susceptible than adults to influence by social and emotional factors (McGivern et al., 2002; Gardner & Steinberg, 2005; Steinberg, 2008). In the current probabilistic decision-making task there was no difference between adolescents and adults in the extent of social bias arising from the emotional expressions shown in the face stimuli. It would be interesting to investigate whether a group difference in social bias would be observed in the Face Decision Task if the stimuli depicted same-age (adolescent) faces, rather than the mature adult faces used in the current study. One hypothesis is that adolescents might be more susceptible than are adults to social influence from same-age individuals (peer influence), but not to social influence from substantially older or younger individuals (Brown, 2004; Steinberg, 2008).

3.4.3 Performance referenced to the ecological observer model: the role of social cues

By referencing participant decisions to those of an ideal observer, it was shown that adult and adolescent behaviour was influenced by the emotion in the face stimuli. However, this result does not tell us anything about the nature of this influence. Therefore, a computational model of participant behaviour was created (the ecological observer model; see **Methods**), containing parameters that encapsulated two separate mechanisms by which the emotion shown in the face stimuli could affect participants' behaviour. These were: (1) a differential weighting of performance feedback based upon the emotional content of the face that was chosen (the evidence or likelihood bias), and (2) a prior bias to select one of the faces i.e. a prior expectancy that a particular face would be associated with a reward.

After fitting both parameters to adult and adolescent datasets, the differential learning (evidence bias) parameter was found to show weak effects across groups and was dropped from the analysis. Previously, this parameter was found to exert a relatively weak effect in adults, so the current result is not surprising (Averbeck & Duchaine, 2009).

The prior bias term was significant in the adolescent group, that is, adolescent participants exhibited a behavioural expectancy that rewards would be associated with the happy face. This expectancy resulted in a greater frequency of choosing the happy face when the ideal observer model specified that the angry face should be chosen than vice versa. This finding extends to a group of adolescents findings from an adult study conducted by Averbeck and Duchaine (2009). The current result suggests that the greater tendency to choose a happy face when the evidence indicates that the angry face should be chosen than vice versa in adolescents is due to a prior expectation that happy faces will be rewarded. This expectation, or bias, may reflect the operation of over-learned social cues present from infancy, or the strongly social context of many real-life decisions (Cosmides & Tooby, 2000; Haley & Fessler, 2005).

The adult participants did not show a prior bias to pick the happy face. However, there was no significant group difference in the impact of the prior bias term, which renders the adult finding difficult to interpret. One explanation is that whereas Averbeck and Duchaine's previous study, which tested a similar number of adult participants, included mainly university students, the current study tested an educationally diverse sample of participants whose heterogeneity introduced greater behavioural variance.

3.4.4 Performance referenced to the ecological observer model: Developmental differences in the role of performance feedback

Participant decisions were referenced to those of an ideal observer, and this showed that both adults and adolescents selected the correct stimulus at a level significantly above chance. However, adults selected the correct stimulus on a greater percentage of trials than did adolescents, which suggests that adults were more sensitive to utilitarian performance feedback (wins and losses) than were adolescents.

It has previously been suggested that the ability to take into account performance feedback continues to develop during adolescence (Huizinga et al., 2007; Byrnes et al., 1999; Crone & van der Molen, 2004) and that, in particular, the time-course of developing sensitivity to performance feedback may differ depending on whether the feedback is negative or positive (Crone et al., 2004, 2008; Huizinga et al., 2006; van Duijenvoorde et al., 2008). The current study investigated whether the age group difference in performance was due to a differential response to positive (win) and negative (loss) performance feedback, by creating a computational model of participant behaviour (the ecological observer model) containing separate parameters encapsulating the behavioural influence of positive ('you win 10 p') and negative ('you lose') performance feedback on behaviour.

Results of this analysis showed that the adolescent and adult groups differed in their behavioural sensitivity to performance feedback. Specifically, the adult group showed a stronger tendency than did the adolescent group to select a face once it had been associated with a reward. In both age groups, receiving negative feedback ('you lose') in response to choosing a face decreased the probability that the face would subsequently be chosen. Thus, adult decisions reflected a composite of both negative and positive performance feedback whereas adolescents showed a bias to respond to negative feedback only.

In the ecological observer model, the effect of performance feedback depended on the belief level of participants when the feedback was given (see **Methods**). If the evidence based on previous trials indicated that participants (as described by the ecological model) were nearly certain that a particular face was correct, then receiving positive feedback in response to the alternative face had very little effect on belief and subsequent behaviour. The effect of performance feedback also depended on current position within each 26-trial block. When participants had received very little performance feedback, at the beginning of a block, each new instance of feedback had a large effect. Later on in the block, each new instance of feedback had proportionally less effect (see Figures 2 and 5 in Averbeck & Duchaine, 2009). Therefore, the developmental result showing greater sensitivity to positive performance feedback in the adult than in the adolescent group may reflect a more mature ability to keep track of and update the history of rewards associated with each stimulus.

3.4.4.1 Adolescent response to positive vs. negative feedback and behavioural strategies

Results from the current study indicate that adolescents aged 12-13 exhibit an unbalanced response to positive vs. negative performance feedback. This finding is in general agreement with studies using rule-switch tasks, which have shown that children and adolescents exhibit greater behavioural asymmetry in their response to positive and negative performance feedback than do adults (Crone et al., 2004, 2008; Huizinga et al., 2006; van Duijenvoorde et al., 2008). However, data from the current study indicate that adults are more sensitive to positive feedback than are adolescents and that both age groups are equally sensitive to negative feedback, whereas studies using rule-switch tasks tend to report the opposite finding that children and adolescents respond better to positive than to negative feedback. For example, while performance in rule-switch tasks is consistently worse following negative ('switch') than positive ('maintain') feedback across age, performance is disproportionately worse following negative feedback in children aged 8-9 (Crone et al., 2008; van Duijenvoorde et al., 2008). However, the tasks used are quite different. In the next paragraph, a possible explanation will be suggested for the divergent findings.

It has been suggested that a developmental shift in strategy is responsible for the age-related changes in behaviour during decision-making tasks. In a study by Huizinga et al. (2007), it was shown that, whereas pre-adolescents (aged 6-9 years) were behaviourally sensitive to the frequency of loss only, adolescents aged 10-15 took into account both the frequency and magnitude of losses. Between mid-adolescence (13-15 years) and young adulthood (18-25 years), the tendency to take into account both the magnitude and frequency of losses continued to increase, and in addition there was evidence for an increase between adolescence and adulthood in the adoption of the maximally unbiased strategy of indifferent choosing between two options that are equally beneficial. Therefore, developmentally immature decision-making may be characterized by a particular set of biases, and focus on a subset of stimulus attributes. The pattern of adolescent behaviour in the Face Decision Task, whereby adolescents take into account negative but not positive feedback, is consistent with a simple behavioural strategy of switching choices after incurring a loss. In contrast, adult participants are able to integrate both wins and losses, showing an increased tendency to switch choices following a loss, but also a tendency to maintain the current choice following a win. The divergent findings between studies may be due to a difference in the strategy employed to accomplish distinct behavioural tasks (context-dependence of strategies). A future study could investigate the factors that cause adolescents to adopt a particular strategy in favour of another, as this could be relevant to adolescent decision-making in naturalistic contexts.

3.5 Conclusion

The current study was carried out to investigate decision-making in adults (aged 21-43) and adolescents (aged 12-13) using a probabilistic Face Decision Task in which happy and angry face stimuli were stochastically associated with reward. A computational method of analysis was implemented, which showed that the decisions of both adolescents and adults can be characterized as a composite of both social and utilitarian factors. Across age, participants showed a similar social bias to choose the happy face; however, the response to utilitarian performance feedback differed across age. Whereas adults integrated both positive and negative performance feedback (wins and losses) to either adjust or maintain ongoing selections, adolescents failed to respond to positive feedback, switching choices after incurring a loss. This suggests that age-related change in the ability to integrate positive and negative stochastic feedback may contribute to the development of decision-making abilities between adolescence and adulthood.

3.5.1 The next chapter

Adolescence is characterized by changes in decision-making, including in the ability to take into account performance feedback. In this chapter, effects of facial emotion cues on the decisions of adults and adolescents were shown. In general, adolescence is said to be characterized by changes in emotion and social understanding, including increased emotional self-awareness and self-consciousness. There is evidence that that pubertal development rather than chronological age *per se* contributes to increased social awareness and self-conscious affect (Simmons et al., 1973; Rosenberg & Simmons, 1975). Furthermore, it has been shown that puberty hormones organise the structure and function of the brain, including parts of the brain involved in emotion and social behaviour (Romeo, 2003; Cahill, 2006; Ahmed et al., 2008; Schulz et al., 2009; Peper et al., 2009; Neufang et al., 2009). Therefore, in the next chapter, a study is described that investigated pubertally-associated development in self-reported emotions. Participants aged 9-16 years were divided into groups on the basis of a puberty development questionnaire, and performed an emotional self-report task. In the task, participants were asked to imagine their emotional responses to a variety of social and basic emotional scenarios. Patterns of emotional responding were investigated, to evaluate the hypothesis that the onset of puberty marks an increase in the awareness of complex, or ‘mixed,’ emotions.

Chapter 4

Development of mixed social emotion understanding across puberty

In the previous chapter, a study was described that investigated the influence of facial emotion cues on decision-making in adolescents and in adults. Results showed that the decisions of both age groups reflected a preference for happy vs. angry faces. However, it has been suggested that developmental differences in emotion processing may be related to puberty as well as chronological age per se. *The current chapter describes a study that was carried out to explore the relationship between puberty stage and a measure of social-emotional understanding. Adolescent females aged nine to 16 years, grouped according to self-reported puberty stage, completed a task in which emotional responses were elicited in response to a series of emotional scenarios. The scenarios were designed to elicit social emotion (embarrassment and guilt) and basic emotions (anger and fear). The relative complexity or 'mixedness' of emotional responses was calculated and compared across puberty groups. This showed evidence that mixed emotion understanding differs across puberty stage, and that this difference may be specific to social emotions.*

4.1 Introduction

4.1.1 Development of social emotion processing

Social emotions, such as guilt, embarrassment and shame, are here defined as emotions that require the representation of another person's mental states (see also Olsson & Ochsner, 2008). In order to feel embarrassed, for example, you must believe that other people think your actions foolish. In contrast, basic emotions constitute immediate affective reactions that do not require consideration of the mental states of others. Studies have indicated that the understanding of basic emotions develops earlier in life than the understanding of social emotions. For example, Harris et al. (1987) have shown that five year old children were able to think of situations in which a basic emotion would be felt, but not situations in which a social emotion would be felt. By the age of seven, children were able to think of situations that would plausibly elicit social emotions, such as pride, jealousy and guilt.

The development of social emotion understanding beyond middle childhood is not well characterised. However, the period from middle childhood to adolescence is thought to be accompanied by an increase in multi-dimensional or abstract thinking about other people, and this includes thinking about the diverse factors that influence people's thoughts and feelings (Wainryb, 2001; Inhelder & Piaget, 1958). Therefore, this age period is likely to be accompanied by an increasingly complex understanding of emotions in self and in others. Furthermore, evidence from behavioural and neuroimaging studies suggests that the interpersonal, physical and hormonal changes associated with puberty may contribute to changes in the behavioural and neural correlates of social emotion processing. This evidence will now be summarised.

4.1.1.1 Social emotion development during puberty

The period of puberty and adolescence represents a time of acute socio-emotional change. Self-awareness and the self-concept undergo profound development during the adolescent years (Sebastian et al., 2008), and the perceived opinions of other social agents, especially peers, are influential in shaping the self-concept and in modulating social behaviour (Brown, 2004). There is evidence that social-emotional development may be linked to puberty stage as well as age *per se*, as self-report studies have shown that young adolescents (particularly girls) from early to mid-puberty are more self-conscious than both pre- and post-pubescent individuals (Simmons et al., 1973; Rosenberg & Simmons, 1975; Elkind & Bower, 1979). It has been suggested that the physical changes of puberty contribute directly to increased self-consciousness, through a mechanism of heightened vulnerability to environmental circumstances that threaten or impinge upon the self-image (Simmons et al., 1973). For example, changes in physical appearance as a result of puberty (e.g. growth spurt) may result in a change in the attitudes expressed by others when they interact with an adolescent, and this will affect the self-image.

Normative and pathological (e.g. Michaud et al. 2006) disruptions in the self-image at puberty are thought to stabilise into adulthood, as physical changes are assimilated into a new adult self-image. In summary, evidence suggests that the period of puberty is an important time for the development of emotions and self-consciousness, and may represent a time window of particular sensitivity to social emotions such as embarrassment and shame.

Recent brain imaging studies suggest that the neural processing of social emotion changes during puberty and adolescence. Structural MRI studies in humans show that certain prefrontal and temporal brain regions supporting emotion understanding and self-awareness undergo protracted structural development until late adolescence and beyond (Giedd et al., 1999; Sowell et al., 1999a,b; Gogtay et al., 2004; Shaw et al., 2008). In particular, there seems to be a reorganisation of grey matter in the frontal cortex that occurs at around the onset of puberty (Giedd et al. 1999; Shaw et al. 2008). Grey matter volume in the frontal lobe increases during childhood, reaching its peak at around puberty onset (approximately 11 years in girls and 12 years in boys), and is followed by a reduction in grey matter volume during the remainder of the pubertal transition. This is hypothesised to have functional consequences.

The majority of human structural MRI studies conducted to date have not included a measure of puberty stage. However, much work in non-human animals indicates a role for puberty in the structural reorganisation of the brain and in neural responsiveness to social and emotional stimuli (e.g. Cahill, 2006; Romeo, 2003). For example, in male rodents, testosterone is thought to mediate effects on cell survival and gross size of the amygdala and hypothalamus (Romeo, 2003). Effects of oestrogen on the hippocampus are also documented (Cahill, 2006). Furthermore, evidence from a number of human MRI studies that have measured puberty stage suggests that the onset of puberty may trigger, or coincide with, a phase of grey matter reorganisation in frontal and temporal regions. For example, Neufang et al. (2009) showed that grey matter volume in the amygdala varied as a function of circulating testosterone and oestrogen, as well as Tanner Stage of puberty (Tanner, 1971). Perrin et al. (2009) showed evidence that self-reported puberty stage correlates with white matter volume in males. Peper et al. (2008, 2009) report correlations between white matter volume and urinary concentrations of luteinising hormone in both sexes, and between grey matter volume and urinary oestradiol in females. This suggests that puberty stage, as well as simply age *per se*, is an important factor in the structural development of the brain during adolescence, including within brain regions implicated in emotion, social processing and self-awareness.

In addition to changes in the structure of the brain, puberty and adolescence is accompanied by changes in the functioning of brain regions involved in emotion and social awareness. For example, functional MRI studies have shown changes in activity within the mentalising system across adolescence (Blakemore, 2008; Pfeifer, 2009). Specifically, adolescents show greater activity than do adults within anterior rostral medial prefrontal cortex (arMPFC), a brain region involved in representing mental states (including feelings, beliefs and desires), during social cognition relative to control tasks (see **Figure 1.8**); including social cognition tasks explicitly assessing self-other-awareness (e.g. how others see you; Pfeifer et al., 2009).

A number of studies show evidence for a relationship between puberty and functional brain activity during social-emotional tasks. For example, fMRI studies comparing typical children/adolescents and those with endocrine disorders (e.g. precocious puberty) indicate a relationship between adrenal hormone levels and amygdala activity during emotional face processing in females (Ernst et al., 2007), and between testosterone levels and hippocampal responsiveness during emotional face processing in males (Mueller et al., 2009). One recent study in hormonally typical adolescent females has demonstrated a link between puberty stage and functional activity within the ventrolateral prefrontal cortex and amygdala during an emotional face processing task (Forbes et al., in press). Thus, evidence from fMRI studies lends support to the notion that there is a relationship between puberty hormones and the cognitive and neural processing of social-emotional information, via effects on the brain.

In summary, there is evidence that puberty stage influences social-emotional processing via psychological effects on the self-image, changes in social-emotional awareness, and effects on the structure and function of the brain. However, pubertal changes in social-emotional awareness are not well characterised. Therefore, the current study investigated the development of social emotion understanding across puberty. Specifically, and in order to limit the scope of this wide subject area, the current study focussed on a single aspect of emotion understanding, the understanding of mixed emotion. This concept will be explained in the following section.

4.1.2 Development of the understanding of mixed emotion

Mixed emotion understanding is the ability to acknowledge that a number of discrete emotions may be simultaneously elicited by a single event. Mixed emotions can be similar in valence, such as feeling both anger and disappointment at a missed opportunity. Mixed emotions can also be oppositely valenced, such as feeling both anger and relief upon the safe return of a wayward child.

There is a body of research on the understanding of mixed emotions in early childhood (Harter & Buddin, 1987; Harris, 1989; Larsen et al., 2007). Studies using a structured interview technique have shown that children around the age of five will deny that mixed emotions occur, or are even possible (Harter 1977; Harter 1983; Harter & Buddin 1987; Harris 1983; Larsen et al., 2007). For example, Harter and Buddin (1987) asked children between the ages of three and 11 to describe situations that would make them feel either opposite valence (happy, sad) or same valence (happy, excited) emotions at the same time. Children aged five reported statements such as "You'd have to be two different people to have two feelings at the same time". Between the ages of six and eight, children initially succeeded in describing situations in which two emotions would be felt in rapid succession, and subsequently, were able to describe situations in which two same-valence emotions would be experienced at the same time. Only between the ages of 10 and 11 were children able to describe situations in which two opposite-valence emotions would be felt simultaneously.

A recent study by Larsen and colleagues (2007) investigated mixed emotion between childhood and the onset adolescence, in children aged five to 12 years. Children were presented with a video clip from a fairy tale (Disney's The Little Mermaid), which culminated in a 'bittersweet' scene in which a father character is portrayed as having to say farewell to his daughter. Children were asked: (a) how the father character would feel, and (b) how the clip made them feel. Children were then given structured prompts to generate more than one emotion, and if they were able to do this, were then asked to indicate whether the emotions would be experienced sequentially or simultaneously (mixed emotions). Results showed a significant linear effect of age on measures of both the tendency to report that the father would experience mixed emotions, and the tendency to report personally experiencing mixed emotions. These data indicate that, in addition to developing a better conceptual understanding of mixed emotion in others (the father), older children also demonstrate a greater tendency to report mixed emotions in themselves.

The development of mixed emotion understanding during puberty has not previously been studied. However, as described above, the adolescent years mark an increase in multi-dimensional thinking about other people and the diverse factors that influence their thoughts and feelings (Wainryb, 2001). This may lead to developments in mixed emotion understanding across puberty, particularly for the understanding of social or self-conscious emotions.

It should be noted at this point that the conceptual understanding of one's own mixed emotions may be distinct from actually experiencing mixed emotions. Emotional ambivalence, that is, the expression of feeling positive and negative emotions simultaneously, is shown by infants aged around age one year (Ainsworth et al., 1978; see also Campos et al., 1983). The observation of a developmental time lag between displaying versus reporting mixed emotions has prompted the suggestion that mixed emotion understanding emerges as children learn to interpret the emotional reactions that they already express, through an increasingly mature appreciation of the complex causal relationships between situations and emotions (Harris 1989). The current study was primarily concerned with the understanding of one's own mixed emotions, insofar as they can be measured by self-report.

4.1.3 The current investigation: mixed emotion during puberty and adolescence

No study to date has investigated the understanding of mixed emotion across puberty. However as indicated above, there is evidence that pubertal development may influence emotional awareness via psychological mechanisms, and via effects on the brain. Therefore, it is reasonable to hypothesise changes in mixed emotion understanding across puberty, especially for social emotions.

The current study investigated the understanding of mixed emotions across puberty, for both social and basic emotions. Eighty-three participants aged between 9.5 and

16.33 years, divided into three Puberty Groups (early, mid- and post-puberty), were tested using an emotional self-report task. During this task, participants were instructed to imagine a series of emotional scenarios and to report how strongly they would feel each of four emotions (anger, fear, embarrassment and guilt) in response to the scenarios. Ratings along these four emotion scales were used to develop a measure of mixedness in emotional responding. It was hypothesised that mixed emotion understanding would develop across puberty.

The scenarios were designed to evoke primarily social emotions (embarrassment or guilt) or primarily basic emotions (anger or fear). In a sense, social emotions are inherently more mixed than are basic emotions, since social emotions require consideration of the mental states of more than one agent (self and other) whereas basic emotions do not. Thus, it was predicted that more highly mixed emotional responses would be observed for social relative to basic emotion scenarios, overall. However, given the changes in social-emotional understanding across puberty, and given the structural and functional developments within brain regions involved in social emotion processing, it was hypothesised that mixed emotional responses to social emotion scenarios in particular would continue to develop across puberty.

4.2 Methods

4.2.1 Participants

Eighty-three female participants aged 9.5 to 16.33 years old took part in the study. Participants were recruited via two comprehensive schools in central Birmingham: a secondary school and a primary feeder school which is located on a site adjacent to the secondary school. This ensured similar educational background and socio-economic status across the age range.

Participants were divided into three Puberty Groups on the basis of a physical development questionnaire that was a version of the Petersen Development Scale adapted from Carskadon and Acebo (Petersen et al., 1988; Carskadon & Acebo, 1993). The three puberty groups were: Early-puberty (*N* = 23, mean (s.d.) age = 11.7 (1.44), range = 9.5-14.08), Mid-puberty (*N* = 40, mean (s.d.) age = 13.0 (1.15), range = 10.5-15.33) and Post-puberty (*N* = 20, mean (s.d.) age = 15.2 (0.70), range =

13.67-16.33). One-way ANOVA showed that chronological age differed significantly between Puberty Groups ($F_{2,82} = 49.914$, $p < 0.05$).

The physical development questionnaire (see **Appendix 4.1**), which comprises questions about menarche and secondary sexual characteristics, was completed by secondary school age participants in a quiet room in school, and was posted to parents of primary school age participants for completion by the parent alone, the parent and child together, or the child alone, according to parental preference. Participants were assigned to the Early-puberty group if they circled 'no' in response to the question 'Have you started having periods?' and also in response to questions regarding secondary sexual characteristics (growth spurt, skin changes and underarm hair). Participants were assigned to the Post-puberty group if they circled 'yes' in response to the question 'Have you started having periods?' and also in response to questions regarding secondary sexual characteristics (growth spurt, skin changes and underarm hair). Participants who did not fit either of these criteria were assigned to the Mid-puberty group.

No information was elicited regarding participants' history of psychiatric or neurological disorder, attention-deficit/hyperactivity disorder, autism or dyscalculia.

The study was restricted to female participants only, for the following reasons. Firstly, the temporal profile of puberty and its impact on social behaviour differs between the sexes (Savin-Williams & Weisfeld, 1989, cited in Spear 2000; Giedd et al. 1999; Romeo, 2003), and therefore participants were restricted to one gender only, to maximise the power to detect an effect in a sample size limited by time and resources. Secondly, it is reported that there are differences between the sexes in expressing emotions (Kring & Gordon, 2007), which could impact on the self-report measure. Specifically, females are reported to be more expressive of most emotions relative to males. If this is the case, then an emotional self-report task might be more engaging for female than in male participants: we therefore selected female rather than male participants.

Prior to the study, written informed consent was obtained from a parent or guardian of adolescent participants. The study was approved by the local Ethics Committee. Participants were not paid.

4.2.2 Procedure

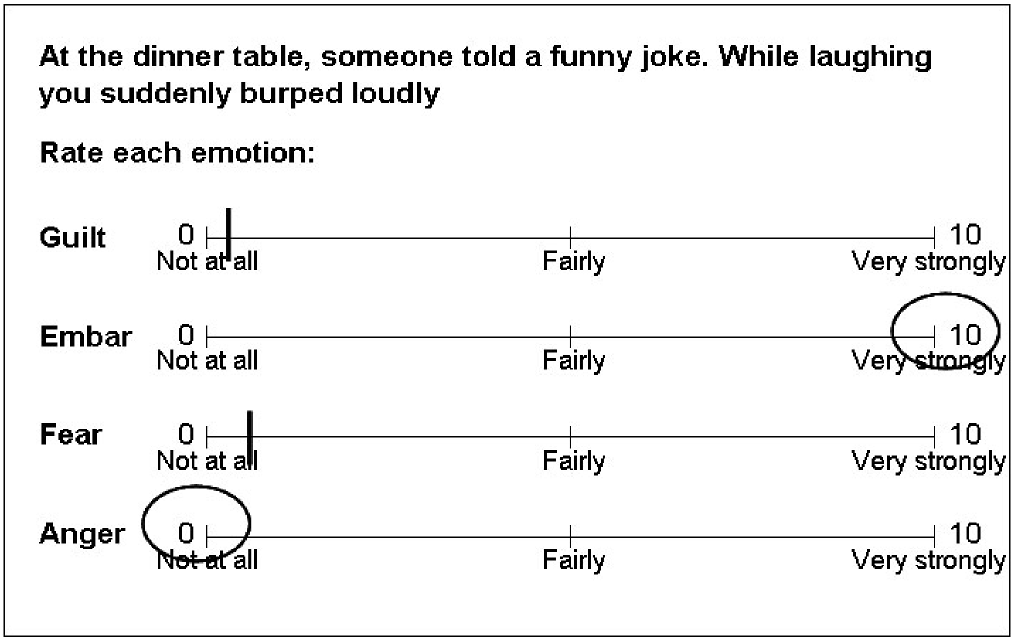
Participants were tested in groups of two to four in a quiet room in school, seated so they were unable to see each others' papers or confer. Participants were each given a paper-based task containing a series of sentences with attached emotion rating scales (see **Figure 4.1** and **Appendix 4.2**). The experimenter instructed participants that they would be reading a number of sentences describing situations in which they might feel emotions such as anger, fear, embarrassment and guilt. Before commencing the experiment, the experimenter defined each of the four emotions, giving examples of situations in which each might be felt (see **Table 4.1**, second column).

Table 4.1 Experimenter-defined emotions and example task scenarios. At the start of the session, the experimenter read aloud a definition and example of each emotion (*column 2*). During the emotion task, participants read a series of 32 emotion scenarios (examples in *column 3*) and rated their imagined emotional response using four rating scales. See **Appendix 4.2** for the complete set of emotion stimuli.

Emotion	*Definition and example*	*Example scenario from the task*
Anger	When you feel mad and annoyed at someone or something, *e.g. You might feel annoyed if the bus is late and you know you are going to mis your appointment*	You saw someone walk by the window. They threw rubbish into your garden
Fear	When you feel scared *e.g. You feel scared when you are walking in a dark quiet street*	You were riding your bike down a hill. Suddenly your brakes stopped working.
Embarrass-ment	When you feel you look silly in front of people *e.g. You trip and fall in front of your friends*	You ate too much cake at a party. You threw up in the living room in front of everyone.
Guilt	When you feel that you have done something wrong and feel bad about it *e.g. You broke your friend's mobile phone.*	You were meant to look after your little brother but you went out. When you got back he was crying.

During the experiment, participants silently read the scenarios while the experimenter read the scenarios aloud. Participants were instructed to imagine how they would feel in each scenario, and to rate their emotional response using four rating scales: anger, fear, embarrassment and guilt. Participants were told that they could place a mark anywhere they wished on the analogue scale, either by drawing a circle around 0 (I would feel the emotion not at all) or 10 (I would feel the emotion very strongly), or by placing a mark anywhere between 0 and 10 (see **Figure 4.1**). Each scenario was designed to evoke primarily one of four emotions: anger, embarrassment, fear or guilt. However, the stimuli were designed such that some sentences might reasonably evoke more than one emotion. The task consisted of 32 scenarios in total, of which 16 were primarily Basic emotion scenarios (eight anger, eight fear) and 16 were primarily Social emotion scenarios (eight embarrassment, eight guilt; see **Table 4.1** and **Appendix 4.2**). The order of emotion words in the rating section for each scenario was counterbalanced between participants. The order of emotions in the instruction phase and the order of scenarios in the task were counterbalanced between the small groups of simultaneously-tested participants.

Figure 4.1 Example of a task scenario. Each scenario was read aloud to participants, who were asked to imagine how they would feel if the scenario happened to them, and then to rate how strongly they would feel each of the four emotions, on a scale of 0 (not at all) to 10 (very strongly).



At the dinner table, someone told a funny joke. While laughing you suddenly burped loudly

Rate each emotion:

Guilt 0 Not at all — Fairly — 10 Very strongly

Embar 0 Not at all — Fairly — [✓ 10 Very strongly]

Fear 0 Not at all — Fairly — 10 Very strongly

Anger [✓ 0 Not at all] — Fairly — 10 Very strongly

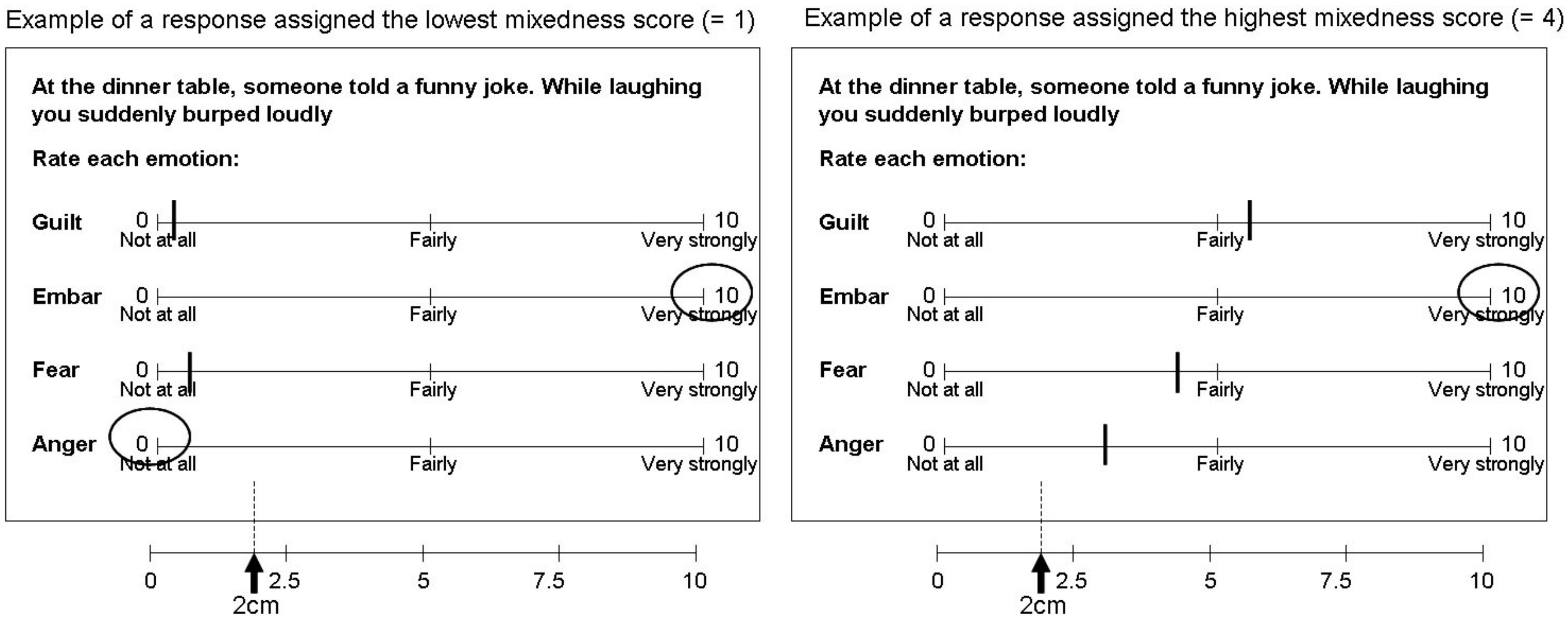
4.2.3 Data analysis

Each scenario was rated along four 10 cm emotion scales for anger, fear, embarrassment and guilt. In order to investigate mixed emotional responses, a measure was developed that encapsulated the extent to which participants used all four rating scales for Social and Basic emotion scenarios. The distance in centimetres of each emotion ratings along each of the four scales for each scenario was measured. These distances were therefore non-integer values ranging from 0 to 10 cm. Next, each scenario was coded according to the number of times a rating >2cm was given. This was an ultimately arbitrary cut-off point, but was chosen on the basis that ratings below 2cm indicate very weak reported feelings of a particular emotion. Rating response codes were assigned as follows:

Rating code 0: none of the four emotions rated >2cm
Rating code 1: one of the four emotions rated >2cm
Rating code 2: two of the four emotions rated >2cm
Rating code 3: three of the four emotions rated >2cm
Rating code 4: four out of four emotions rated >2cm

A response assigned a rating code of 4 is maximally mixed, since all four emotions are rated >2cm (see **Figure 4.2**). A rating code of 1 indicates a minimally mixed response, since only one of the four emotions is rated >2cm. Responses assigned a rating code of zero, i.e. in which no emotion was rated >2cm, were omitted from the analysis, since it was considered that this response pattern indicated a lack of emotion.

Figure 4.2 Scoring of responses. Each response (32 per participant: 16 Social, 16 Basic) was given a mixedness score that took into account how many times a rating >2cm had been given. A maximally mixed emotional response (e.g. below right) was one in which all four emotions were rated >2cm. We compared mean mixedness scores for social and basic emotion scenarios across puberty groups.


Example of a response assigned the lowest mixedness score (= 1)

Example of a response assigned the highest mixedness score (= 4)

For each participant, mean mixedness scores were calculated for Social and Basic emotion scenarios separately, resulting in a range of possible mean mixedness scores between 4 (maximum mixedness) and 1 (minimum mixedness). After checking for normality and excluding outliers lying >3 s.d. from the group mean for Social and Basic scenarios separately (one Basic, Post-puberty mixedness score excluded), mixed design repeated measures 3x2 ANOVA was conducted to test for Puberty Group differences in mean mixedness scores for Social and Basic emotion scenarios. There was one between-subjects factor with three levels: Puberty Group (Early-puberty, Mid-puberty and Post-puberty); and one within-subjects factor with two levels: Emotion Type (Social, Basic). A threshold for significance of $p < 0.05$ was used throughout, and *post hoc* Bonferroni-corrected t-tests were used to explore paired differences.

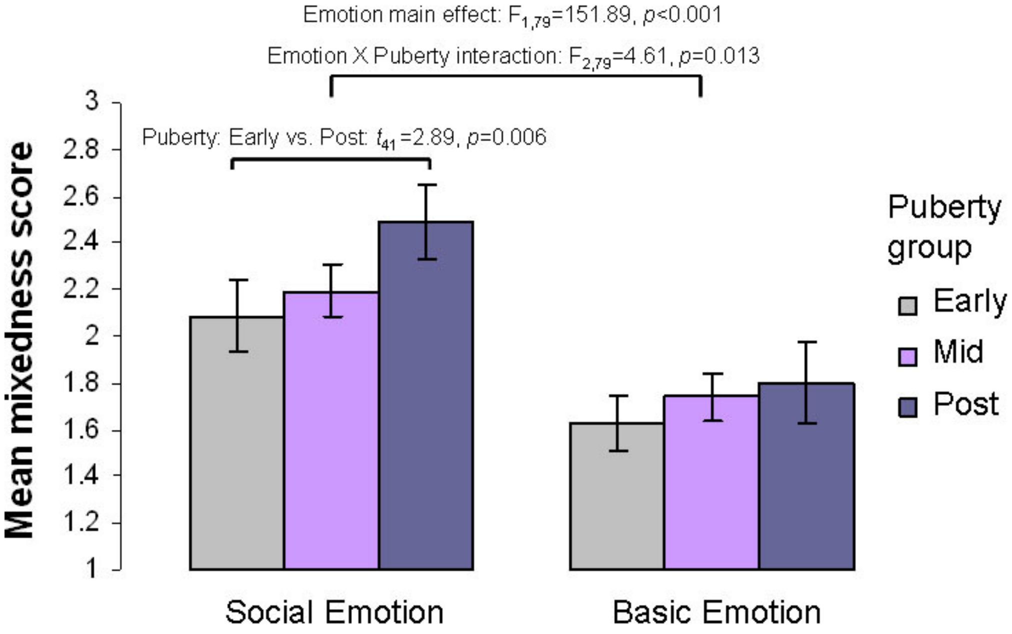
4.3 Results

Mean mixedness scores for Social and Basic emotion scenarios by Puberty Group are shown in **Figure 4.3**. Skew and kurtosis for Social and Basic mixedness scores were between +2 and -2, indicating that the distribution of the data was satisfactorily close to normal. One Post-puberty outlier >3 s.d. from the group mean for Basic mixedness was excluded. Repeated measures ANOVA revealed a main effect of Emotion Type on mixedness scores ($F_{1,79} = 151.89$, $p < 0.05$) such that more highly mixed emotional responses were given for Social than for Basic emotion scenarios (Social: mean (s.d.) mixedness = 2.21 (0.70); Basic: mean (s.d.) mixedness = 1.68 (0.61)). Paired samples t-tests showed that mixedness for Social Emotion scenarios was significantly higher than mixedness for Basic Emotion scenarios in all three Puberty Groups (Early: $t_{22} = 6.82$, $p < 0.05$; Mid: $t_{39} = 7.71$, $p < 0.05$; Post: $t_{19} = 7.02$, $p < 0.05$).

There was no main effect of Puberty Group ($F_{2,79} = 1.901$, $p = 0.16$). However, there was a significant interaction between Puberty Group and Emotion Type ($F_{2,79} = 4.614$, $p < 0.05$). The interaction was driven by higher mixedness scores in the Post-puberty group than in the Early-puberty group for Social Emotion scenarios ($t_{41} = 2.89$, $p < 0.05$), but not for Basic Emotion scenarios ($t_{40} = 1.07$, $p = 0.291$). The Mid-puberty group did not differ from the Early- or Post-puberty groups on mixedness score for either Social or Basic Emotions (Social: Early vs. Mid: $t_{61} =$

1.40, $p = 0.167$; Mid vs. Post: $t_{58} = 1.83$, $p = 0.072$; Basic: Early vs. Mid: $t_{61} = 1.40$, $p = 0.184$; Mid vs. Post: $t_{57} = 0.06$, $p = 0.955$).

Figure 4.3 Mean mixed emotion score for Social (left) and Basic (right) emotion scenarios in each Puberty Group. The maximum possible mixedness score was 4 (four emotions rated >2cm) and the minimum was 1 (one emotion rated >2cm). There was an interaction between Puberty Group and Emotion driven by higher mixedness scores for social relative to basic emotions in the Post-puberty group relative to the Early-puberty group.



4.4 Discussion

Previous research has demonstrated that the ability to acknowledge that a number of discrete emotions may be elicited by a single event, or the understanding of ‘mixed’ emotion, first emerges in middle childhood and continues to develop up to age 12 (Harter, 1983; Harter & Buddin, 1987; Harris et al., 1986; Larsen et al. 2007). On the basis that pubertal development is related to social awareness and self-conscious affect (Simmons et al., 1973; Rosenberg & Simmons, 1975), and in view of evidence that puberty hormones organise the structure and function of the brain, including regions of the brain involved in social behaviour and emotion (Romeo, 2003; Cahill, 2006; Schulz et al., 2009; Peper et al., 2008, 2009; Neufang et al., 2009), the current study investigated mixed emotion understanding across puberty. Mixed emotion understanding was assessed by taking a measure of the number of discrete emotions reported in response to imagined social or basic emotion scenarios.

4.4.1 Mixedness in social emotion

The current results revealed two main findings. First, and as predicted, responses were significantly more mixed for social emotions than for basic emotions across puberty groups. Social emotions, such as guilt and embarrassment, require the representation of another person's mental states. In contrast, no mental state representation is required to experience basic emotions. Thus, social emotions can be seen as inherently more representationally complex than basic emotions. Social emotions usually involve the consideration of social norms and conventions, as well as the social or moral implications of one's own actions. For example, the feeling of guilt involves the consideration of one's mental states and actions resulting perhaps in anger and shame directed at the self, but also the feelings of the wronged party and perhaps the real or imagined opinions of a judging third party. In contrast, the feeling of fear minimally involves an immediate emotional reaction to a threatening stimulus. Therefore, it can be concluded that the current result showing greater mixed emotional responding to social emotion scenarios than to basic emotion scenarios across all puberty groups reflects the greater inherent emotional complexity, and requirement for representing multiple mental states, in social relative to basic emotions.

4.4.2 Development of mixed emotion understanding

The second result in the current study was the significant interaction between puberty group and emotion condition. Results showed that the degree of mixedness in the emotional response to social, but not basic, emotion scenarios increased between early- and post-puberty. This result provides evidence for the continued development of mixed emotion understanding across the period of puberty, and indicates that this development may be specific to social emotions.

Previous research has shown that the understanding of basic emotions precedes the understanding of social emotions developmentally, and that mixed emotion understanding continues to develop during childhood and up to the age of 12 (Harris et al., 1986; Harter & Buddin, 1987; Larson et al., 2007). The results of the current study are consistent with, and extend, this developmental picture. This study showed no change in mixed emotion reporting for basic emotions after late childhood (early-puberty), at around 11 years, but a change in mixed emotion reporting for social emotions across the puberty range included here, and up to the age of 16. One caveat in the current study is that puberty stage was significantly related to chronological age. This issue should be addressed in a subsequent study in which groups are matched for age but differ in puberty stage (e.g. Tanner Stage of puberty). Methods and issues in pubertal measurement will be covered in the **Discussion** (section **7.2.3**).

Another caveat is with the method of assessing emotional mixedness. Previous studies using structured interviews are consistent with the current finding, and show that mixed emotion understanding shows protracted development throughout childhood (Harter, 1983; Harter & Buddin, 1987; Harris 1989; Larsen et al., 2007). Another study has shown age differences during adulthood in mixed emotion, specifically, in self-reported discomfort in response to watching adverts that elicit mixed emotions between young and older adulthood (Williams & Aaker, 2002). Thus, the result from the current chapter showing an increase in the reporting of mixed social emotions across puberty is consistent with extant findings. However, the method by which mixedness was assessed in the current chapter requires validation. The current result also needs to be replicated using the previously-employed structured interview technique.

4.4.3 Structural and functional brain development and puberty

Bearing in mind the abovementioned caveats, the current result showing evidence for the development across puberty of mixed emotion responding for social emotion scenarios could be a due to a number of factors. As mentioned in section **4.1.1**, there are changes in emotion and self-awareness during adolescence that have been attributed to pubertal development (Simmons et al., 1973; Rosenberg & Simmons, 1975; Michaud et al. 2006). In addition, development within regions of the brain implicated in self-awareness, social cognition and emotion occurs during adolescence, and studies suggest that at least some of these changes are related to puberty. For example, Neufang et al. (2009) showed that grey matter volume in the amygdala varied as a function of circulating testosterone and oestrogen, as well as Tanner Stage of puberty (Tanner, 1971), and Peper et al. (2008, 2009) report correlations between white matter volume and puberty hormones. Multimodal studies are now needed that investigate the separate contributions of puberty and chronological age to measures of structural brain development and social-emotional processing.

Changes in the structure of brain regions involved in emotion understanding and self-awareness are proposed to result in changes in the information processing carried out in these regions, and in the resultant cognitive and behavioural capabilities of the developing individual (Olesen et al., 2003; Schmithorst et al., 2005; Stevens et al., 2007; 2009; Olson et al., 2009). Several functional imaging studies have shown a change in patterns of neural activity during social cognition tasks between adolescence and adulthood. In particular, these fMRI studies have shown that activity in arMPFC decreases between adolescence and adulthood during social cognition (including social emotion) tasks (see Blakemore, 2008, for review; and **Figure 1.8** for meta-analysis). It is not known how these changes in social brain activity are related to puberty stage. One recent study has demonstrated a link between puberty stage and brain activity during a social task (Forbes et al., in press). An interesting avenue for future research will be to look at the relationships between puberty stage and functional brain activity during social emotion and mixed emotion tasks.

4.4.4 Mixedness and cognitive development

In addition to changes in hormones and neuroanatomy, the cognitive changes that occur during puberty and adolescence may pave the way for a more sophisticated understanding of mixed emotion. Early cognitive-developmental research suggested that the period from middle childhood to adolescence is characterised by an increased capacity for abstract reasoning (Inhelder & Piaget, 1958). This may result in a more sophisticated conceptual understanding of emotions, including mixedness in emotions. Relatedly, it has been suggested that the capacity for counterfactual reasoning continues to develop during adolescence (Baird & Fugelsang, 2004). This could enable development in mixed emotion understanding, since a single situation needs to be interpreted in different (e.g. counterfactual) ways for it to yield a mixed emotional evaluation. Finally, there is evidence that the social cognitive ability to take into account the perspectives of other social agents develops throughout the adolescent years (Dumontheil et al., 2009; Choudhury et al., 2006; see section **1.6.1.2).** In Dumontheil et al. (2009), continuing development during late adolescence was reported in a visual perspective task requiring the online use of mental state (visual perspective) information. Social emotions require one to take into account another individual's emotional perspective (thinking about how someone else would feel, or how they would think about you, as a consequence of your actions). Therefore, development of perspective-taking ability across puberty and adolescence might contribute to developments in the awareness of mixed feelings in social emotion situations. Further studies should investigate the relationship between cognitive development and the development of mixed emotion understanding, across puberty and age.

4.5 Conclusion

The current chapter presents evidence that mixed emotion understanding develops across puberty in females, and that this development may be specific to social emotion scenarios. As discussed above, this result could be due to changes in social-emotional awareness, cognition, and development in the structure and function of the brain. However, since puberty stage was related to chronological age in the current study, a follow-up study should be conducted in which puberty groups are matched for age. In addition, follow-up studies are needed to extend these findings in males and to evaluate the current methodology.

4.5.1 The next chapter

In the next chapter, the emotional scenarios described in the current chapter were adapted to investigate the neural processing of social and basic emotions using fMRI. In line with the current definition of social emotions as emotions that require mental state processing, it was predicted that participants would show activity during social vs. basic emotion processing within the mentalising system, comprising arMPFC, pSTS/TPJ and ATC. However, an age-related shift in activity has been reported within the mentalising system, between adolescence and adulthood (Blakemore, 2008; see section **1.5.2.2.2**). Relative to adults, adolescents (aged 10-18) show stronger activity within arMPFC during mentalising relative to control conditions. It was of interest to ascertain whether a comparable developmental shift would be seen for social vs. basic emotion processing. Therefore, in **Chapter 5,** adolescent and adult participants were scanned with fMRI while processing a set of social and basic emotion scenarios adapted from **Chapter 4,** and it was predicted that activity within the arMPFC would be stronger in adolescents than in adults during social vs. basic emotion processing.

Unlike in the current chapter, in **Chapter 5** participants were grouped according to age rather than puberty. This was because a relatively small number of participants took part in the fMRI study (19 adolescents and 10 adults) and the adolescent group was not considered large enough for subdivision according to puberty measures, and in addition given the age range (from 10 to 18 years) puberty stage was likely to correlate strongly with age. In addition, previous fMRI studies have shown an age-associated shift in activity within the mentalising system (puberty has not previously been assessed with regards mentalising), and it was of interest to conduct a study whose results could be compared with previous fMRI studies of mentalising and emotion.

Chapter 5

A functional magnetic resonance imaging study of social emotion processing in adolescents and in adults

The previous chapter described a study that investigated a behavioural measure of social emotion understanding across puberty. This showed evidence that the understanding of social emotions continues to develop across puberty, which was related to age in the experimental sample. In the current chapter, a study is described that investigated developmental differences in the neural processing of social emotions, using fMRI. Female adolescents and adults underwent fMRI scanning while processing scenarios in which either a social or a basic emotion would be felt. The results indicate that both age groups showed activity during social vs. basic emotion processing within brain regions implicated in mentalising, including the anterior rostral medial prefrontal cortex (arMPFC). However, a region of arMPFC was activated more strongly by adolescents than by adults for this contrast, and conversely the left anterior temporal cortex (ATC) was activated more strongly by adults than by adolescents. This set of results provides evidence that the neural strategy for social vs. basic emotion processing develops between adolescence and adulthood. In agreement with previous developmental fMRI studies of social cognition, activity shifts from frontal (arMPFC) to temporal brain regions with age. Further studies should investigate possible relationships between this age group difference in functional brain activity, and both cognitive and neuroanatomical development.

5.1 Introduction

5.1.1 fMRI studies of mentalising in adults

A number of functional imaging and neuropsychological studies in adults have shown that mentalising tasks, i.e. tasks that require processing of internal states including beliefs, feelings and desires, activate or rely upon a circumscribed set of brain regions known as the mentalising system (Frith & Frith, 2003). This set of brain regions comprises the anterior rostral medial prefrontal cortex (arMPFC), the posterior superior temporal sulcus (pSTS) bordering on the temporo-parietal junction (TPJ) and the anterior temporal cortex (ATC). The purported role of each of these brain regions is as follows:

The ATC, or temporal polar cortex, is thought to be a multimodal convergence zone where information about complex social (as well as non-social) stimuli is integrated with emotional signals (Olson et al., 2007). Functional imaging and neuropsychological studies (e.g. in fronto-temporal dementia patients) show evidence that the ATC represents complex semantic knowledge that is needed to navigate social situations and respond in a socially and emotionally appropriate manner. Thus, it has been suggested that the ATC represents 'social scripts', that is, semantic information relevant to specific social encounters (Frith, 2007).

The pSTS is responsive to complex movements, including biological movements of the eyes, face and hands. This brain region is more active when predictions based on these movements are in error, relative to when they are correct (Pelphrey et al., 2004a, 2004b). Therefore, the pSTS is thought to play a role in decoding social gestures and signals, and using these to form predictions of action or intent (Frith, 2007).

There seems to be overlap in the roles of the pSTS and the TPJ. However it has been suggested that, in contrast to the pSTS which decodes complex (including biological) movements, the TPJ is more concerned with spatial perspective information (Aichhorn et al., 2006; Frith, 2007). Spatial perspective information is necessary for understanding the epistemic states of social agents based on what they can and cannot see. This knowledge forms a part of mentalising, which is the ability to attribute mental states to social agents.

The arMPFC (BA 10) is also thought to play a role in representing or using mental state information. These include the emotional, motivational and epistemic mental states of self and other (Amodio & Frith, 2006; Gilbert et al., 2006). Frith (2007) has suggested that the more general role of arMPFC in representing mental states is to enable human communicative interactions. Perspectives on the role of arMPFC in mentalising will be discussed in a later section (**5.4.1.1**).

The mentalising system is of interest with regards emotion development, since it has been suggested that mentalising plays a key role in learning about emotions (Olsson & Ochsner, 2008). FMRI studies in which adult participants reflect upon social emotions have shown activity within components of the mentalising system (e.g. arMPFC; Moll, Grafman et al., 2005; Takahashi et al., 2004; Berthoz et al., 2002; Moll et al., 2002; Shin et al., 2000). In the current study a social emotion task was employed to investigate age-related changes in activity within the mentalising system.

5.1.2 Developmental fMRI studies of mentalising

Several recent fMRI studies have shown an age-related shift in activity within the mentalising system during social cognition tasks that have a mentalising component. In particular, a number of studies have shown evidence for an age-related decrease in activity within arMPFC during social cognition tasks with a mentalising component, between adolescence and adulthood (Blakemore et al. 2007; Pfeifer et al. 2007; Wang et al. 2006; Pfeifer et al., 2009; also between childhood and adolescence: Moriguchi et al., 2007). Specifically, activity within the arMPFC during mentalising relative to control tasks decreases between adolescence and adulthood (see Blakemore, 2008 for a meta-analysis). The current study was designed to test whether a comparable developmental shift would be observed for social emotions, which are defined as emotions which require the consideration of others' mental states.

Unlike in the previous chapter, participants in the current chapter were grouped according to age (adolescent vs. adult), rather than puberty stage. This was because a relatively small number of participants took part in the fMRI study (19 adolescents and 10 adults) and the adolescent group was not considered large enough for subdivision according to puberty measures, and in addition given the age range (from 10 to 18 years) puberty stage was likely to correlate strongly with age. In addition, since previous fMRI studies have shown an age-associated shift in activity within the mentalising system (puberty has not previously been assessed with regards mentalising), the aim of the current chapter was to conduct a study whose results could be compared with findings from previous fMRI studies. Findings from these previous studies will now be summarised.

Previous studies have demonstrated remarkably consistent differences in activity within the mentalising system between adolescence and adulthood (see **Figure 1.8**; Blakemore et al. 2007; Wang et al. 2006; Pfeifer et al. 2007; Pfeifer et al., 2009; see Blakemore, 2008 for a meta-analysis). For example, in Blakemore et al. (2007), adolescents (aged 12-18) and adults (aged 22-38) were scanned with fMRI while they read sentences about intentions (e.g. "You want to go to the cinema. Do you look in the newspaper?"), relative to sentences featuring unintentional physical events (e.g. "It has been raining all night. Is the ground warm?"). Results showed that part of arMPFC was more active in adolescents than in adults during intentions vs. physical events (**Figure 1.8**, blue dots), whereas the adult group showed more activity than did adolescents within a region of right STS during this comparison.

A similar developmental shift in brain activity was found using a task based on decoding communicative intentions (Wang et al., 2006). When children/adolescents (aged 9-14 years) and adults (aged 23-33 years) judged whether a series of communications were sincere or ironic (sarcastic), the child/adolescent group showed stronger activity within arMPFC than did adults (**Figure 1.8**, green dots). Adults activated more posterior brain regions, including the superior temporal and fusiform gyri, more.

Two studies that focussed on the processing of self-related sentences showed a similar age-related decrease in arMPFC activity. In Pfeifer et al. (2007), children (aged 9-11 years) and adults (aged 23-32 years) silently read phrases such as 'I like to read just for fun'. It was shown that the arMPFC and ACC were more active in children than in adults (**Figure 1.8**, yellow) when these phrases were applied to the self, relative to when they were applied to a familiar other (Harry Potter). The authors suggest that this pattern of activity may reflect a greater degree of online, self-reflective processing (performed by the arMPFC) in children vs. adults. In Pfeifer et al. (2009), adolescents (aged 11-14 years) and adults (aged 23-30 years) processed self-related sentences from their own vs. another's perspective (parent, best friend, or class; e.g. 'My best friend thinks I am good at maths'). Age group differences were observed in arMPFC (**Figure 1.8**, grey dot). Activity in the medial fronto-parietal network was also enhanced when adolescents took the perspective of someone more relevant to a given domain (e.g. ‘My mother/my class thinks I am popular at school’).

Finally, in a study conducted by Moriguchi et al. (2007), child and adolescent participants watched the Frith-Happé mentalising animations (Castelli et al., 2000), in which simple geometric shapes (triangles) move in such a way as to suggest the presence of mental states (e.g. a desire to hide from another triangle, a desire to play with another triangle). In control (non-mentalising) animations, the same geometric shapes move in a manner that suggests they are merely inanimate objects operating under the physical laws of gravity and inertia. Moriguchi et al. showed that, during mentalising relative to control animations, activity within a ventral portion of arMPFC decreased with age across childhood and adolescence (**Figure 1.8**, red dot), whereas activity within a more dorsal portion of arMPFC showed an age-related increase in activity. This study had no adult comparison group, but the age-associated changes in arMFPC activity are consistent with adolescent vs. adult studies.

Thus, a number of recent studies have consistently shown that activity within arMPFC during mentalising or social cognition tasks is greater in adolescents than in adults, whereas activity in certain posterior brain regions shows the opposite developmental pattern. The current study was designed to test whether this developmental pattern is also seen during a social emotion task.

5.1.3 Development of social emotion

As discussed in **Chapter 4**, the understanding of social emotion develops during early to middle childhood. Studies have shown that at around the age of seven, a child is able to describe situations in which a social emotion such as pride or embarrassment will be experienced (Harris et al., 1987). However at around puberty, individuals become increasingly aware of and concerned with people’s opinions of them, which suggests a heightened experience of social emotions or perhaps greater self-relevance of social emotions (Parker et al., 2006; Adams & Berzonsky, 2003; Elkind, 1967; Elkind & Bower, 1979; Zeman et al., 2006). The adolescent years are marked by an increasing dependence of the self-image upon perceived social reputation (Davey et al., 2008), especially reputation with peer groups (Brown, 2004). Finally, a variety of socialization experiences with parents and peers mean that adolescence is a key time for learning about how social emotions should be expressed in different social contexts (Zeman & Shipman, 1997).

5.1.4 Predictions

It is unknown whether the neural correlates of social emotion processing develop between adolescence and adulthood. To investigate this question, an fMRI study was conducted in which 19 adolescents (aged 10–18 years) and 10 adults (aged 23–32 years) were scanned as they read a series of sentences (adapted from **Chapter 4**) that were designed to elicit either a social emotion (guilt or embarrassment) or a basic emotion (disgust or fear). The replacement of anger by disgust was effected because it was decided that anger has a greater social component, and therefore a greater likelihood of eliciting mentalising, than disgust.

In line with previous studies, it was predicted that social vs. basic emotion processing would be associated with greater activity within the mentalising system, including arMPFC (Moll, de Oliveira-Souza, et al., 2005; Moll, Zahn, et al., 2005; Takahashi et al., 2004; Moll et al., 2002). A second prediction was that adolescents would activate arMPFC more strongly than adults during social relative to basic emotion processing, in line with previous developmental fMRI studies of mentalising (Blakemore, 2008).

In the current study, social and basic emotion scenarios pertained either to the self or to another person. This additional component was included because adults show differences in neural activity within parts of the mentalising system when processing emotions in the first vs. third-person perspective (Ruby & Decety, 2004), and because children show differences relative to adults in neural activity within parts of the mentalising system when processing statements in the first vs. third-person perspective (Pfeifer et al., 2007; 2009). For example, Pfeifer et al. (2007) showed that attributing statements to self vs. Harry Potter was associated with greater activity in arMPFC in children, but greater activity in the lateral temporal cortex in adults. Therefore the current study included both first and third-person social and basic emotion processing conditions. It was decided that third-person protagonist (the ‘other’) in this study would be the participant’s mother, as this protagonist would be sufficiently familiar to participants to enable the adoption of her emotional perspective, but sufficiently distinct from self that participants would not necessarily use their own perspective as an heuristic for their mother's (cf. Ruby & Decety, 2004). To quantify how similar each participant perceived herself to be to her mother, the NEO-V Factor Personality Inventory (Costa & McCrae, 1991) was completed from the self and mother perspective by participants (see **Methods, 5.2.2.4**).

The study was conducted with female participants only, for the following reasons. First, structural differences between the sexes have been observed within brain regions involved in emotion and social cognition (Schmithorst et al., 2008; Lenroot et al., 2007). Specifically, there are significant sex differences in the age at which grey matter volume peaks in the frontal and parietal cortices (11 years in girls vs. 13 years in boys; Giedd et al., 1999), and sex differences in trajectories of white matter development (Schmithorst et al. 2008). Second, sex differences have been observed in fMRI studies of emotion, in both adolescents and in adults (Yurgelun-Todd & Killgore, 2006; Hall et al., 2004; Killgore & Yurgelun-Todd, 2004), as well as in fMRI studies of specifically social emotion processing in adults (Moll, de Oliveira-Souza, et al., 2005; Moll, Zahn, et al., 2005). Third, there are differences between the sexes in expressing emotions (Kring & Gordon, 2007), which could either impact on, or be a result of, sex-specific neurocognitive strategies. This sex difference in emotion expression becomes accentuated with age, as sex-specific, culturally-defined rules for the expression of emotion are learned and internalised during childhood and beyond (see Brody, 1985, for a review). That is, the relationship between feeling and expressing emotions not only differs between the sexes, it also changes with age in a sex-specific way. Including both sexes would therefore have added unquantifiable variance to the between-groups fMRI data.

The choice of females rather than males in the current study was related to the documented sex differences in the expression of emotion. Specifically, females are reported to be more expressive of emotions than males (Kring & Gordon, 2007). If this is indeed the case, a social emotion task may be more engaging for female than for male participants.

5.2 Methods

5.2.1 Participants

Nineteen female adolescents (age range = 10.83 to 18.17 years; mean age = 14.8 years) and 10 female adults (age range = 22.92 to 31.83 years; mean age = 26.41 years) took part in the study. Adult participants were recruited from the local community via posters and a community website, as well as from the UCL Psychology Department participant database and via personal contacts. Adolescent participants were recruited from a database of interested potential volunteers who had previously contacted the research group, via teacher contacts in a number of London schools, and from the local community via posters (e.g. in the Institute of Education common room).

Participants had no history of psychiatric or neurological disorder, and none had received a diagnosis of attention-deficit/hyperactivity disorder, autism or dyscalculia.

Participants' general ability was assessed by administering the 4-subtest form of the Wechsler Abbreviated Scale of Intelligence (WASI; Harcourt, 1999), prior to or after the MRI scanning session. Mean (± s.d.) full-scale IQ (FSIQ) was 115.52 (± 6.63) for the adolescent group and 111.14 (± 14.10) for the adult group. An independent-samples *t*-test revealed no significant difference in FSIQ between groups ($t(22) = 1.052$, $p > 0.3$). Three adult participants did not complete the WASI, but since they had completed university-level education at a leading university, their general ability level was judged to be comparable to or higher than the mean for the adult group.

Prior to the study, written informed consent was obtained from adult participants, and from a parent or guardian of participants younger than 18. The study was approved by the local Ethics Committee. Adult participants received a modest financial compensation for their time and adolescent participants were not paid. Prior to the experimental session, it was ascertained that all participants had a living, healthy mother.

5.2.2 Experimental Design

The fMRI experiment had a 2x2x2 mixed factorial design. There were two within-subjects factors: Emotion (social emotion vs. basic emotion) and Protagonist (self vs. other perspective). The between-subjects factor was Group (adolescent vs. adult).

During functional MR-imaging, participants silently read 144 emotional sentences which described social or basic emotion scenarios pertaining either to self or mother (**Figure 5.1a**; see **Appendix 5.1** for the emotion scenarios). Participants were instructed to imagine each scenario. After reading each scenario, participants rated how much the protagonist (self/mother) would feel the named emotion, on a discrete rating scale from 1 (not at all) to 4 (very much), using a button box. The mean (plus the range) word length and the number of clauses in the emotion sentences were equated between conditions.

5.2.2.1 Emotion factor

Each scenario primarily featured either a social emotion or a basic emotion. The social emotions were embarrassment and guilt, and the basic emotions were disgust and fear. Emotion sentences from **Chapter 4** were adapted to maximize the difference in mentalising requirement between social and basic emotion conditions. Therefore, the basic emotion sentences featured immediate and viscerally evocative situations. Whereas in **Chapter 4**, the basic emotions were anger and fear, in the current chapter the basic emotions were fear and disgust. The replacement of anger by disgust was effected because it was decided that anger has a greater social component, and therefore a greater likelihood of eliciting mentalising, than disgust.

The sentences were chosen from a larger set of sentences that was presented in the form of a questionnaire to 17 female adolescents and 7 female adults (see **Appendix 5.2** for pilot questionnaire). Pilot participants, who were different from the participants in the fMRI study, rated their emotional response to each sentence on a discrete rating scale from 1 (I would not feel the emotion at all) to 4 (I would feel the emotion a lot). For all sentences in the pilot questionnaire, the emotion to be rated (embarrassment, guilt, disgust or fear) was specified, and the protagonist in each sentence was the self ('you'). Any sentence that was given a rating of one by any participant in the pilot study was discarded. Then, for each age group, the remaining sentences were ranked according to group mean emotion ratings. Sentences that were rated highly by both age groups were chosen for use in the fMRI study.

Sentences rated highly by one group only were discarded. This was to ensure that the emotion sentences used in fMRI were similarly effective for both age groups.

Both social and basic emotion scenarios featured the main protagonist plus one other person (e.g. a friend, family member or unnamed onlooker). This was to ensure that the difference between social and basic emotion conditions was the need to *take into account* another person's mental state, not the mere presence of another person in the scenario (which is thought to result in activity in TPJ; Abraham et al. 2008, Coricelli & Nagel, 2009).

5.2.2.2 Protagonist factor

The protagonist in each scenario was either the participant (self, or 'you') or the participant's mother (other, or 'your mum'). The same emotional scenarios were used for the self and other conditions, but sentence construction and vocabulary was altered to preserve equal word length between conditions.

5.2.2.3 Task structure

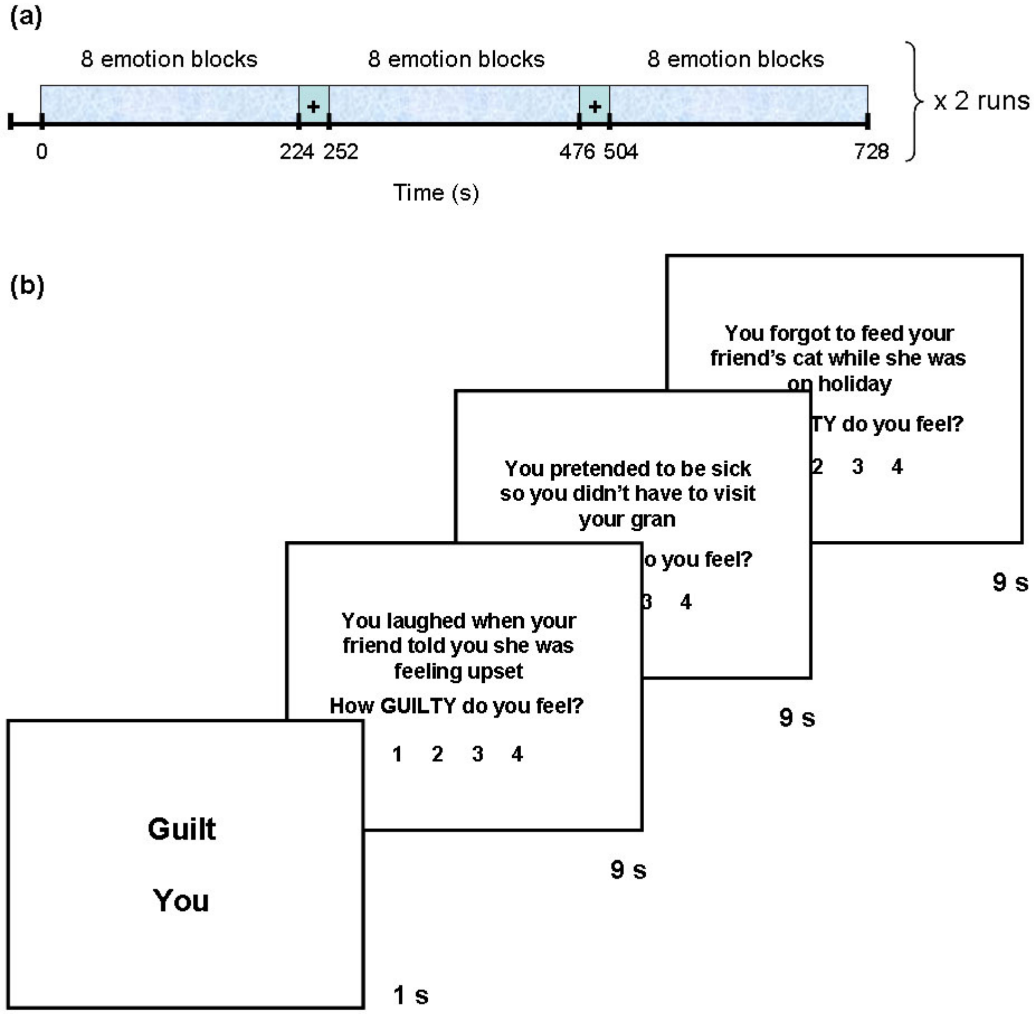
Sentences were presented in blocks of three (see **Figure 5.1b**). Participants had 9 seconds to read silently, imagine, and rate their response to each emotion sentence. The experiment was blocked by emotion and protagonist such that within a block, all three scenarios featured the same emotion (disgust, embarrassment, fear, or guilt) and the same protagonist (self or other). This was to maximise the strength of the imagined emotions, while minimising carry-over effects between sentences featuring different emotions and protagonists. Sentence, block and condition orders were fully randomized.

At the start of each block, a 1 second cue screen informed participants which emotion and which protagonist the proceeding three sentences would feature. This was to minimise the effect on BOLD response to the first sentence in each block of possible age differences in latency to identify the relevant emotion/protagonist.

Each 12 minute session of the fMRI experiment contained 24 emotion blocks, and each block lasted 28 sec (see **Figure 5.1a**). In addition, there were two 28 sec visual fixation blocks per session, occurring one third and two thirds of the way through each of the two sessions. Stimulus presentation was programmed in Cogent (www.vislab.ucl.ac.uk/Cogent/index.html) running in Matlab 6.5, which recorded participant responses.

Prior to scanning, all participants completed a practice session outside the scanner room. The practice session consisted of four emotion scenarios (one from each of the four specific emotions). The sentences used in the practice task did not appear inside the scanner.

Figure 5.1 Structure of the experiment (a) Participants completed two runs of the task, lasting 728 sec per run. During each run, 24 emotion blocks and 2 fixation blocks were presented. There were three emotion sentences per block **(b)**, which appeared for 9 sec each; participants therefore had 9 sec to read and respond to each sentence. Each emotion block was preceded by a 1 sec cue screen. Within a block, all three sentences featured the same emotion (disgust, embarrassment, fear or guilt) and the same protagonist (self or mother).



5.2.2.4 Participants' perceived similarity to their mothers

To quantify any age-related differences in participants' perceived similarity to their mothers, which might cause between-group differences in brain activity in the protagonist condition e.g. within arMPFC (Mitchell et al. 2006), participants' perceived similarity to their mothers was quantified by administering after the scanning session two separate versions of the NEO-V personality questionnaire (Costa & McCrae, 1991). The two versions of the questionnaire were identical except that in one version participants answered personality questions about themselves, and in the other version they answered the same questions about their mother.

5.2.3 Data Acquisition

A 1.5-T Siemens Sonata head MRI scanner was used to acquire both 3-D T1-weighted fast-field echo structural images and multi-slice T2*-weighted echo-planar volumes, with blood oxygenation level-dependent (BOLD) contrast. Each T2 functional volume was composed of thirty-three 3-mm axial slices with a 1.5-mm gap and in-plane resolution of 3x3 mm, angled at 308 to cover the whole brain and minimize signal dropout from the facial sinuses. Repetition time was 3 sec. Functional volumes were acquired in two scanning sessions of approximately 12 minutes each, in which a total of 554 volumes were acquired, or 277 scans per session. The acquisition of a T1-weighted anatomical image occurred after the two functional scanning sessions for each participant. The total duration of scanning was approximately 35 minutes for each participant.

5.2.4 Data Analysis

Behavioural and fMRI data were analyzed by collapsing the four emotions – disgust, embarrassment, fear, and guilt – into two emotion conditions, social and basic. This was because the experimental hypotheses related to differential neural effects of social vs. basic emotion, not to the neural effects of specific emotions.

Behavioural data (emotion ratings and NEO-V) were analyzed using the SPSS statistical package. Emotion ratings were analysed to investigate main effects of Emotion and Protagonist in both groups, as well as two- and three-way interactions between Emotion, Protagonist, and Group, using mixed-model repeated measures

ANOVA with within-subjects factors Emotion and Protagonist and between-subjects factor Group. NEO-V data were analysed to yield perceived self-mother difference (PSMD) scores, by calculating the square root of the summed squared self-mother difference scores for all five dimensions of the NEO-V 'self' and 'mother' personality questionnaires. A median test of PSMD score vs. age group, and linear regression between PSMD score and age, were carried out to investigate possible relationships. A significance threshold of $p < .05$ was used for behavioural data.

Imaging data were analyzed using SPM2 (www.fil.ion.ucl.ac.uk/spm). The first six functional image volumes from each run were discarded to allow for T1 equilibrium effects, leaving 542 image volumes per participant. Preprocessing included rigid-body transformation (realignment) and slice timing to correct for head movement and slice acquisition delays. The images were then stereotactically normalized into the standard space defined by the Montreal Neurological Institute (MNI) template using the mean of the functional volumes, and smoothed with a Gaussian filter of 6 mm full width at half maximum to increase the signal-to-noise ratio and facilitate group-level analysis. The time series for each participant were high-pass filtered at 128 sec to remove low-frequency drifts.

The analysis of the functional imaging data entailed the creation of statistical parametric maps representing a statistical assessment of hypothesized condition-specific effects (Friston et al., 1994b), which were estimated with the general linear model. The effects of interest were the four scenario block types (2 emotion x 2 protagonist) and the visual fixation blocks. The six realignment parameters were modelled as effects of no interest, in order to account for any group differences in head movement. Each component of the model served as a regressor in a multiple regression analysis for each participant. The resulting parameter estimates for each regressor at each voxel were then entered into a second level analysis, where 'participant' served as a random effect in a within-subjects ANOVA, enabling population inferences to be made.

The main effects and interactions between conditions were specified by appropriately weighted linear contrasts, and determined using the *t*-statistic on a voxel-by-voxel basis. Statistical analysis at the second level was performed for each group separately to first examine the main effect of all scenarios vs. fixation in order to check that the expected brain regions (visual, motor, reading) were activated in this contrast. Next, in order to test the main hypotheses, the three-way interaction between emotion, protagonist, and group was investigated. A significant result permitted the implementation of a series of planned *t*-contrasts to investigate the main effects of condition for the two groups separately, as well as two-way interactions between group and condition. Specifically, for each group separately, *t*-tests were carried out to investigate the main effect of Emotion (social > basic, basic > social) and Protagonist (self > other, other > self), interactions between Group and Emotion, using the contrast [adult (social > basic)–adolescent (social > basic)], and *vice versa*, and interactions between Group and Protagonist, using the contrast [adult (self > other)–adolescent (self > other)] and *vice versa*. Finally, we the interaction between Protagonist and Emotion was investigated in each Group separately using the contrasts [adult ([self > other]–[social > basic])] and *vice versa*, and [adolescent ([self > other]–[social > basic])] and *vice versa*.

Statistical contrasts were used to create an SPM{t}, which was transformed into an SPM{Z} and thresholded at *P* < .05 (corrected on the basis of the theory of random Gaussian fields for multiple comparisons across the whole brain volume examined). Regions are reported that survive correction at *P* < .05, as well as activations within regions for which there was an *a priori* hypothesis: For these regions, a small-volume correction was applied (SVC; 12 mm radius sphere, unless otherwise specified) at *P* < .05. *A priori* regions of interest were the arMPFC (Blakemore et al., 2007; Gilbert et al., 2006, 8 mm), the pSTS/TPJ (Aichhorn et al. 2006; Frith & Frith, 2003), the ATC (Blakemore et al., 2007; 8 mm), and the precuneus (Blakemore et al., 2007) for social > basic emotion; the anterior insula (Moll et al., 2002) and the inferior frontal gyrus (Moll, de Oliveira-Souza, et al., 2005; Moll, Zahn, et al., 2005) for basic > social emotion; the postcentral gyrus for self > other (Ruby & Decety, 2004); and the medial fronto-polar gyrus, the left STS, the left ATC, the posterior cingulate gyrus, and the right inferior parietal lobule for other > self (Ruby & Decety, 2004).

5.3 Results

5.3.1 Behavioural Results

5.3.1.1 Emotion Ratings

Participants rated the extent to which the protagonist of each scenario (self, mother) would feel the named emotion on a discrete rating scale from 1 (not at all) to 4 (very much). Mixed design, repeated measures 2x2x2 ANOVA showed that mean emotion ratings did not differ between groups ($F_{1,26} = 0.60$; $p > 0.4$; see **Table 5.1**). There were no significant two- or three-way interactions between age Group and the factors Emotion and Protagonist (all $p > 0.2$). For both groups, basic emotion scenarios were given higher ratings than social emotion scenarios ($F_{1,26} = 9.44$, $p < 0.05$), and other scenarios were given higher intensity ratings than self scenarios ($F_{1,26} = 4.47$, $p < 0.05$). Therefore, there is no evidence for any age Group differences in the intensity of imagined emotions.

Table 5.1 Mean and standard deviation of the emotion ratings (from 1 to 4), by Group (adult, adolescent), Emotion (social, basic), and Protagonist (self, other). Ratings for basic emotions were significantly higher than for social emotions, and ratings from the other perspective were significantly higher than from the self perspective. There were no significant group differences, and no interactions.

Emotion	Protagonist	Group	Mean	Std. Deviatio
Social	Self	Adult	2.98	0.349
		Adolescent	2.94	0.397
	Other	Adult	3.34	0.343
		Adolescent	3.07	0.514
Basic	Self	Adult	3.16	0.283
		Adolescent	3.11	0.417
	Other	Adult	3.29	0.395
		Adolescent	3.24	0.427

5.3.1.2 Perceived Self–Mother Difference

Data were not available for one adult participant. For the remaining participants, perceived self-mother difference (PSMD) scores were computed by calculating the square root of the summed squared self-mother difference scores for all five dimensions of the NEO-V 'self' and 'mother' personality questionnaires. This yielded PSMD scores ranging from 5.57 to 37.03 (mean ± SD = 20.34 ± 9.14). A median test of the PSMD scores revealed no difference between adult and adolescent participant groups ($X^2 = 0$, $p > 0.99$). Linear regression revealed no relationship between age and PSMD score ($r^2 = .009$, $p > 0.6$). There is therefore no evidence for age group differences in perceived similarity of self to mother.

However, possible neural effects of perceived similarity of self to (m)other were of interest. We therefore used the PSMD scores as a regressor in the SPM analysis (see **Appendix 5.3**).

5.3.2 Functional Imaging Results

Data from both imaging runs of one adolescent participant and one run of a second adolescent participant were excluded due to excessive head movement (> 5 mm). After these data were excluded, there were no statistical differences in mean head movement between the two age groups for any of the six dimensions of movement (independent-samples *t*-tests ($df = 26$): all $p > 0.15$). However for caution's sake, the six realignment parameters were modelled as effects of no interest in the general linear model.

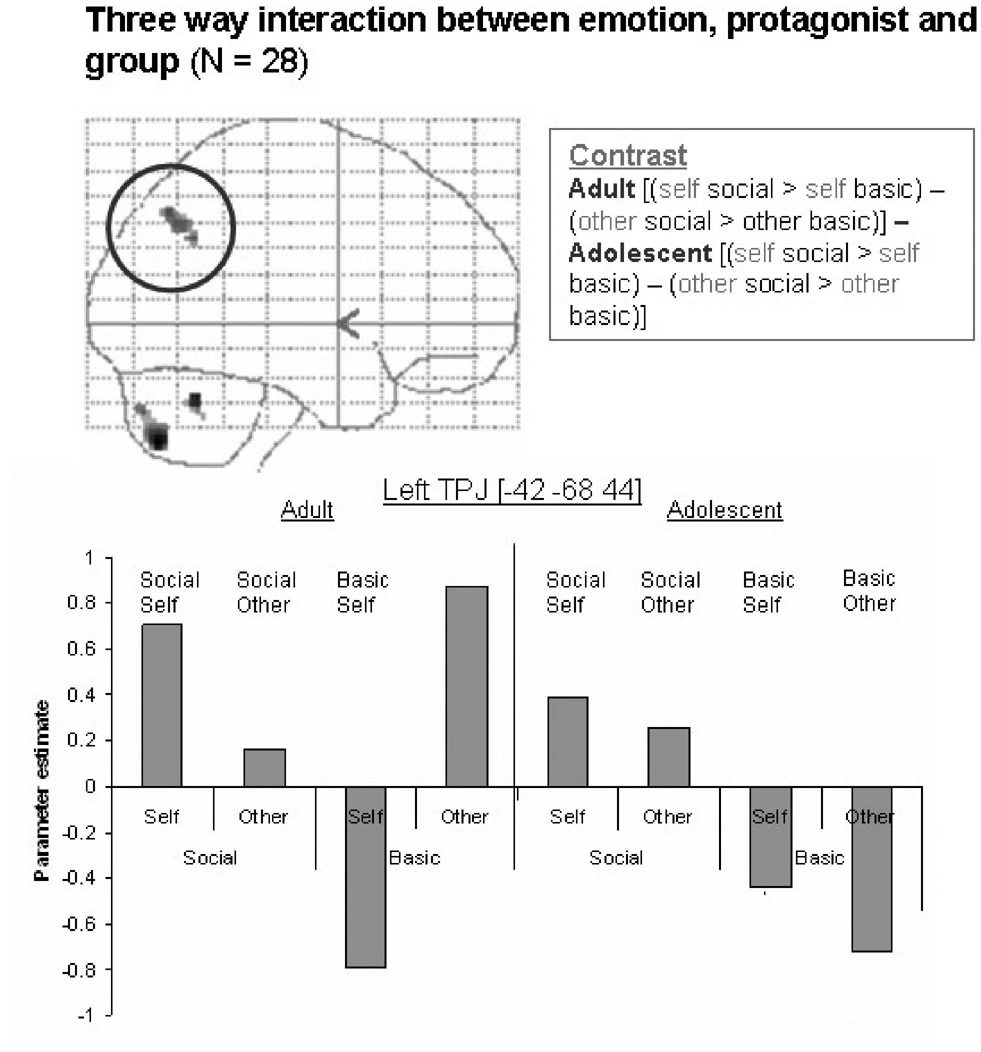
5.3.2.1 Main effect of sentences vs. visual fixation

In both adult and adolescent groups, the main effect of all scenarios vs. visual fixation resulted in expected activation of visual and motor areas, as well as areas involved in reading.

5.3.2.2 Three-way interaction between Emotion, Protagonist, and Group

The three-way interaction between Protagonist (self > other), Emotion (social > basic), and Group (adult > adolescent) yielded a significant region of activation in the left TPJ (MNI coordinates [-42 -68 44]; $Z = 3.60$, $p < 0.05$ SVC; **Figure 5.2**, top left. For illustration purposes, parameter estimates are shown relative to visual fixation). Activity in this region was driven by a main effect of social > basic emotion in adolescents, and an interaction between emotion and protagonist in the adult group (**Figure 5.2**, bottom). The opposite contrast with respect to Group (adolescent > adult, social > basic, self > other) did not yield any significant activations.

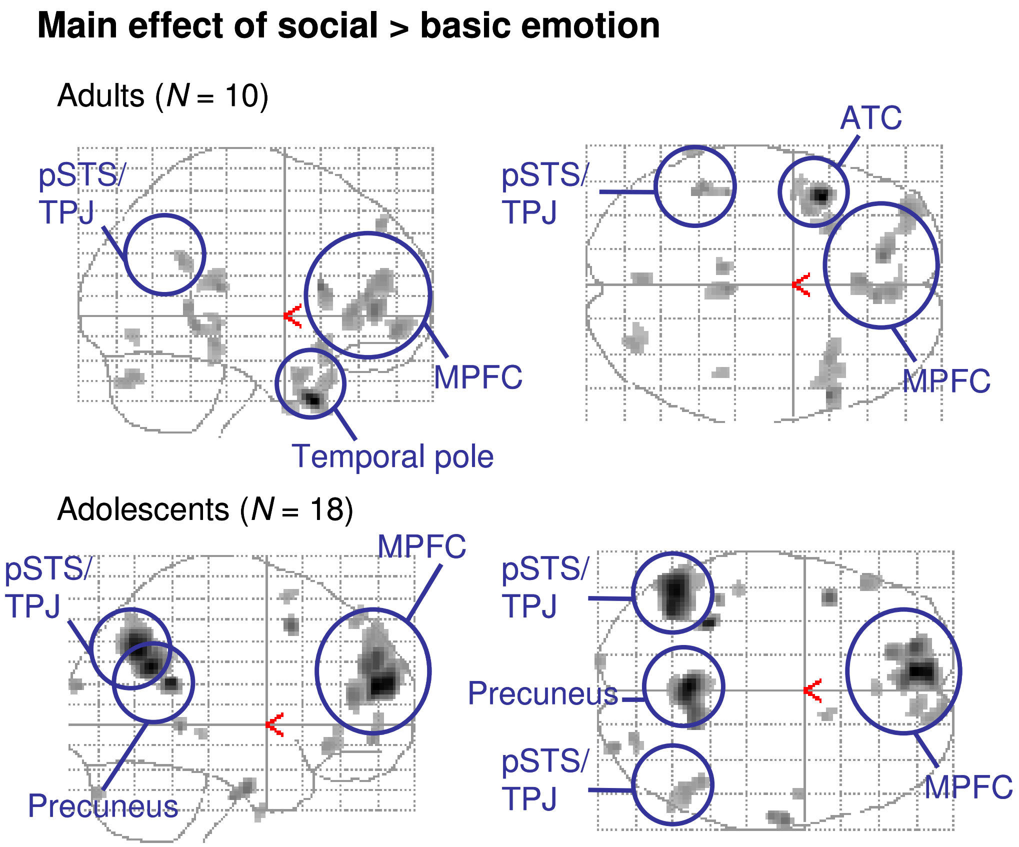
Figure 5.2 Three way interaction between Emotion, Protagonist and Group in left TPJ, shown at $P < 0.001$ on a sagittal glass brain projection. Parameter estimates for each condition are shown for each group. This region of the left TPJ is most active in adult self-social emotions and other-basic emotions, and in adolescent self- and other-social emotions.



5.3.2.3 Main effect of Emotion in each Group

In the adult group, the main effect of social > basic emotion resulted in activation of the arMPFC, the left pSTS/TPJ, and the left ATC (**Table 5.2**, **Figure 5.3**). In the adolescent group, the main effect of social emotion (social > basic) resulted in activation of the arMPFC, the left and right pSTS/TPJ, and the precuneus (**Table 5.2**, **Figure 5.3**).

Figure 5.3 Main effect of Emotion (social > basic) in each Group. Sagittal and transverse glass brains showing average group activation for adults and adolescents. Shown at $P < 0.005$; minimum spatial extent = 10 voxels; smoothed with a filter of 6mm full width at half-maximum at the second level.



5.3.2.4 Interactions between Group and Emotion

To identify group differences in brain activity to social > basic emotion, interactions between Group (adult, adolescent) and Emotion (social, basic) were investigated.

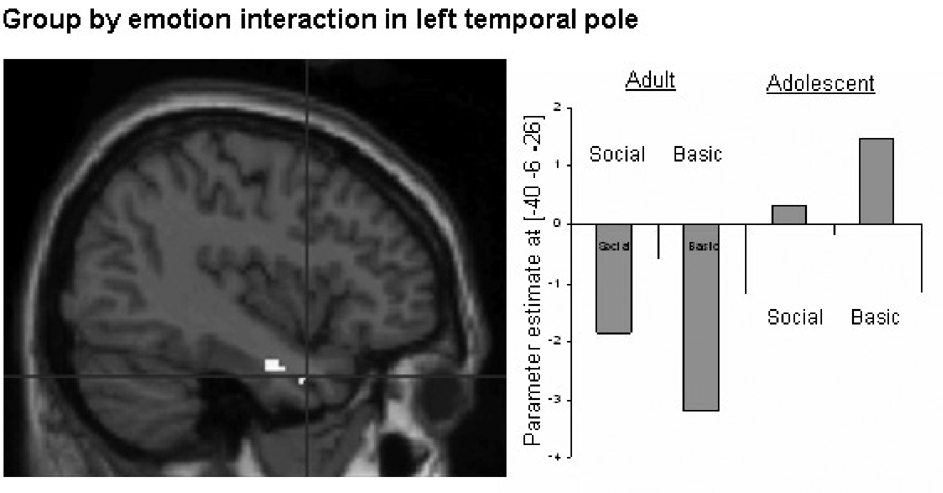
[Adult (social > basic)–adolescent (social > basic)]

This analysis revealed a cluster in the left ATC (**Table 5.2**, **Figure 5.4**). Inspection of parameter estimates, as well as inclusive masking (with adult social > basic), showed that this region was more active during social than basic emotions in adults, and more active to basic than to social emotions in adolescents (**Figure 5.4**).

[Adolescent (social > basic)–adult (social > basic)]

A cluster in left lateral arMPFC (**Table 5.2**, **Figure 5.5**) was active during the contrast [adolescent (social > basic)–adult (social > basic)]. Inspection of the parameter estimates, as well as inclusive masking (with adolescent social > basic), showed that this region was more active during social than during basic emotions in adolescents, and more active during basic than during social emotions in adults (**Figure 5.5**).

Figure 5.4 Interaction between Group (adult > adolescent) and Emotion (social > basic). Top left: activity in left ATC ([-40 -6 -26]) resulting from the contrast [adult (social > basic) - adolescent (social > basic)], shown at $P < 0.005$ projected onto a sagittal T1 image, with crosshair at [-40 8 -30]; top right: graph showing parameter estimates in left ATC for social and basic emotion, in both groups; bottom panel: positive correlation between age and adjusted BOLD signal in left ATC ([-40 -6 -26]) in the contrast [social > basic]; $r = 0.572$; $p < 0.05$).



Group by emotion interaction in left temporal pole

Regression between age and activity to social > basic emotion in left temporal pole [-40 -6 -26]

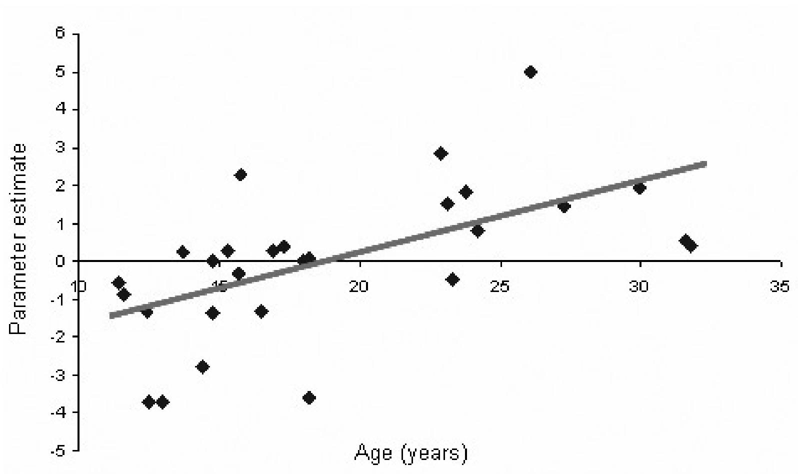
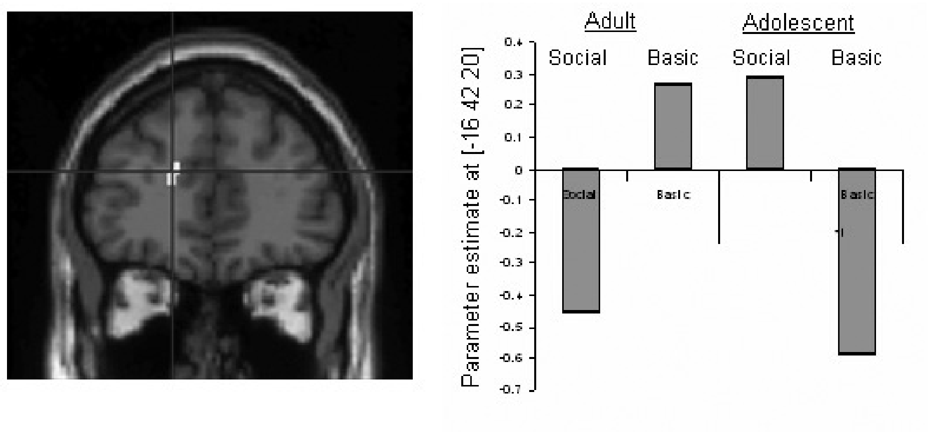
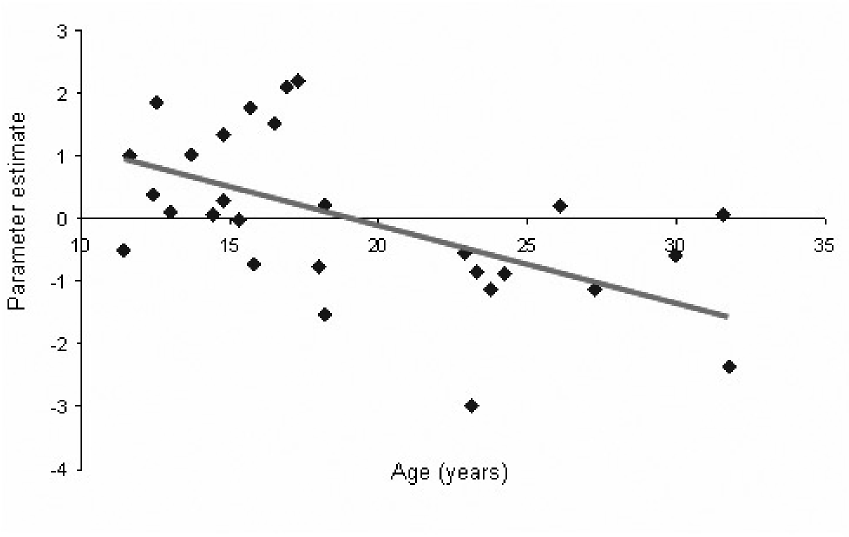


Figure 5.5 Interaction between Group (adolescent > adult) and Emotion (social > basic). Top left: activity in arMPFC ([-16 42 20]) resulting from the contrast [adolescent (social > basic) - adult (social > basic)], shown at $p < 0.005$ projected onto a sagittal T1 image, with crosshair at [-16 42 20]); top right: graph showing parameter estimates of activity in arMPFC for basic and social emotion conditions, in both groups; bottom panel: negative correlation between age and adjusted BOLD signal in arMPFC ([-16 42 20]) in the contrast [social > basic] ($r = 0.541$; $p < 0.05$).

Group by emotion interaction in lateral anterior rostral MPFC



Regression between age and activity to social > basic emotion in MPFC [-16 42 20]



5.3.2.5 Main effect of Protagonist in each Group

In the adult group, the main effect of self (self > other) did not yield any significant activations. In the adolescent group, the main effect of self (self > other) resulted in activation of the left postcentral gyrus (**Table 5.2**). The main effect of other (other >

self) did not yield any significant activations in either the adult or the adolescent group (however, see **Appendix 5.3**).

5.3.2.6 Interactions between Protagonist and Group

No brain regions showed a significant interaction between Protagonist and Group.

5.3.2.7 Interactions between Emotion and Protagonist

To identify differences in brain activity to social > basic emotion which differed as a function of Protagonist (self, other), interactions were between Emotion (social, basic) and Protagonist (self, other) were assessed within each age group separately.

Adult [(self social > self basic)–(other social > other basic)]

The adult group activated the left TPJ in this contrast (**Table 5.2**; **Figure 5.2**, top left). At an uncorrected threshold of $P < 0.001$, the adult group activated an antero-dorsal portion of the MPFC for this contrast (**Table 5.2**; **Figure 5.6**, top left). Inspection of the parameter estimates, as well as inclusive masking (with social > basic for self only; and basic > social for other only), showed that this antero-dorsal region of MPFC was more active during self-social emotions than in any other condition (**Figure 5.6**, bottom left). In contrast, the left TPJ was more active during self-social emotions and other-basic emotions than in the other conditions (shown in the graph in **Figure 5.6**).

Adolescent [(self social > self basic)–(other social > other basic)]

At an uncorrected threshold of $P < 0.001$, the adolescent group showed activity within an antero-dorsal region of the MPFC for this contrast, at a similar location to that found in adults (**Table 5.2**; **Figure 5.6**, top right). Inspection of the parameter estimates, as well as inclusive masking (with social > basic for self only; and basic > social for other only), showed that this antero-dorsal MPFC region was more active during self-social emotions than in any other condition (**Figure 5.6**, bottom right).

Adult and adolescent [(other social> other basic)–(self social > self basic)]

No brain regions were significantly active for this contrast, in either group.

Figure 5.6 Interaction between Emotion (social > basic) and Protagonist (self > other) in each age Group. Top panel: adult (left) and adolescent (right) activity in antero-dorsal MPFC in the contrast [(self social > self basic) - (other social > other basic)], shown at $p < 0.005$ on sagittal glass brain projections. The adult interaction in left TPJ, containing the region showing a three-way interaction, can also be seen. Bottom panel: parameter estimates for the interaction between Emotion and Protagonist in antero-dorsal MPFC in adults (left) and adolescents (right) are shown. In both groups, this antero-dorsal region of MPFC is most active during self-social emotions.

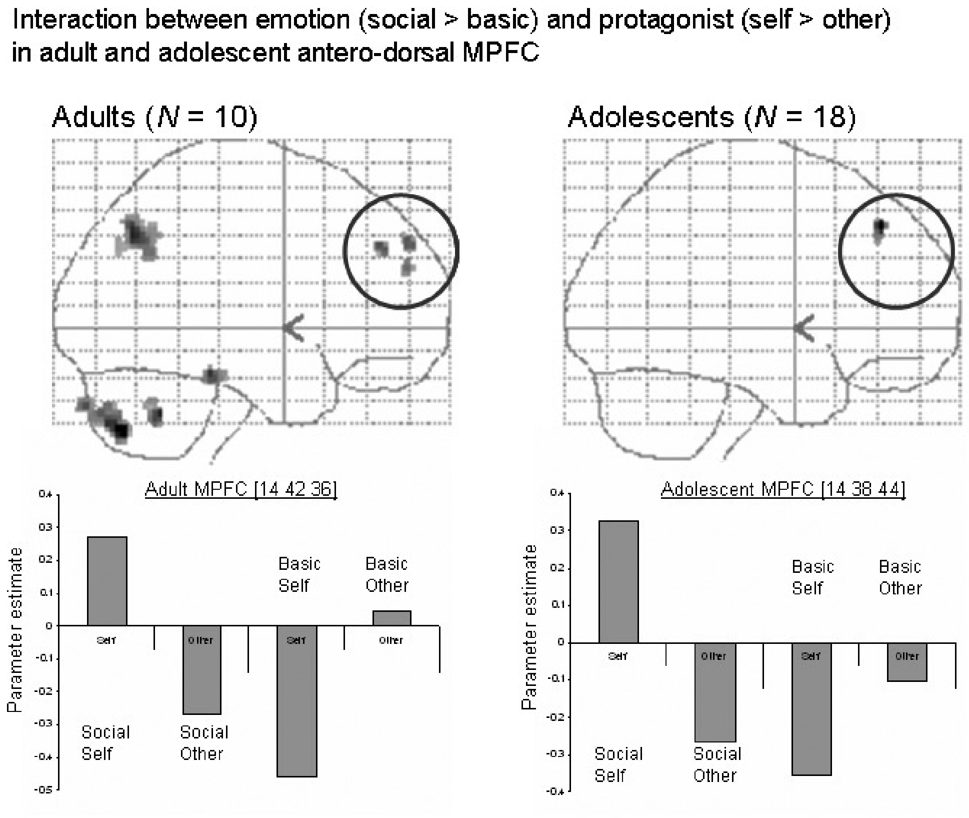


Table 5.2 MNI co-ordinates, Z-values and cluster size (in mm^3) for regions of activation in the main effect of Emotion, the interaction between Emotion and Group, the main effect of Protagonist, the interaction between Protagonist and Group, and the three-way interaction between all three factors.

Contrast	Region of activation	MNI co-ordinates	Z value	Size in mm^3 at $p < 0.001$
Emotion: social>basic	***Adults***			
	Anterior rostral MPFC	-14 44 2	3.82	96
		4 48 18	3.56	216
		6 42 12	3.28	(part of above cluster)
	Left pSTS/TPJ	-56 -62 28	3.48	32
	Left anterior temporal cortex	-36 8 -30	3.43	24
	Adolescents			
	Anterior rostral MPFC	-10 52 18	4.13	1600
		-6 62 22	4.03	(part of above cluster)
		-4 50 28	3.64	(part of above cluster)
		-18 42 16	3.65	128
		-4 52 -8	3.43	64
		-16 48 34	3.37	40
	Precuneus	-4 -56 28	4.64	1360
		14 -56 34	3.49	(part of above cluster)
		-4 -62 40	3.32	64
	Left TPJ	-38 -66 42	4.00	2032
		-48 -62 36	3.98	(part of above cluster)
		-38 -62 32	3.62	(part of above cluster)
	Right pSTS/TPJ	44 -48 28	3.31	40
Interaction between emotion and group	***[Adult (social>basic) – adolescent (social>basic)]***			
	Left anterior temporal cortex	-40 -6 -26	3.43	32
	[Adolescent (social>basic) – adult (social>basic)]			
	Left lateral anterior rostral MPFC	-16 42 20	3.39	32
Protagonist: self>other	***Adolescents***			
	Left postcentral gyrus	-24 -40 52	4.32	112
Interaction between emotion and protagonist *[(Self social > self basic) - (other social > other basic)]*	***Adults***			
	Left TPJ	-42 -66 40	3.83	264
	Antero-dorsal MPFC	14 42 36	3.38*	5
	Adolescents			
	Antero-dorsal MPFC	14 38 44	3.29*	8
Interaction between emotion, protagonist an group	***(For contrast, see Figure 5.2)***			
	Left TPJ	-42 -68 44	3.60	264
		-52 -58 34	3.50	40

* = active at $P < 0.001$, uncorrected

5.4 Discussion

The current fMRI study conducted to investigate the neural correlates of social vs. basic emotion processing in adolescents and in adults. It was predicted that both age groups would show activity within the mentalising network during social vs. basic emotion processing, but that adolescents would show greater activity within arMPFC for this contrast. The fMRI results uphold this prediction.

Adults activated a region of left ATC more than did adolescents during social vs. basic emotion, and this result is novel. The self vs. other contrast did not show a clear pattern of results, either within or between age groups.

5.4.1 FMRI correlates of social emotion processing in both groups

5.4.1.1 Anterior rostral MPFC

Social emotions require a representation of the mental states of others (mentalising). That is, social emotions require insight into the emotions, beliefs and opinions of other people—whether they are physically present, imagined, or perhaps represented by the concept of societal norms (Moll, de Oliveira-Souza, et al., 2005; Moll, Zahn, et al., 2005). For example, guilt is experienced when one believes that one's actions warrant disapproval or punishment, or that they have caused harm to another individual. In contrast, basic emotions such as 'visceral' fear and disgust entail a lesser degree of mentalising, since they only require insight into one's own instantaneous internal state. In line with this distinction between social and basic emotions, the current study found that both age groups activated brain regions involved in mentalising, namely, the arMPFC and the pSTS/TPJ (Amodio & Frith, 2006; Frith & Frith, 2003; Saxe & Kanwisher, 2003), during social vs. basic emotion processing. In a recent review paper, Olsson and Ochsner (2008) have drawn attention to the partial overlap between brain regions involved in social cognition and in social emotion. The results of the current study concur with this picture.

Parts of the arMPFC, which has been identified as the portion of MPFC most consistently active in studies involving mental state attribution (MNI y-coordinates from 30 to 60; z-coordinates from 0 to 40; Amodio & Frith, 2006; Gilbert et al., 2006), were active in both groups for social vs. basic emotion. This result is therefore in agreement with a large body of evidence. More narrowly, this result is in agreement with studies of social emotion in adults, which have reported activity within the arMPFC (Takahashi et al., 2004; Berthoz et al., 2002; Moll et al., 2002[8]). This finding is consistent with the notion that a cognitive process, that is, mental state attribution, is involved in certain emotional tasks including imagining social emotion situations (cf. Olsson & Ochsner, 2008). This is not surprising, given the current stimuli were explicitly designed to maximise the difference in mentalising requirement between social and basic emotion conditions. The current pattern of results in arMPFC does not shed any light on the cognitive components of social emotional processing (see Poldrack, 2008, re. reverse inference). They do, however, support the notion that arMPFC is associated with mentalising in an emotional context, whereas many previous adult and developmental studies have focussed on mentalising in an unemotional context (e.g. den Ouden et al., 2005, Blakemore et al., 2007).

The implication of the current finding in arMPFC depends on what role the arMPFC plays in mentalising. It has been proposed that the cognitive role of arMPFC in mentalising is to ‘decouple mental states from physical reality’ (Frith, 2007). Recent evidence from Gilbert et al. (S. Gilbert, personal communication) supports this notion[9]. An alternative, not necessarily incompatible view of the role of arMPFC is that it represents the motivational relevance (Moll, de Oliveira-Souza, et al., 2005; Moll, Zahn, et al., 2005), the value (Rushworth et al., 2007) or changing action values (Matsumoto et al. 2007) of social behaviors. A broader conceptualization of the role of MPFC in general (not just the anterior rostral portion), which has just been put forward in the literature, is that this large region of the brain is concerned with representing ‘fuzzy’, inexact and shifting realities – including social information, which is highly context-dependent and mutable (Mitchell, 2009). The

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[8] Although see Moll et al. (2005a), who did not report activity in arMPFC during social/moral disgust (indignation) vs. basic visceral disgust

[9] An fMRI study conducted by S. Gilbert et al. (personal communication) used a multivariate technique to map the representation of distinct mental states in arMPFC and other regions of the brain. Patterns of activity corresponding to distinct mental states could not be identified in arMPFC (although this region was generally activated during mentalising conditions). However, patterns of activity corresponding to distinct mental states could be identified in the medial temporal lobe. One explanation for this finding could be that the arMPFC enables mentalising, drawing information on specific mental state representations from medial temporal regions of the brain.

current study was not designed to distinguish between these possibilities. However, a role for arMPFC in self-relevant social information, needed for social actions, would be consistent with the social vs. basic contrast in the current study.

An alternative explanation for the finding that arMPFC is more active in social than basic emotions, is that the social emotion condition is more engaging and evocative (see Mitchell, 2009). Although we found no evidence for higher emotion ratings in social than basic emotions (in fact, the opposite was found), self-rated emotion is a notoriously slippery and unreliable measure. This explanation, however, is also compatible with the notion that arMPFC is representing self-relevant social information, as this information is engaging. Clearly, further work is needed on the precise role of the arMPFC in social-emotional tasks, and implications for models of social cognitive functioning and emotion processing.

Finally, several previous studies have demonstrated activity within child and adolescent arMPFC during mentalising relative to control conditions (Blakemore et al., 2007; Moriguchi et al., 2007; Wang et al., 2006). These previous studies have variously investigated mentalising using intentional vs. physical causality statements, animated shapes moving in a manner that suggest characters with intentions, and judgments of sincere vs. sarcastic statements. The current result extends this developmental finding to show that arMPFC is also active in adolescent participants during mentalising in a strongly emotional context.

5.4.1.2 Posterior superior temporal sulcus/ temporo-parietal junction

Adults and adolescents activated the pSTS/TPJ for social vs. basic emotion, with activity greater on the left than on the right. The left TPJ is consistently reported for its involvement in mentalising tasks, and is thought to play a role in reasoning about the beliefs of others (Samson et al., 2004; Frith & Frith, 2003; Saxe & Kanwisher, 2003). Elsewhere, it has been argued that pSTS/TPJ represents a prediction error (or ‘pay attention!’) signal for updating social information (Hampton et al., 2008; Kawawaki et al., 2006). This is not in consistent with the current result.

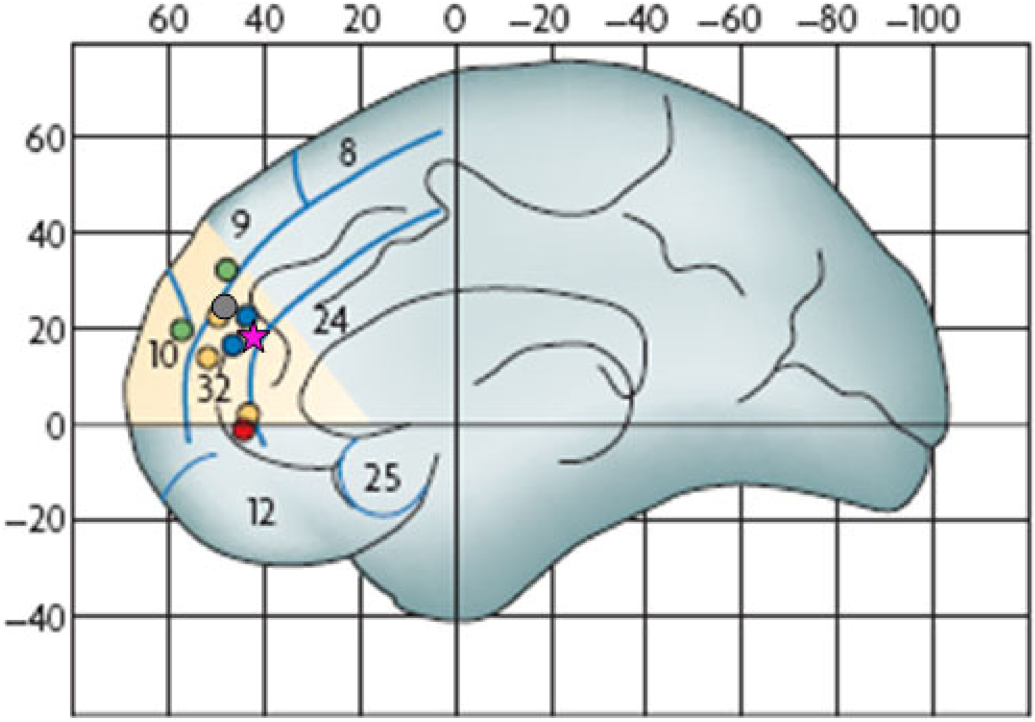
The pSTS/TPJ has been reported to be activated during mentalising in adolescents (Blakemore et al., 2007; Moriguchi et al., 2007). Activity within this region in the social relative to basic emotion condition may be related to the need for representing or reasoning about other people's beliefs when imagining social vs. basic emotion situations.

5.4.2 Group differences in the fMRI correlates of social emotion processing

5.4.2.1 Anterior rostral MPFC

Although both age groups activated parts of the anterior rostral MPFC for social vs. basic emotion, a more lateral part of this region was activated for social vs. basic by the adolescent group, but not by the adult group (**Figure 5.5**). This region was contiguous with the region activated by adolescents in the main effect of social vs. basic emotion. Activity to social vs. basic emotion at this locus was also negatively correlated with age. This result suggests that, as well as showing greater activity than adults within parts of arMPFC for social vs. basic emotion, adolescents also activate a greater volume of the arMPFC for social emotion processing, or activate additional parts of arMPFC that adults do not. This result is consistent with recent developmental neuroimaging studies looking at other aspects of social cognition, such as thinking about how intentions cause behaviour (Blakemore et al., 2007) and understanding the intended meanings of ironic remarks (Wang et al., 2006). These previous studies demonstrated an age-related decrease in activity in social relative to control conditions in arMPFC, in a similar location to that found in the current study (see Blakemore, 2008 for meta-analysis).

Figure 5.7 arMPFC shows greater activity in adolescents relative to adults during mentalising tasks. The current study found greater mentalising-related activity in a region of arMPFC in the adolescent than in the adult group, at a similar location (pink star) to that found in previous studies (Blakemore, 2008; Pfeifer et al., 2009; **Figure 1.8**).



5.4.2.2 Anterior temporal cortex

The left ATC demonstrated a significant group by condition interaction (**Figure 5.4**) such that the adult group showed more activation of this region than did adolescents for social vs. basic emotion processing. Activity to social vs. basic emotion in the left ATC was also positively correlated with age. The ATC is thought to store semantic social-emotional knowledge, or 'social scripts' (Frith, 2007; Zahn et al., 2007; Olsson et al., 2007), and it has been suggested that activation of the ATC during mentalising tasks in adults is due to the accessing and use of this stored knowledge (Frith, 2007).

5.4.2.3 Interpretation of group differences

One interpretation of the difference in activation pattern between age groups is that it reflects a difference in the cognitive strategy for social vs. basic emotion processing, and for mentalising or social cognition in general. A region of MPFC implicated in mentalising was found to be more active in adolescents than in adults during social vs. basic emotion processing. Therefore it could be the case that during adolescence, either a greater degree of mental state attribution, or a more effortful and less automatic form of mental state attribution, takes place in social-emotional situations. Later, during mature adulthood, the role of mentalising in social-emotional situations is diminished, because accumulated social experience allows for a greater reliance on semantic social-emotional knowledge (e.g. represented in anterior temporal cortex). This is a purely speculative interpretation (see Poldrack, 2008), but it could be investigated using cognitive-psychological paradigms.

An alternative explanation for the age group difference in arMPFC is that in adults, recruitment of the arMPFC during mentalising is more metabolically or neurally efficient (Durston et al., 2006). This explanation would make it difficult to explain the age-related increase in activity within the left ATC, and further studies are needed to look at developmental trajectories of functional activity across the brain. This issue is explored in more detail in the general **Discussion**, **Chapter 7** (section **7.2.4).**

5.4.3 FMRI correlates of self/other processing

In the current study, participants imagined emotion scenarios either from a first-person (self) or a third person (mother) perspective. This additional factor was included because previous studies have shown that neural activity to emotion (in adults) and semantic knowledge (in adults vs. adolescents) differs between self and other perspectives (Ruby & Decety, 2004; Pfeifer et al., 2007). In the current study, thinking about emotion from a first-person vs. third-person perspective resulted in activation in the right postcentral gyrus in adolescents. Activation of this region is consistent with previous studies (Ruby & Decety, 2004), and may be related to imagining the sensory consequences of emotional scenarios. A region of the MPFC showed a significant interaction between protagonist and emotion in both groups. This region of the MPFC was similarly located in both groups, and was more anterodorsal than the main foci of activation to social vs. basic emotion and self vs. other processing. Inspection of the parameter estimates for this region revealed that, in both groups, the anterodorsal MPFC was most active to social emotion in the first-person perspective.

A region of activation was seen in the left TPJ for the three-way interaction between emotion, protagonist, and group. Although the left TPJ was more active for social vs. basic emotion in the adolescent group, the adult group showed highest activation of this region for basic emotion in the third-person perspective and for social emotion in the first-person perspective. The role of this brain region in thinking about others' beliefs has been highlighted in adult neuroimaging and lesion studies (Samson et al., 2004; Frith & Frith, 2003). The differential recruitment of the left TPJ in adults and adolescents in the current study may indicate that different cognitive strategies are being used for the attribution of social and basic emotions to self and other. For a given emotion, the left TPJ seems to differentiate better between self and other in adults than it does in adolescents. A possible interpretation of these data, which has been proposed elsewhere (Moriguchi et al., 2007), is that adolescents rely more heavily on a simulation-based strategy when imagining another person's emotional response than adults do. It is notable that this difference in brain activity occurred despite a lack of group difference in perceived self–mother similarity (see **Results,** section **5.3.1.2**).

5.4.4 Role of the arMPFC in social cognitive development

An interesting perspective on the role of the arMPFC in social cognition has recently been raised in the adult lesion and neuroimaging literature. Although the arMPFC is robustly activated by mentalising tasks, and adults presenting with MPFC lesions usually show mentalising deficits (Frith & Frith, 2003; see Frith, 2007), there is one report of an individual who suffered extensive bilateral MPFC damage during adulthood but who was unimpaired on mentalising tasks (Bird et al., 2004). The arMPFC is not recruited when adults make semantic discriminations among abstract social concepts, such as 'brave' or 'stingy' (Zahn et al., 2007). Rather, this process is associated with activity within superior ATC. In addition, a small number of social emotion studies in adults fail to find arMPFC activation, but do find activity within other regions of the mentalising network such as the STS and the ATC, as well as in more ventral and/or anterior prefrontal regions such as the fronto-polar and orbito-frontal cortex (Moll, de Oliveira-Souza, et al., 2005; Moll, Zahn, et al., 2005; Takahashi et al., 2004). The current study, as well as previous studies, found greater arMPFC activity in adolescents than in adults for mentalising relative to control tasks (Blakemore et al., 2007; Pfeifer et al., 2007; Wang et al., 2006). One interpretation of this collection of findings is that the role of arMPFC in mentalising tasks becomes less crucial across age. Studies investigating mentalising ability in individuals who have sustained lesions to arMPFC during childhood, adolescence or adulthood would be important in evaluating this hypothesis.

Further work is needed on the development during adolescence of the cognitive strategies for understanding people. For example, it is not known whether the type of mentalising needed for social emotion understanding changes with development. It may be the case that a more explicit mentalising process is needed to learn about social emotions initially, but that more scripted, heuristic, or intuitive strategies are employed later on (Haidt, 2001).

Another factor which may contribute to a change in the role of the arMPFC with age is anatomical brain development. Volumetric MRI studies show that gray matter volume in social brain regions such as the MPFC and the TPJ decreases during adolescence, whereas white matter volume increases (Shaw et al., 2008; Gogtay et al., 2004; Giedd et al., 1999; Paus et al., 1999; Sowell et al., 1999). These changes are thought to be due to synaptic pruning and axonal myelination/increases in axonal calibre (see **Introduction,** sections **1.4.2** and **1.4.3.2.1.1/.2.2**), and may result in increased coordination between components of the social brain network and greater processing efficiency within brain regions mediating social cognition.

5.5 Conclusion

This fMRI study showed evidence that the neural processing of social emotion develops between adolescence and adulthood. Although components of the mentalising system including the arMPFC were active in both groups, adolescents activated the lateral rostral MPFC more for social vs. basic emotion whereas adults did not. Adults activated the left ATC more for social vs. basic emotion than did adolescents. These results indicate that the neural processing of social emotion continues to develop between adolescence and adulthood, such that the predominant activity moves from anterior (arMPFC) to more posterior (temporal) regions with age. Further work is needed to ascertain how this is related to neuroanatomical development within social brain regions, and to possible changes in cognitive strategies. Only female participants were included in the current study. It would be interesting to conduct a study with male participants.

The current study shows evidence that adolescents and adults use a similar neural network for social emotion processing, but with relative differences. However, the functional relevance of this developmental shift across adolescence is not clear. The current experiment did not look for behavioural differences between the age groups. Indeed, it was important that performance between groups was matched because, had performance differed between groups, it would have been impossible to interpret any differences in neural activity, which might have been a cause or a consequence of differences in task performance. Very few empirical studies have reported significant behavioural development during adolescence that is specific to social cognition and which cannot be explained by general improvement in attention, concentration, memory, and so on. The reasons for this are probably multifactorial. One possibility is that, in the lab, adolescents are able to pass complicated social cognitive tasks, which in everyday life they do not accomplish successfully. More naturalistic paradigms might be useful in addressing this issue.

5.5.1 The next chapter

In the current chapter, evidence was presented that the fMRI correlates of social emotion differ between adolescent and adult groups. Further studies are needed to establish the extent to which this age group difference is due to a shift in cognitive strategies, and/or changes in brain activity as a result of neuroanatomical development. However, an outstanding issue that should be addressed as a priority is the extent to which the collection of brain regions referred to as the mentalising system, or “mentalising network” (e.g. Frith & Frith, 2003), indeed function as a network during mentalising tasks relative to control tasks. A network is defined as a set of brain regions that demonstrate functional integration despite spatial separation, but there is currently limited evidence that the so-called mentalising network does indeed show functional integration.

The study described in the next chapter was conducted to address this outstanding issue. In **Chapter 6**, fMRI data from **Chapter 5** were reanalysed to investigate functional integration between brain regions involved in mentalising. The technique which was chosen to address this research question is known as psychophysiological interaction (PPI) analysis. This method was used to test the hypothesis that there would be greater functional integration, i.e. connectivity, as assessed using PPI analysis, between the arMPFC and the pSTS/TPJ and ATC during mentalising (social emotion) relative to a control condition (basic emotion). In addition, it was hypothesised that functional integration within the mentalising system would differ between adult and adolescent age groups, in line with evidence from developmental connectivity studies using non-mentalising tasks (see **section 6.1.3**), and given the evidence that white matter tracts connecting spatially distant brain regions undergo continuing maturation across adolescence (e.g. Paus et al., 1999; Giedd et al., 1999a; Giorgio et al., 2008; Barnea-Goraly et al., 2005).

Chapter 6

Effective connectivity during social emotion processing in adolescents and in adults

In the previous chapter, results were reported from an fMRI study of social and basic emotion processing in adolescents and in adults. Activity was observed within parts of the mentalising system including arMPFC in both age groups. However, there were age group differences in activity, such that adolescents activated a region of arMPFC more strongly than did adults for social vs. basic emotion, and adults activated part of the left ATC more strongly than did adolescents during this contrast. The current chapter describes a reanalysis of this fMRI dataset that was implemented to investigate effective connectivity within the mentalising system. Effective connectivity, defined as the influence that one neuronal system exerts over another, can be assessed using a statistical technique known as psychophysiological interaction (PPI) analysis. Using this technique, evidence is presented that components of the mentalising system interact functionally during social emotion processing, and furthermore that there are age group differences in connectivity. Further studies are needed to replicate and extend these findings, and to investigate the structural pathways responsible for within-mentalising system interactions and their development.

6.1 Introduction

Many studies have reported co-activation of the anterior rostral medial prefrontal cortex (arMPFC), posterior superior temporal sulcus (pSTS) bordering on the temporo-parietal junction (TPJ) and anterior temporal cortex (ATC) during mentalising tasks, and as a consequence this set of brain regions is often referred to as the mentalising 'network' (Frith & Frith, 2003). However, a network is defined as a set of brain regions that demonstrate functional integration despite spatial separation. It would appear from the mentalising literature that no study to date has tested whether this set of brain regions indeed demonstrate functional integration. There is evidence that components of the mentalising system are connected anatomically in rhesus macaques (e.g. MPFC receives projections from the temporal pole and superior temporal gyrus: Bachevalier et al., 1997; MPFC reciprocally connected with superior temporal cortex: Barbas et al., 1999), and a resting-state connectivity study in humans has shown correlations in activity between arMPFC and both ATC and the TPJ during 'rest' (i.e. unconstrained task conditions; Kelly et al., 2009).

It would appear that the only study to date that has looked at connectivity during a mentalising task is a positron emission tomography study by Castelli et al. (2002). This study demonstrated task-dependent correlations in activity between pSTS/TPJ and an extrastriate region implicated in biological motion, during a mentalising task in which participants attributed mental states to moving two-dimensional shapes. Indeed, surprisingly in view of the wealth of functional imaging data collected during mentalising tasks (Frith & Frith, 2003; Mitchell, 2009), no study to date has investigated within-mentalising system connectivity during mentalising tasks. It is conceivable that these regions are co-activated during mentalising tasks, but do not directly interact. Therefore, the first aim of the current study was to test whether the brain regions which comprise the mentalising system show evidence of functional interactions during a mentalising task.

6.1.1 PPI analysis

The technique which was chosen to address this research question is known as PPI analysis, or the analysis of 'psychophysiological interactions' (Friston et al. 1997).

PPI analysis is a way of explaining responses in one brain region in terms of an interaction between the influence of another region, and some experimental parameter (e.g. task; cognitive process). PPI analysis, along with other techniques for analysing effective connectivity[10], allow one to make inferences about the *influence* that one neuronal system could be exerting over another. This is in contrast to analyses of *functional* connectivity, in which conclusions may only be drawn about simple correlations in activity between brain regions – correlations which

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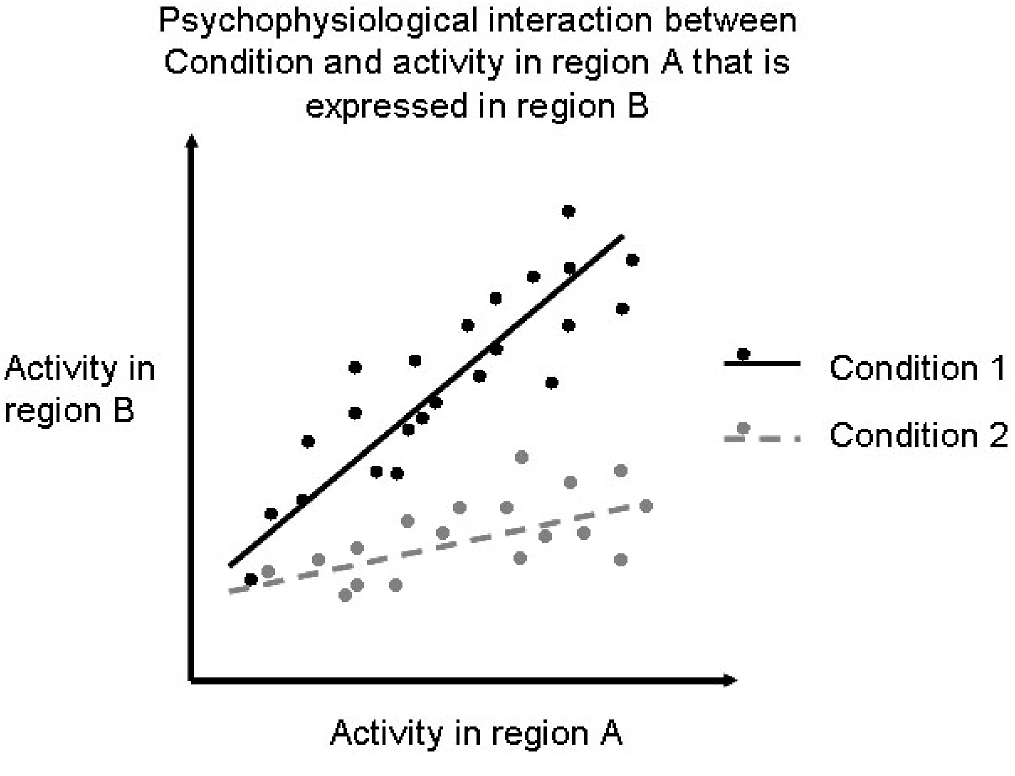
[10] E.g. structural equation modelling, dynamic causal modelling

could be spurious or uninteresting, such as stimulus-evoked transients, and the correlations that are measured in resting-state functional connectivity studies.

In PPI analysis, hypothesised effective connectivity is predicated on a model of the influence that one neuronal system is exerting over another. The parameters of the model (the connection strengths) are identified as those which allow the model to emulate the observed regional activities, or interregional correlations. The essential idea behind PPI analysis (see **Figure 6.1**) is this: If one were to regress the activity of one brain region (call it region B) on the activity of another brain region (region A), the slope of this regression would reflect the influence the second region (A) could be exerting over the first region (B). If this regression were then repeated using data acquired in a different experimental context, the slope might change, and this change in slope is a PPI. The degree to which activity in region B can be predicted on the basis of activity in region A corresponds to the *contribution* of region A to region B, where this contribution can be related to effective connectivity.

Figure 6.1 Graphical depiction of a fictitious psychophysiological interaction (PPI). There is a PPI between Condition (1 vs. 2) and activity in region A that is expressed in region B.



For a given PPI there are two statistically equivalent explanations (which may differ in physiological plausibility). The first explanation is that the experimental context (e.g. task, cognitive process) is modulating the contribution of activity in region A to activity in region B (i.e. there is a context-specific change in effective connectivity). For example, mentalising vs. no-mentalising may modulate the effect that activity in region A has on activity in region B. The second explanation is that activity in region A is modulating the impact of experimental context on activity in brain region B (i.e. effective connectivity modulates stimulus-specific responses). For example, the extent of activity in region A may modulate the impact of mentalising on activity in region B. Therefore the results from the current PPI analysis will not distinguish statistically between these possibilities.

6.1.2 Mentalising system connectivity

In the current **Chapter**, fMRI data from **Chapter 5**, collected while participants silently read a series of scenarios designed to evoke social emotions (embarrassment or guilt) or basic emotions (disgust or fear), were reanalysed in order to test whether effective connectivity within the mentalising system would be greater during social than basic emotions. Specifically, PPI analysis was used to test the prediction that arMPFC activity would more strongly predict activity in pSTS/TPJ and ATC during social than during basic emotions[11].

6.1.3 Age group differences in connectivity

The second aim of the current study was to investigate age group differences in effective connectivity. Recent fMRI studies of social cognition in adolescents and in adults, analysed in the conventional manner to look at mean activity levels in social and non-social conditions (Burnett et al., 2009, Blakemore et al. 2007, Wang et al. 2006, Pfeifer et al. 2007; Pfeifer et al., 2009), have demonstrated an apparent shift in activity between late childhood/adolescence (age 9-18) and adulthood (age 22-38). Specifically, these studies show an age-related decrease in activity within arMPFC, and an increase in activity in temporal portions of the mentalising system (pSTS/TPJ or ATC; for review, see Blakemore, 2008). In the current study, it was hypothesised that this shift in mean activity would be accompanied by a developmental shift in effective connectivity.

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[11] Or, equivalently, that social > basic emotion would more strongly predict activity in pSTS/TPJ and ATC while MPFC was more vs. less activated

This hypothesis was prompted by recent evidence from non-social tasks that age-related changes in mean activity during fMRI are accompanied by changes in functional and/or effective connectivity. For example, Stevens et al. (2007, 2009) demonstrated adult vs. adolescent group differences in both mean activity and effective connectivity, in brain regions engaged during performance of the go/no-go task[12]. Hare et al. (2008) found that the amygdala was more active in adolescents relative to adults while viewing fearful faces, and that across age, functional connectivity between ventral prefrontal cortex and the amygdala was correlated with a 'habituation' of amygdala activity upon repeated exposure to the faces. Finally, Menon et al. (2005) showed an age-related decrease in activity within the left medial temporal lobe during memory encoding (in 11-19 year olds) which was accompanied by increased functional connectivity with dorsolateral prefrontal cortex. However, no previous study has investigated the development between adolescence and adulthood of effective (or indeed functional) connectivity within the mentalising system, during social cognition tasks. This, therefore, was the second aim of the current PPI investigation.

6.2 Methods

6.2.1 Participants, experimental design and data acquisition

The participants, task and scanning parameters were as described in **Chapter 5,** sections **5.2.1-5.2.3**: Nineteen female adolescents (age range = 10.83 to 18.17 years; mean age = 14.8 years) and 10 female adults (age range = 22.92 to 31.83 years; mean age = 26.41 years) underwent fMRI scanning as they read sentences describing scenarios in which a social or a basic emotion would be felt. For each participant, 554 functional volumes were acquired over two consecutive scanning sessions lasting 12 min each.

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[12] Brain regions: Correct responses engaged a network comprising left lateral prefrontal cortex, left postcentral gyrus/inferior parietal lobule, striatum, and left cerebellum. A similar network was engaged during errors, but this network was not integrated with activity in regions believed to be engaged for higher-order cognitive control. In addition, a medial/dorsolateral prefrontal-parietal network responded to all no-go stimuli, but with greater activity to errors. ICA analyses also identified a third error-related circuit comprised of ATL, limbic and pregenual cingulate cortices, possibly representing an affective response to errors.

In the conventional analysis of the fMRI data (**Chapter 5,** section **5.2.4**), mean signal in adults vs. adolescents was analysed during social vs. basic emotion, and from the perspective of self vs. other, in a 2x2x2 mixed factorial design. However for the current PPI analysis, a 2x2 mixed factorial design was employed, with between-subjects factor age group (adolescent vs. adult) and within-subjects factor emotion (social vs. basic), by collapsing the self/other levels of the protagonist factor. The reason for collapsing self and other scenarios in the current PPI analysis was because no significant differences were found in activity within any mentalising regions for self > other or other > self in either age group, and to increase power.

6.2.2 PPI Analysis

PPI analysis assesses the hypothesis that activity in one or a set of brain regions can be explained by an interaction between activity in another part of the brain (the physiological source), and the presence of a cognitive process (the psychological context). This is implemented by denoting activity in the source region as the physiological regressor, and psychological context is the psychological regressor. A third regressor in the analysis represents the interaction between the first and second regressor, and brain regions are identified for which the interaction regressor predicts BOLD signal.

6.2.2.1 Definition of physiological source and PPI target regions

In the conventional analysis reported in **Chapter 5,** the arMPFC, pSTS/TPJ and ATC were active in either or both age groups during social relative to basic emotions. Overlapping portions of arMPFC were active in both age groups, as were portions of left pSTS/TPJ; the right pSTS/TPJ was active in the adolescent group only, and left ATC was active in the adult group only.

In the current PPI analysis, the arMPFC was selected as the source of the physiological regressor due to (a) its confirmed involvement in mentalising (Amodio & Frith, 2006), and (b) because overlapping regions of arMPFC were active in both age groups during social vs. basic emotion in **Chapter 5**, whereas the same was not true of pSTS/TPJ and ATC. Effective connectivity between the source region and target regions of interest, during social relative to basic emotions, was then investigated. Target regions of interest were pSTS/TPJ and ATC.

The precise region of arMPFC from which the physiological regressor (BOLD signal) was extracted was defined in the following manner. First, taking as a reference the mentalising region of arMPFC (BA 10) delineated in Gilbert et al. (2007), arMPFC was defined as the volume from -8 to +8 on the x-axis, from +40 to +56 on the y-axis and from -12 to +30 on the z-axis. Then, in each single-subject *t*-contrast map for the emotion contrast (social > basic), thresholded at $P < 0.005$ uncorrected (minimum voxel extent 4), SPM2 was used to locate the nearest local maximum to the centre of this volume (i.e. the nearest single-subject peak to the co-ordinate [0 48 9]). A volume of interest was then created in the form of a sphere of radius 8 mm centred on the single-subject peak. If there was no significantly active cluster within arMPFC at this threshold ($N = 7$ datasets, of which 6 were from the adolescent group), the threshold was lowered to $P < 0.05$ uncorrected (minimum voxel extent 4). Two datasets that did not contain a peak within the defined arMPFC volume at this significance level were excluded (1 adolescent, 1 adult), leaving 17 adolescent and nine adult datasets in the PPI analysis. Finally, each single-subject social > basic *t*-contrast map was smoothed to facilitate group level analysis, and the BOLD signal time-series was extracted from each subject's 8 mm sphere of interest in arMPFC.

6.2.2.2 Group level PPI analysis

Voxel-wise PPI analysis was conducted at the combined group level ($N = 26$), in order to identify target brain regions that showed a significant increase in correlated activity with the arMPFC volumes of interest (VOI) during social relative to basic emotion, at an uncorrected threshold of $P < 0.01$ with minimum voxel extent 4 (Penny et al., 2003). For non-hypothesised target regions, a threshold of $P < 0.05$ (minimum voxel extent 4) was applied with family-wise error correction. Target regions were defined as pSTS/TPJ (co-ordinates as in Aichhorn et al., 2006) plus the caudal portion of STS that extends into TPJ (as in Frith & Frith, 2003; Hein & Knight, 2008), as well as the ATC (as in Frith & Frith, 2003; Burnett et al., 2009; Hein & Knight, 2008).

After the combined group-level analysis, voxel-wise PPI analysis was conducted within each age group (adolescent: $N = 17$, aged 11-18, mean (s.d.) age = 14.83 (2.16) years; adult: $N = 9$, aged 22-32, mean (s.d.) age = 26.69 (3.66) years) separately. To directly compare group differences in effective connectivity, the interaction between PPI (the interaction between arMPFC VOI activity and emotion) and group (adolescent vs. adult) was investigated. Finally, *t*-contrasts were used to investigate, within each group separately, effective connectivity during social > basic emotion within brain regions that showed this group-by-PPI interaction.

6.3 Results

6.3.1 Psychophysiological interaction across participants

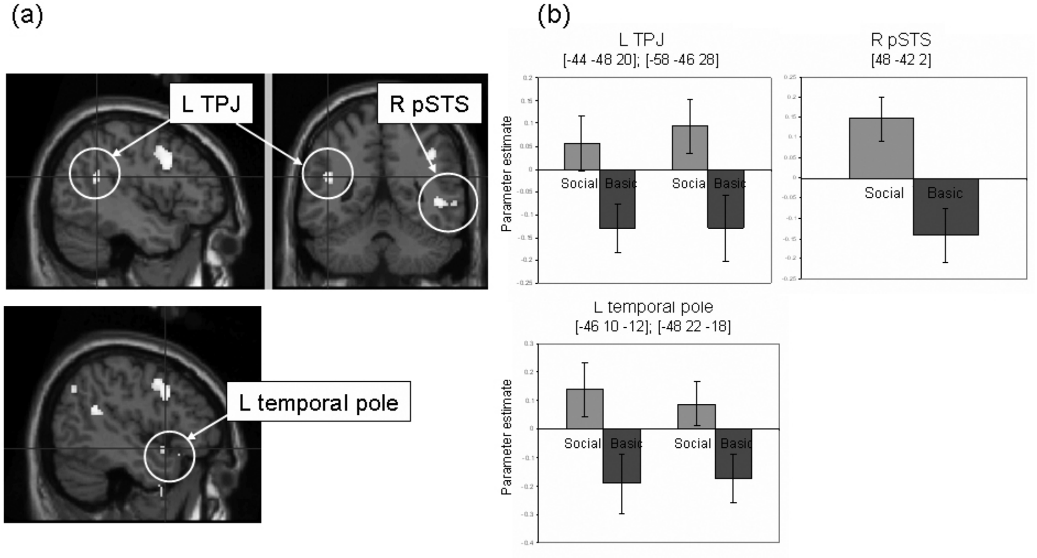
At the combined group level (*N* = 26 participants, aged 11 to 32), PPI analysis revealed a significant interaction between emotion (social > basic) and signal in the arMPFC volumes of interest (VOI), expressed in other regions of the mentalising system. Specifically, the left TPJ, right pSTS and left ATC showed greater connectivity with arMPFC during social than during basic emotion scenarios (**Table 6.1**; **Fig. 6.2**). No other regions showed significant interaction with the arMPFC VOI during social vs. basic emotions.

Table 6.1

PPI results: brain regions expressing an interactio between activity within arMPFC and emotion condition (social vs. basic) across participants (*N* = 26)

		P	*T*	*Z*	Size in voxels at < 0.01
R pSTS	[48 -42 2]	<0.001	4.21	3.63	343
	[60 -42 2]	0.001	3.62	3.21	(part of above)
	[62 -32 -4]	0.002	3.21	2.91	(part of above)
L TPJ	[-44 -48 20]	0.002	3.25	2.94	51
	[-42 -46 28]	0.007	2.66	2.48	(part of above)
	[-58 -46 28]	0.003	2.96	2.71	10
	[-46 -66 38]	0.005	2.76	2.56	8
L anterior temporal cortex	[-46 10 -12]	0.005	2.75	2.55	14
	[-46 8 -12]	0.006	2.7	2.51	7
	[-66 -4 -22]	0.003	3.08	2.81	50
	[-48 22 -18]	0.005	2.77	2.56	6

Figure 6.2 PPI results across participants: (a) regions of significant interaction between emotion (social > basic) and activity in arMPFC, shown at $P < 0.01$ projected onto transverse and sagittal T1 images; (b) graphs showing parameter estimates for regions of significant interaction between emotion (social > basic) and activity in arMPFC.



6.3.2 Psychophysiological interactions within each age group separately

Within the adult group ($N = 9$, aged 22 to 32), PPI analysis revealed a significant interaction between emotion (social > basic) and signal in the arMPFC VOI, expressed in the ATC bilaterally and in the right pSTS/TPJ (**Table 6.2a**). That is, in the adult group, these regions showed greater effective connectivity with arMPFC during social than during basic emotions.

Within the adolescent group ($N = 17$, aged 11 to 18), PPI analysis revealed a significant interaction between emotion (social > basic) and signal in the arMPFC VOI, expressed in the left pSTS extending into left TPJ, in left TPJ proper, in right pSTS and in the left ATC (**Table 6.2a**). That is, in the adolescent group, these regions showed greater effective connectivity with arMPFC during social than during basic emotions.

6.3.3 Interaction between the arMPFC-emotion PPI and age group

In the conventional analysis of the fMRI data (**Chapter 5**), adolescents were found to show stronger mean activity within arMPFC during social > basic emotion than did adults, whereas adults showed stronger mean activity within left ATC for this contrast compared to adolescents. In the current PPI analysis, the aim was to determine whether effective connectivity between arMPFC and other regions of the mentalising system also varied as a function of age group. Indeed, PPI analysis revealed a significant interaction between age group and the PPI between emotion condition and signal within the arMPFC VOI, expressed within a region of left pSTS extending into TPJ (**Table 6.2b**; **Figure 6.3**). In other words, effective connectivity between left pSTS/TPJ and the arMPFC VOI during social > basic emotion differed between adolescent and adult groups.

In order to investigate the directionality of this age group difference, *post hoc* *t*-tests were conducted. These tests revealed greater adolescent connectivity between the arMPFC VOI and the central portion of left pSTS/TPJ during social relative to basic emotion (region (iii) in **Figure 6.3**: [-44 -34 10]; adolescents: paired samples *t*-test, $t_{16} = -1.83$, $P = 0.04$; adults: paired samples *t*-test, $t_8 = -0.76$, $P = 0.24$). In a more peripheral portion of the left pSTS/TPJ region, adults showed the opposite pattern (region (ii) in **Figure 6.3**: [-38 -34 20]; adults: paired samples *t*-test, $t_8 = -2.31$, $P = 0.02$; adolescents: paired samples *t*-test, $t_{16} = -1.15$, $P = 0.13$). No other regions showed a significant interaction between age group and the emotion-arMPFC PPI.

Table 6.2

(a)

PPI results: brain regions expressing an interaction between arMPF signal and emotion condition (social vs. basic) within each age grou separately

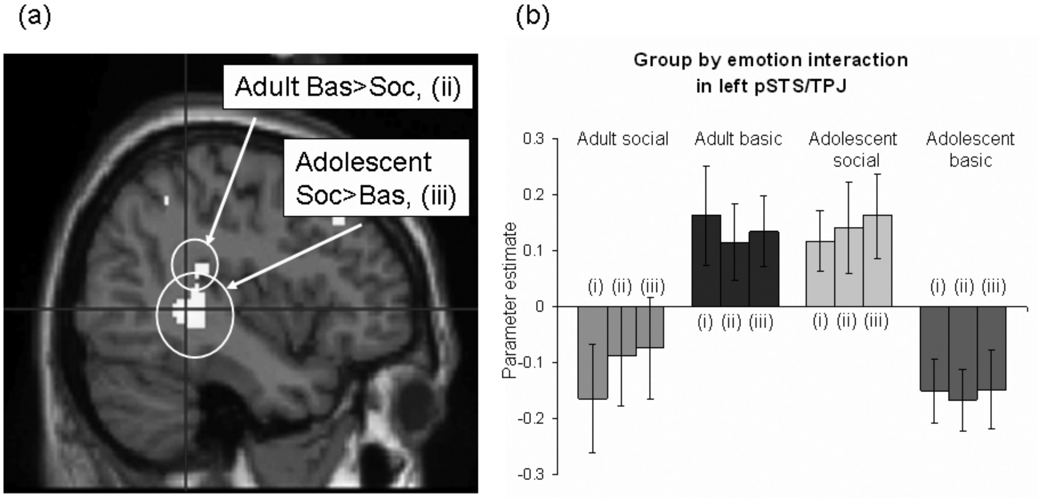
*Adult (*N = *9)*		*P*	*T*	*Z*	Size in voxels *P* < 0.01
R pSTS/TPJ	[62 -44 4]	0.002	4.12	2.93	71
	[68 -44 4]	0.002	3.97	2.87	(part of above)
L anterior temporal cortex	[-48 16 -20]	0.002	3.99	2.88	31
R anterior temporal cortex	[58 6 -32]	0.003	3.83	2.81	8
*Adolescent (*N = *17)*					
L pSTS extending into L TPJ	[-36 -36 8]	0.001	3.93	3.24	402
	[-48 -38 8]	0.001	3.69	3.09	(part of above)
	[-44 -44 0]	0.002	3.47	2.95	(part of above)
L TPJ	[-58 -48 26]	0.006	2.86	2.53	8
R pSTS/TPJ	[60 -30 -4]	0.001	3.64	3.06	249
	[36 -28 18]	0.001	3.62	3.05	(part of above)
	[60 -38 0]	0.003	3.15	2.74	(part of above)
L anterior temporal cortex	[-44 -4 -24]	0.003	3.1	2.7	11

(b)

Group-by-PPI interaction: Brain regions expressing an interaction between arMPFC activit emotion condition (social vs. basic) and group (adolescent vs. adult)

		P	*T*	*Z*	Size in voxels at < 0.01
L pSTS extending into L TPJ	[-40 -42 2]	<0.001	3.75	3.29	247
	[-44 -34 10]	0.001	3.45	3.08	(part of above)
	[-38 -34 20]	0.003	2.97	2.72	(part of above)

Figure 6.3 Interaction between group, emotion and arMPFC signal in left pSTS/TPJ (a) Region showing significant interaction between group (adolescent vs. adult), emotion (social vs. basic) and activity in anterior rostral MPFC, shown at $P < 0.01$ projected onto a sagittal T1 image. Crosshair is at peak voxel [-40 -42 2]. Regions in which there was also an effect of social vs. basic emotion within each group separately are circled; (b) graph showing parameter estimates for this interaction. Key: (i) peak voxel [-40 -42 2]; (ii) secondary peak voxel [-44 -34 10]; (iii) secondary peak voxel [-38 -34 20]



6.4 Discussion

The current study had two aims. The first aim was to investigate effective connectivity within the mentalising system during a social emotion task, using PPI analysis. A previous, conventional analysis of the same fMRI data had shown that components of the mentalising system, namely parts of the arMPFC, pSTS/TPJ and the ATC, were more active during social than during basic emotion processing in adolescents and/or adults (**Chapter 5**). In the current study, it was additionally found that pSTS/TPJ and ATC showed greater connectivity with arMPFC during social than during basic emotions. It would appear that this is the first study to demonstrate effective connectivity within the mentalising system.

The second aim of the current study was to investigate age group differences in mentalising system connectivity. In **Chapter 5**, it was shown that activity in a region of arMPFC during social relative to basic emotions was greater in adolescents than in adults, whereas activity in left ATC was greater in adults for this contrast. The current PPI analysis adds to this developmental picture by showing greater effective connectivity between arMPFC and the left pSTS/TPJ during social relative to basic emotion processing in adolescents than in adults, while ATC shows task-dependent connectivity with arMPFC in both age groups.

6.4.1 Effective connectivity within the mentalising system

Conventional neuroimaging analysis provides information about how some index of brain activity within a set of brain regions differs between groups and conditions. PPI analysis, on the other hand, provides information regarding correlations in activity between brain regions, and how these correlations differ between groups and conditions (Friston et al., 1997). A task-dependent correlation between two brain regions is taken to imply that these brain regions interact more during one experimental condition than during another.

The previous, conventional analysis showed that components of the mentalising system were more active during social than during basic emotion processing. The current PPI analysis shows that components of the mentalising system also show effective connectivity. Specifically, bilateral pSTS/TPJ and the left ATC show stronger connectivity with arMPFC during social relative to basic emotion processing. This finding adds weight to the notion that these brain regions may function as a network during mentalising tasks. It is possible that, at a neurophysiological level, effective connectivity is mediated by direct anatomical connections between arMPFC and both pSTS/TPJ and ATC, as have been identified in rhesus macaques (Bachevalier et al., 1997; Barbas et al., 1999). However, more evidence is needed.

The current study shows evidence for effective connectivity between arMPFC and parts of the left ATC in both adult and adolescent groups. The previous, conventional analysis indicated that adults activated left ATC for social relative to basic emotion, whereas adolescents did not (even at reduced significance threshold). Because conventional and PPI analyses test different constructs, these two sets of results provide complementary information. Indeed, the current finding mirrors those from other PPI studies reported in the literature, in which effective connectivity between two brain regions has been demonstrated when conventional analysis had shown no activity in one or both regions during a particular experimental context. For example, Rao et al. (2008) showed that, whereas no regions within prefrontal cortex were active during an executive sensorimotor task[13], there was nevertheless demonstrable effective connectivity between parts of lateral PFC and relevant sensorimotor regions during task performance. Rao et al. interpreted this result as showing evidence that PFC plays a regulatory (rather than direct) role in the task. Thus, one possibility in the current study is that during social relative to basic emotion processing, arMPFC and the ATC are engaged in a regulatory rather than a direct relationship. Exactly what this means, however, is unclear. Further studies are needed to investigate the directionality of this arMPFC-ATC relationship, and explore in more detail its functional role.

6.4.2 Adolescent vs. adult effective connectivity

The second aim of this study was to investigate whether effective connectivity within the mentalising system differed between adolescent and adult groups. To the author's knowledge, no previous fMRI study has examined age group differences in effective connectivity during a mentalising task. The current study shows evidence for an age-related decrease in effective connectivity between arMPFC and left pSTS/TPJ during social relative to basic emotion processing.

This finding is at odds with the small number of developmental studies of functional and effective connectivity in the literature, which report age-related *increases* in correlated activity. However, all previous studies have been restricted to non-social domains, so it is not clear how comparable the findings are. Effective connectivity has been investigated in adolescents vs. adults during go/no-go task performance (Stevens et al., 2007, 2009) and during memory encoding (Menon et al. 2005). In these studies, age-related increases in connectivity were shown between brain regions instrumental in performing the tasks[14]. Other studies have investigated the development of functional connectivity during 'rest', or unconstrained task conditions (Fair et al., 2007, 2008; Kelly et al., 2009). These studies have shown that some within-network correlations increase, whereas some decrease with age. The

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[13] A puzzling result, given that lesions to this part of PFC interfere with performance of the task.

[14] In Stevens et al., age-associated increases in the strength of within-network connectivity were accompanied by a decrease in strength of between-network connectivity. In the current study, we do not know whether the set of brain regions we are interested in participates in a single discrete network, or a set of interacting networks.

current finding that social emotion-dependent arMPFC-pSTS/TPJ connectivity is greater in adolescents than in adults needs to be replicated, and then tested for generalisability using other mentalising tasks.

6.4.3 Implications for the development of mentalising

An interpretation of the age-related decrease in connectivity between arMPFC and left pSTS/TPJ during social relative to basic emotions is that, in order to accomplish this task, adolescents require not only higher activity in arMPFC (as found in **Chapter 5**) but also stronger co-activation of the mentalising system, relative to adults. This may be because the maturing network in adolescents is less efficient in accomplishing the task. Continuing synaptic elimination and axonal myelination during adolescence (Yakovlev & Lecours, 1967; Huttenlocher, 1979; Huttenlocher et al., 1982; Benes et al., 1994; Huttenlocher & Dabholkar, 1997), and perhaps developing axonal calibre (Paus et al., 2008) may act to increase the efficiency of the system. Another (not mutually exclusive) possibility is that the shift in functional connectivity between arMPFC and left pSTS/TPJ with age is related to a change in the type of mentalising used in social cognition tasks such as these. More naturalistic tests of mentalising, on which adolescents do not show ceiling performance, are needed to test this hypothesis. Performance on a visual perspective-taking task has recently been shown to develop throughout adolescence (Dumontheil et al. 2009; see **Introduction**). Follow-up studies should ascertain whether this is accompanied by changes in functional (including connectivity) brain measures. Studies are also needed that combine measures of functional connectivity during with static anatomical measures of grey and white matter volume, and white matter integrity (e.g. voxel-based morphometry and diffusion-tensor imaging; Olesen et al., 2003; see **Discussion,** sections **7.2.4** and **7.2.5**).

PPI analysis is used for investigating how an experimental manipulation modulates functional connectivity between brain regions, or alternatively how one brain region modulates the impact of an experimental manipulation on activity within a second brain region (Friston et al., 1997). In the current study, it could be the case that the social emotion task causes differences in connectivity between the mentalising regions, or instead that activity within arMPFC modulates the response of other mentalising regions to the social emotion task. The directionality of the functional connectivity reported here is unknown; whether arMPFC is influencing activity in the rest of the mentalising network, or vice versa, cannot be determined by PPI analysis.

6.5 Conclusion

Several recent fMRI studies (including **Chapter 5**) have shown evidence for the development during adolescence of activity within the mentalising system. However, the development of effective connectivity within the mentalising system has not previously been studied in adolescents, or indeed in adults. This study represents an initial step in this direction, by demonstrating that arMPFC shows task-dependent connectivity with pSTS/TPJ and ATC, during social relative to basic emotion processing, in adolescents and in adults. Future studies are needed to extend this finding, and to replicate the developmental result that functional connectivity between arMPFC and pSTS/TPJ during social relative to basic emotions decreases between adolescence and adulthood.

Chapter 7

Discussion

This Discussion will summarise, place in context and draw out implications of findings from each of the preceding chapters. Subsequently, outstanding issues will be discussed, with general and specific suggestions for future investigation.

7.1 Summary of findings

7.1.1 Chapter 2: The development of expected value maximising, risk-seeking and counterfactual emotion in a probabilistic gambling task

Adolescents are said to be risk-seeking, and this is thought to underlie real-life adolescent engagement in ‘risky’ activities, that is exciting activities which have a relatively high risk of causing harm (Geier & Luna, 2009). However, engagement in such activities, which include experimentation with substances and unsafe sex, is likely to occur for a variety of reasons. One possibility is that adolescents show a genuine preference for risk (e.g. Casey et al., 2008). However, another possibility is that the ability to estimate and weigh up potential consequences is still developing. The study described in **Chapter 2** investigated behavioural economic operationalisations of each of these two hypotheses, in participants aged nine to 35. The propensity to seek risk was investigated by measuring the tendency to maximise outcome variance in a gambling task, and the ability to choose the optimal set of possible consequences was investigated in the same task by measuring the tendency to maximise expected value (EV). EV is the sum of possible outcomes of a decision (e.g. a quantity of points or money) weighted by their probabilities.

The results show that both components of decision-making, the ability to maximise EV and the tendency to seek risk, continue to develop during adolescence. However, these two components showed distinct developmental trajectories. The tendency to maximise EV increased linearly between the ages of nine and 35 years (see **Figure**

2.2), whereas the tendency to make risky choices showed a nonlinear (inverted-U shaped) developmental trajectory with its peak in adolescence (age 14.38; see **Figure 2.3**). This set of results implies that adolescent engagement in risky activities in real life may be partly due to a true underlying preference for risk, relative to children and adults. Furthermore, the distinct trajectories for risk and EV imply that adolescent risk-seeking does not arise due to a simple deficit in EV-maximising. The study in **Chapter 2** is one of few (or indeed the first) experimental studies to show evidence for the often-cited inverted-U shaped developmental trajectory of risk-seeking, with its peak in adolescence (Casey et al., 2008; Steinberg, 2008; see Figner et al. 2009; O'Brien & Steinberg, 2009).

In naturalistic situations, decision-making involves additional components beyond the ability to calculate EV and risk. Thus, age differences in the tendency to engage in risky activities may also be due to development of the ability to detect possible outcomes and estimate their respective probabilities (e.g. Crone & van der Molen, 2004), or age differences in the subjective value of certain decision outcomes. The latter is of course difficult to compare across individuals, but the task used in **Chapter 2** assessed one aspect of subjective value, i.e. emotion. After the outcome of each gambling decision was revealed, participants reported their emotional response using a linear rating scale, and these responses were assumed to approximate participants' actual emotional responses. The absence of overall age differences in emotion evaluations suggests there were no overall age group differences in the use of the rating scale, and/or that adolescents were not hyper-emotional in general, as has been suggested elsewhere. However, interestingly, there was an age group difference in the impact of counterfactual context on the emotion evaluations. Relative to children (aged 9-11), young adolescents (aged 12-15) reported feeling more positive (/negative) in response to winning (/losing) a small number of points when the alternative decision could have resulted in a loss (/gain) of points (relief/regret), and in particular, young adolescents showed a heightened evaluative response to relief outcomes, or 'lucky escapes' relative to children. Further studies should investigate whether this emotional response contributes directly to adolescent risk-taking. In addition, reasons for the age-related decline in risk-taking between adolescence and adulthood should be explored (see section **7.2.1**).

7.1.2 Chapter 3: Development of the integration of social and utilitarian cues in a probabilistic decision-making task

A number of studies, including the study described in **Chapter 2,** have shown that young adolescents are not yet mature in their ability to choose optimally in decision-making tasks. It has been suggested that one reason for this is that, relative to adults, adolescents are disproportionately influenced by social-emotional factors. However, this may be expected to operate to a greater extent in real life situations or in laboratory-based tasks with a strong emotional component, and to a lesser extent in simple, relatively unemotional decision-making tasks. In the decision-making task used in **Chapter 3,** adults outperformed young adolescents (aged 12-13), but this was not attributable to a heightened influence of social-emotional factors on the decision-making process. Computational modelling of adult and adolescent behaviour showed that the emotional content of the forced-choice stimuli (happy and angry facial expressions) influenced decisions in both age groups, and there was no difference in the extent or nature of this influence. This study represents a first step towards investigating the interaction between social and non-social influences on decision-making across development. Further applications of this approach are outlined in section **7.2.2**.

The study described in **Chapter 3** showed no age group differences in the impact of a social cue on decision-making in a simple forced-choice task. Therefore, other explanations for the age group difference in performance were sought. One interesting possibility from the literature is that adolescents approach decision-making tasks using relatively less cognitively sophisticated strategies, compared with adults. For example, studies including those by Huizinga et al. (2007) and Harbaugh et al. (2002) have shown that age-related improvements in performance on decision-making tasks are accompanied by (or due to) a decrease in decision-making bias, and an increase in the tendency to take into account all relevant sources of utilitarian information (performance feedback). Therefore, the study described in **Chapter 3** adopted a computational modelling approach to evaluate this suggestion. Performance was analysed computationally to show evidence that, while both adolescent and adult groups were able to take into account probabilistic reward feedback (wins and losses) in order to perform at a level above chance, there was a developmental asymmetry in the response to positive vs. negative performance feedback (wins and losses). Whereas adults integrated across both wins and losses in order to adjust or maintain ongoing selections, adolescents were not significantly responsive to positive feedback, a pattern that was consistent with a simple behavioural strategy of switching choices after incurring a loss.

Further studies are needed to explore this suggestion, in particular with regards its generalisability to other decision-making tasks. It would be interesting to explore possible relationships between the extent of developmental bias in decision-making, and executive function development. For example, the extent of bias in sensitivity to sources of performance feedback could be hypothesised to be related to the development of working memory efficiency (Romine & Reynolds, 2005) and perhaps to the ability to shift set (Davidson et al., 2006; Romine & Reynolds, 2005). Again, the application of a computational modelling approach to this problem could be fruitful (see section **7.2.2**).

7.1.3 Chapter 4: Development of mixed social emotion understanding across puberty

The studies described above were carried out to investigate the development of decision-making, including the influence of emotion on decision-making, in adolescence. However, it has been suggested that puberty stage rather than chronological age influences aspects of development across adolescence. In particular, the hormonal and psychosocial changes of puberty are thought to interact with emotional development, including via effects on the brain (see **Introduction** and **Chapter 4**). Therefore in **Chapter 4,** an exploratory study was carried out to explore the relationship between puberty stage and a measure of emotion understanding. Adolescent females aged nine to 16 years were divided into early, mid- and post-puberty groups on the basis of a pubertal self-report questionnaire, and then completed an emotion task. In this task, participants read and imagined a series of emotional scenarios that were designed to elicit social emotions (embarrassment and guilt) and basic emotions (anger and fear). Participants were instructed to imagine each scenario and to rate their imagined emotional response using four discrete rating scales, one for each of the four emotions. The ratings were then analysed using a novel measure that encapsulated the relative complexity or ‘mixedness’ in emotional responses, since previous work has suggested that the understanding of mixed emotion shows a protracted developmental trajectory (Harter & Buddin, 1987; Larsen et al., 2007). The results of this analysis showed greater mixed emotional responses (use of multiple rating scales) in the post-puberty than in the early-puberty group. This difference was seen for the social emotion scenarios featuring guilt and embarrassment, and not for the basic emotion scenarios featuring anger and fear.

This result is consistent with, and extends, previous work on mixed emotion and on social vs. basic emotion. For example, a study by Larsen et al. (2007) used structured interviews to show continuing development between the ages of seven and 12 in the tendency to report mixed emotional responses to a bittersweet video clip. Studies by Harter and colleagues have shown that the ability to describe situations in which a social emotion would be experienced emerges roughly two years later than the same for basic emotion (age 7 vs. age 5, respectively). The study described in **Chapter 4** extends this work, using a different methodology and age range, and by investigating relationships between emotional development and puberty stage. However, puberty stage was significantly related to age in the study. Further studies should investigate mixed emotion understanding in groups which differ in puberty stage but not in age.

The development of mixed social emotion understanding could be related to changes in self- and social awareness, which have been shown to occur across age and are thought to be related to puberty development. In addition, cognitive development during adolescence may also play a role in the development of mixed emotion understanding, by facilitating the representation of multiple emotional and mental states. However, there are a number of outstanding issues with the study conducted in **Chapter 4** and as such the results are tentative. The method of assessing mixed emotion understanding needs to be validated, for example by comparing previous structured interview methods and the self-report rating scale method within the same study. Another issue is the measurement of puberty. Self-report questionnaires assessing Tanner stage of puberty are appropriate for assessing the psychosocial effects of puberty, as their results reflect the respondent's body image and self-perceptions (Dorn et al., 2006). However they are less reliable in terms of identifying and differentiating between stages of puberty. The issue of puberty measurement will be explored in section **7.2.3**. Further studies are needed to assess the relationship between pubertal development and social-emotional awareness, given evidence for interactions between puberty hormones and regions of the brain important for emotion and social cognition (see section **4.1.1.1**).

7.1.4 Chapter 5: A functional magnetic resonance imaging study of social emotion processing in adolescents and in adults

Chapter 4 described a study that assessed the development during puberty of an understanding of social emotion. In **Chapter 5**, a study was carried out to investigate development of the functional neural correlates of social emotion processing using fMRI. Note that in order to compare the results with previously-published fMRI studies of social cognition, **Chapter 5** investigated the relationship between adolescent age rather than puberty stage on the fMRI pattern of results. Previous fMRI studies have shown an age-associated shift in activity between adolescence and adulthood within brain regions associated with mentalising (representing and processing mental states such as beliefs, feelings and desires), during mentalising/social cognition relative to control tasks. The study described in **Chapter 5** was carried out to investigate whether a comparable developmental shift would be observed during an overtly emotional mentalising task, i.e. social vs. basic emotion processing. As in **Chapter 4**, social emotions are defined as emotions that require representation of others' mental states, and the social emotions used in the task were embarrassment and guilt, as in **Chapter 4**. Basic emotions were defined as emotions that do not require a representation of others' mental states, and the basic emotions used in the task were fear (as in **Chapter 4**), and disgust (the replacement for **Chapter 4**'s anger; see **Chapter 5** section **5.2.2.1**).

The results in **Chapter 5** provide evidence that both adolescent and adult age groups showed activity (BOLD signal change) during social vs. basic emotion processing within mentalising regions of the brain, including the anterior rostral medial prefrontal cortex (arMPFC) and the posterior superior temporal sulcus (pSTS) bordering on the temporo-parietal junction (TPJ). However, there were age group differences in activity during social vs. basic emotion. Whereas a region of arMPFC was activated more strongly by adolescents than by adults for social vs. basic emotion (**Figure 5.5**), adults activated the left anterior temporal cortex (ATC) more strongly than did adolescents during this contrast (**Figure 5.4**). This set of results is in agreement with previous developmental fMRI studies of social cognition (see **Figure 5.7**; Wang et al., 2006; Blakemore et al., 2007; Pfeifer et al., 2007;

Moriguchi et al., 2007; Pfeifer et al., 2009; see Blakemore 2008 for review). The result in ATC is novel, but consistent with the adult mentalising fMRI literature (e.g. Frith & Frith, 2003; Frith, 2007).

In summary, **Chapter 5**, as well other recent fMRI studies, has shown an age-related decrease in activity within arMPFC during mentalising/social cognition relative to control tasks, whereas activity within more posterior, temporal cortex regions shows the opposite developmental pattern. There are several possible explanations for this pattern of results. First, there may be an age group difference in the cognitive strategy employed during these tasks, as has been shown using a different mentalising task (Dumontheil et al., 2009). Second, this change in cognitive strategy or proficiency might be accompanied by a shift in the recruitment of specialised brain regions, and/or may be related to neuroanatomical development. These possibilities will be discussed in more detail in section **7.2.4**.

7.1.5 Chapter 6: Effective connectivity during social emotion processing in adolescents and in adults

In **Chapter 6**, fMRI data from the functional imaging study of social and basic emotion processing in adolescents and in adults in **Chapter 5** were re-analysed to investigate effective connectivity within the mentalising system (arMPFC, pSTS/TPJ, ATC; Frith & Frith, 2003). Effective connectivity, defined as the influence that one neuronal system exerts over another, can be assessed using a statistical technique known as psychophysiological interaction (PPI) analysis (Friston et al., 1997). This analysis revealed evidence for functional integration between components of the mentalising system, during social relative to basic emotion processing, in that task-dependent interactions were shown between activity in the seed volume in arMPFC, and regions within the right pSTS, left TPJ and the left ATC.

This is the first study to show effective connectivity within the mentalising system, which is surprising given the wide availability of effective connectivity methods (available since at least 10 years ago), the large number of published fMRI studies showing activity within this circumscribed set of brain regions during mentalising relative to control tasks (Frith & Frith, 2003), and the fact that this collection of brain regions is frequently referred to as a ‘network’. Further studies should now be conducted to replicate the current finding using more standard and well-validated mentalising tasks (e.g. the Frith-Happé animations: Castelli et al., 2000). This could be done relatively easily using existing fMRI datasets, and could be supplemented using diffusion tensor imaging (DTI) to infer connecting white matter tracts.

Chapter 6 also showed evidence for age group differences in effective connectivity. The adolescent group showed stronger task-dependent connectivity between the arMPFC seed region and the left pSTS/TPJ, relative to adults. Further research is required before this result can be interpreted convincingly (see sections **7.2.4-5**). In particular, the developmental difference in **Chapter 6** is at odds with a (small) number of existing developmental connectivity studies, which show age-related increases in network correlations (Stevens et al., 2007, 2009; Menon et al. 2005). However, these studies investigated non-social domains of cognition, and it is not clear how comparable the findings are. Studies that have investigated the development of functional connectivity during 'rest' (Fair et al., 2007, 2008; Kelly et al., 2009) have shown that some within-network correlations increase with age, whereas others show age-related decreases. The current result should be replicated (e.g. using more standard mentalising tasks) before interpretations can justifiably be proposed.

Also of interest from **Chapter 6** is the finding that the adolescent group showed a significant PPI between arMPFC and the ATC during social vs. basic emotion, despite showing no mean activity within ATC during social relative to basic emotion processing (see **Chapter 5**). One possible explanation for this finding is that, prior to the ATC becoming functionally mature during development, it is engaged in a subthreshold or regulatory relationship with arMPFC. A similar interpretation was suggested in a study by Rao et al. (2008). In this study, no regions within PFC were active during an executive sensorimotor task thought to rely on PFC, but there was effective connectivity between parts of lateral PFC and relevant sensorimotor regions, suggesting that PFC plays a regulatory (rather than direct) role in the task. However, as stated in the preceding paragraph, follow-up studies should extend the current pattern of developmental findings in ATC using a variety of social cognition and mentalising tasks (e.g. Grosbras et al., 2007). DTI studies should investigate white matter pathways responsible for purported functional interactions between spatially distant components of the mentalising system (e.g. Kelly et al., 2009;

Giorgio et al., 2009), and the development of their contribution to functional brain activity across age.

7.2 Outstanding issues and future directions

7.2.1 Reasons behind adolescent risk-taking in decision-making tasks

Further studies should investigate which aspects of the task used in **Chapter 2** were key in producing the non-linear developmental profile of risk-taking. One possibility is that the emotional aspect of the task played a role. A previous study by Figner et al. (2009) has shown elevated adolescent relative to adult risk-taking in a 'hot', emotional version of the Columbia Card Task (CCT), and not in 'cold', less emotional version of the task. Similarly elevated adolescent vs. adult risk-taking was reported in a study in which participants made risky or safe decisions in a car driving game: adolescents took more risks than adults in a hot, social-emotional condition in which their friends were present, relative to a cold condition in which they played alone (Gardner & Steinberg, 2005). Therefore in **Chapter 2,** adolescent risk-taking may have arisen due to the emotional aspect of the task.

However, there is an outstanding issue with this explanation. In **Chapter 2,** as well as in Figner et al. (2009), in Gardner and Steinberg (2005) and in Eshel et al. (2007), elevated risk-taking was demonstrated in adolescents relative to adults in emotional tasks, but adolescents also take more risks than children. This has been shown in **Chapter 2**, in which the logit regression results shown an increase in the impact of risk on decisions increases between childhood and adolescence, and in an as yet unpublished study by O'Brien and Steinberg (2009) which showed heightened risk-taking in adolescents relative to children. In **Chapter 2**, an increase in counterfactual emotion was shown between childhood and young adolescence, but thus far, neither this nor any other study has shown evidence to suggest that emotional factors can explain the increase in risk-taking from childhood to adolescence, *and* its decrease into adulthood. Similarly, it has been suggested that sensitivity to peer influence may underlie adolescent risk-taking, but a self-report study has shown that children are indeed more sensitive to peer influence than are adolescents (Steinberg & Monahan, 2007). Therefore neither peer influence, not emotion, can solely account for the increase in risk-taking into adolescence *and* for its decrease into adulthood.

A solution to this issue, and one that has been suggested elsewhere, is to propose a dual-process model of the development of risk-taking (Casey et al., 2008; Steinberg, 2008). In this model, emotional factors such as heightened sensation-seeking, and social factors such as alignment with peers are suggested to cause an increase in risk-taking between childhood and adolescence, but cognitive factors (e.g. better judgment and control) are thought to contribute to the decline of risk-taking into adulthood. This dual-process model needs to be tested by conducting studies comparing adolescents with both children *and* adults, as in **Chapter 2**. Studies should take the approach used in Figner et al. (2009) and compare risk-taking under emotional and less-emotional task conditions. Emotionally engaging tasks are needed to more closely emulate the real-life conditions in which adolescents take risks, as studies including Steinberg's car driving experiment have shown that under calm, unemotional circumstances in a laboratory, adolescents are no more risk-taking than are adults. Further application of logit regression and other statistical approaches will be useful in evaluating separately the distinct factors that contribute to risky behaviour across age. Another fruitful approach could be to adopt a computational modelling approach, as was implemented in **Chapter 3**.

7.2.2 Adopting a computational approach to investigate factors influencing adolescent (social) decision-making

In **Chapter 3,** behaviour in a simple decision-making task was analysed computationally to disentangle and test specific hypotheses regarding the influence of discrete factors that may underlie behaviour. This approach should now be applied more widely to test hypotheses regarding the development of decision-making and social-emotional influences in adolescence. The approach is more flexible than many analytic techniques currently used to investigate behaviour, and can be implemented to test specific hypotheses in a focussed manner. The usefulness of the computational approach to understanding behaviour is particularly apparent in experimental situations in which several intertwined cognitive factors are all thought to influence a simple behavioural measure (e.g. Averbeck & Duchaine, 2009). Therefore, this approach could now be used to test the dual-system model of adolescent risk-taking, in which emotional factors such as heightened sensation-seeking are suggested to cause an increase in risk-taking between childhood and adolescence, but cognitive control factors are thought to contribute to its decline into adulthood (Casey et al., 2008; Steinberg, 2008). Another application could be to continue to model social influences on behaviour in adolescence as in **Chapter 3**, but using for example a version of the task in **Chapter 3** in which the face stimuli depict 'popular' same-age individuals (rather than older-age Ekman faces). An interesting extension to this study would be to include a component in the task that allows participants to choose to act in a risk-seeking or in a risk-averse/neutral manner. It would be interesting to model computationally the impact of social factors (e.g. popular/attractive vs. unpopular/unattractive faces) on the tendency to take risks in a decision-making task.

7.2.3 The measurement of puberty stage for use in adolescent cognitive development and cognitive neuroscience research

As summarised in **Chapter 4**, studies with non-human and human samples, including normal and clinical samples (e.g. with hormone abnormalities), have shown that aspects of adolescent neuroanatomical and functional brain development are related to the physical and hormonal changes of puberty. In addition, certain aspects of social-emotional development are thought to be related to puberty. These are hypothesised to occur via effects on the brain, and also by altering the body which impacts on social roles and self-image. Therefore, it is important to include puberty measures in adolescent cognitive development and cognitive neuroscience research, for two distinct reasons: 1) to directly investigate the effects of puberty, and 2) to reduce noise and control for possible confounds.

However, puberty is challenging to measure. For a start, puberty is neither a brief event nor a unitary phenomenon. Puberty lasts for several years, and comprises a number of distinct, partially independent and incompletely overlapping processes (Dorn et al., 2006). These processes include activation of adrenal and gonadal hormone systems, as well as physical growth, a shift in metabolism, changing social roles, and neuroanatomical development. The most appropriate measure of puberty will therefore depend in part on the specific research question.

A commonly used measure of puberty is Tanner Stage. Tanner staging categorises individuals along an ordinal puberty scale from 1 to 5, on the basis of breast and pubic hair development in females, and genital and pubic hair development in males (Tanner, 1971; Tanner & Whitehouse, 1976). Tanner staging should be carried out by a trained clinician. There are limitations to Tanner staging, in that the scale was developed with reference to a single ethnic group (there may be cross-ethnic differences) and in a relatively small sample of 200 children. Overweight girls will tend to be inaccurately staged, as breast development will be over-estimated. More fundamentally, Tanner staging only takes into account the physical effects of gonadal hormones, whereas in the early stages of puberty adrenal hormones are particularly important; therefore, Tanner staging has limited usefulness in distinguishing between the earlier stages of puberty, which may be of most interest with regards effects upstream or parallel hormonal effects on the brain. However, Tanner staging is currently the gold standard for puberty measurement, and is favoured by clinicians and researchers (Dorn et al., 2006).

In light of the above concerns, it might be expected that Tanner staging by physical examination could be usefully supplemented by hormonal assays, since this will measure adrenal and gonadal (or adrenal/gonadal-releasing) hormones upstream from their external physical effects. However, while hormone assays may be useful for measuring puberty stage in the future, at the present time it is unclear how hormone measurements should be combined with Tanner stages to give a measure of puberty stage. The levels of different puberty hormones fluctuate in monthly, circadian and even minute-to-minute cycles, and some hormones (e.g. testosterone) have more than one cycle; therefore, experimental control is difficult to establish (Cauter, 2001; Dorn et al., 2006). Little research has been done comparing hormone levels in different biological samples (saliva, blood, urine) with clinician-assessed Tanner stages (see e.g. Dorn et al. 2006), so it is unclear how much weight should be given to hormone levels, e.g. if these conflict with clinician-assessed Tanner stage. Therefore more research is needed in this area, and at present, hormone assays are not a valid alternative to clinician-assessed Tanner stage.

Tanner staging by external physical examination is not always practical or appropriate, e.g. when a behavioural study is carried out in school. Unless the research question is clinically urgent, it is unlikely that a school will accept the inconvenience of setting up a physical examination procedure (preparing the children and parents, establishing the necessary ethical and legal procedures). Therefore in these situations, Tanner stage can be assessed by self-report questionnaire. A relatively large number of studies, including the study in **Chapter**

4, have assessed self-rated (or parent-rated) Tanner stage using the Petersen Development Scale (PDS; Petersen et al., 1988). This is a questionnaire that includes items assessing hair growth, skin changes and growth spurt, with sex-specific items i.e. menarche and breast development in female, and genital growth and facial hair in males (see **Appendix 4.1** for an adaptation of the female version). As such, the PDS measures a composite puberty score that includes the effects of adrenal and growth hormones, as well as gonadal hormones. Correlations with clinician-assessed Tanner stage are not especially high: one study found correlations between 0.61 and 0.67 in 11-13 year old girls for the self-report PDS (Brooks-Gunn et al. 1987; correlations are even lower for parent-report PDS). The extent to which these relatively low correlations are due to inaccurate self-rating vs. the distinct effects of adrenal/growth vs. gonadal hormones needs to be evaluated. Therefore, the PDS should be used with caution to estimate Tanner stage when a physical examination is not possible. However, on a different note, it could be the case that if the research question does not concern hormone levels and Tanner stage, but instead relates to self-image, self-consciousness or social awareness (as in **Chapter 4**), it can be argued that the PDS is the most relevant measure, as it directly assesses self-perceived puberty stage (see Dorn et al. 2006 for discussion).

In summary, there is much scope for investigating relationships between the brain, cognition, behaviour and puberty[15]. However, methodological research evaluating and comparing different puberty measures should be conducted alongside this research. Researchers should consider which aspect of puberty is most relevant to their research question and select their measure of puberty accordingly.

7.2.5 Age group differences in functional brain activity: what do they mean?

A number of developmental fMRI studies of social cognition, including the study described in **Chapter 5**, have shown greater BOLD signal change within adolescent relative to adult arMPFC, during mentalising relative to control tasks. There are a

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[15] The candidate is currently involved in a study investigating relationships between functional (fMRI) and structural (VBM) brain measures, and puberty stage (assessed using salivary hormone samples, clinician-assessed Tanner stage and self-report PDS), in two groups of females matched for age but differing in puberty stage. Inverse relationships are predicted between puberty stage and (a) cortical grey matter, (b) BOLD signal in arMPFC. It is predicted that some of the variability within the adolescent sample in **Chapter 5** will be attributable to pubertal development.

number of possible (and not mutually exclusive) explanations for this developmental finding.

One possibility is that developmental differences in BOLD response arise due to an age group difference in the cognitive strategy employed during these tasks, which might be associated with differential recruitment of functionally-specialised brain regions. For example, in the study in **Chapter 5**, adolescents may employ a more effortful, on-line mentalising-based strategy to imagine social emotion situations, which may recruit 'mentalising region' arMPFC more strongly. Adults may employ a strategy based more heavily on semantic social knowledge, and thus recruit the ATC, a region that is thought to represent social semantic knowledge. Similar interpretations could be applied to similar studies such as Blakemore et al. (2007).

However, this cognitive interpretation of the fMRI data is at present mere reasoned speculation (see Poldrack, 2008) and indeed could be construed as a confound in published developmental fMRI studies. Therefore, a more thorough cognitive characterisation of how adolescents perform social cognition tasks is now needed. This endeavour should be approached using appropriate social cognition tasks, including those which can be analysed using computational models (**7.2.2**; **Chapter 3**). For example, in order to evaluate the specific cognitive hypothesis proposed in the preceding paragraph and in **Chapter 5**, behavioural studies could be conducted testing script usage vs. on-line mentalising in adolescents vs. adults. Computational models could be developed predicting probable behaviour in such a task, given reliance on scripts vs. reliance on on-line mentalising. These could subsequently be extended to test the contributions of region-specific functional brain activity to scripts vs. on-line mental state usage (as in Hampton et al., 2008; Behrens et al. 2009), in addition to other cognitive components of mentalising which are thought to develop during adolescence (e.g. executive-social interactions, Dumontheil et al. 2009). In adults, a study could be conducted using transcranial magnetic stimulation to assess disruption of mentalising performance when social semantic processing regions are targeted. The research could be supplemented where possible with cognitive profiling of patients who have sustained lesions to different parts of the social brain, e.g. ATC vs. arMPFC, during adolescence and adulthood (c.f. Anderson et al., 1999).

However, age group differences in BOLD response during social cognition (or indeed any) tasks could be elicited in the absence of any differences in cognitive competence or strategy (Kuhn, 2006). Age group differences in electrical or metabolic responsiveness within task-associated brain regions could give rise to age differences in BOLD response. Given evidence for neuroanatomical (including synaptic) development during adolescence, this factor is likely at least to contribute to age group differences in BOLD response, if not entirely account for them. For example, the precise time-course and nature of neuronal-vascular coupling (Peppiatt et al., 2006) is likely to differ between brain regions, and these regional differences may emerge at different points during development. If there are indeed region-specific trajectories of synaptic pruning during adolescence, as have been hypothesised, this may lead to increased 'efficiency' of regional brain activity (Durston et al., 2006; see **1.4.3.1**), in terms of increases in both information processing efficiency (e.g. efficiency to accomplish the same cognitive task), and metabolic efficiency (note that the two are likely to be linked; Attwell & Laughlin, 2001). In addition, global increases in myelination and axon calibre are hypothesised to contribute to increased efficiency of network integration, including increased precision of temporal encoding (Paus et al., 2008; see **Introduction,** section **1.4.3.2**). Further research is needed on developmental changes in region-specific metabolic demands and information processing efficiency, as well as neuronal-vascular coupling, in order to interpret developmental fMRI findings.

7.2.6 Future directions using a multimodal approach to study the development of social cognition and its neural basis: Effective connectivity, structural and diffusion neuroimaging, behavioural testing

Chapter 6 showed evidence for an age group difference in effective connectivity between components of the mentalising system. This result, pending replication, is one step towards demonstrating that age group differences in BOLD signal have functional relevance – whether this is due to cognitive development and resultant changes in the recruitment of functionally specialised (social) brain regions, or development in metabolic/information processing efficiency due to neuroanatomical development in social brain regions, or both.

Studies should now be conducted to investigate the development of effective connectivity during social cognition tasks, starting with existing social fMRI datasets (e.g. Blakemore et al., 2007). Developmental relationships between regional BOLD signal and network function should then be investigated. Subsequently, social cognition tasks in which performance can be more accurately quantified than in the social emotion task used in this thesis should be used in fMRI to investigate relationships between regional BOLD signal, functional integration, and task proficiency.

In addition, it would be interesting to conduct the above studies in combination with measures of grey and white matter structure and integrity (e.g. VBM, DTI). Similar developmental studies have been conducted in non-social cognitive domains: for example, Olson et al. (2009) showed that DTI-assessed white matter integrity in tracts serving frontal lobe regions predicted delay discounting behaviour in participants aged nine to 23. Liston et al. (2005) showed that DTI-assessed fronto-striatal white matter integrity was related to accuracy in performing a go/no-go task. It is predicted that proficiency in mentalising tasks will be related to white matter integrity within tracts connecting regions of the mentalising system. Proficiency in the mentalising task in Dumontheil et al. (2009), which requires integration of executive functions and visual perspective information, is predicted to correlate with the integrity of white matter tracts connecting regions of the mentalising system with executive control regions.

Other studies have shown correlations between BOLD signal increases during executive tasks, and white matter integrity in presumed task-related tracts (e.g. Olesen et al., 2003). Similar studies should now be conducted in the domain of social cognition. This could be conducted alongside DTI studies in adults that have begun to parcellate white matter connectivity of a number of brain regions (Beckmann et al., 2009).

7.3 Wider implications

This section will discuss wider implications of developmental cognitive neuroscience research and developmental psychology research in this thesis and elsewhere.

7.3.1 Education

Knowledge of brain development, and how this development influences cognition and learning could, and indeed does, have an impact on education (see Blakemore & Frith, 2005). The understanding of how the brain mechanisms that underlie learning and memory change across age, and how this impacts cognition, is vital for optimizing education for individuals of different ages. This applies to the various stages of adulthood, as well as childhood and adolescence. Lifespan considerations on education, including encouraging and optimizing life-long learning, have recently been areas for government policy initiatives (e.g. Beyond Current Horizons project, see Burnett et al. 2009b). Relatedly, it is important to understand how learning in individuals of different ages is influenced by aspects of the environment, including its social and emotional context.

Social-emotional factors have been shown to play an important role in shaping learning and academic performance, as well as *vice versa*. It is possible that the social, potentially emotionally charged context of many educational environments may interfere with the cognitive resources that can be devoted to academic learning. For example, a secondary school classroom environment could be overwhelmingly social for the less socially-competent, and the reported recent rising incidence of face-to-face and cyber-bullying by schoolchildren is likely to have wide impact. However, learning to cope with a complex social environment is an important part of development, and must not be neglected. Constructive avenues for future educational policy could draw on evidence that adolescence is an important period for learning about emotions and opinions of the self and others, and therefore might be a particularly fruitful time for educational programmes to focus on fostering empathy and social support.

Another finding that could have impact is the notion that the brain is still developing substantially during adolescence. Previously, early childhood was seen as a major opportunity (a ‘sensitive period’) for teaching, due to the brain development which was thought to be restricted to this period. Therefore, the finding that parts of the brain are reorganized during the teenaged years suggests that this period might be seen as part of an extended ‘sensitive period’ for learning. Aspects of learning which may be particularly malleable during adolescence, and which education could focus on, are those which rely on parts of the brain that undergo protracted anatomical development: for example, internal control, multi-tasking and planning – which to an extent, secondary education already focuses on – but also self-awareness and social cognitive skills, such as perspective-taking and understanding complex social emotions.

Finally, it could be fruitful to include in the educational curriculum for adolescents some teaching on the changes occurring in the brain during puberty and adolescence. Adolescents might be interested in, and could benefit from, learning about the changes that are going on in their own brains.

7.3.2 Psychiatric disorders

A better understanding of adolescent brain development and cognition is also vital for understanding psychiatric disorders, many of which have their peak age of onset during adolescence (Paus et al., 2008; see **Figure 7.1**). It has been suggested that the emergence of certain disorders in adolescence is directly linked to brain development (e.g. schizophrenia, Feinberg, 1982; depression, Davey et al., 2008), and to the maturation of certain cognitive functions such as planning and counterfactual thinking (e.g. depression and social anxiety, Davey et al. 2008). Work presented in this thesis is particularly relevant to the emergence of (i) disorders of incentive processing, and (ii) disorders of social processing. These will briefly be discussed in the next sections.

Figure 7.1 The onset of many psychiatric disorders occurs during adolescence. Mean age of onset of a number of psychiatric disorders in the USA in recent years. Graph from Paus et al. (2008).

7.3.2.1 Disorders of incentive processing

Certain disorders of incentive processing commonly arise during adolescence, and cognitive neuroscience research will inform the understanding of these disorders. This section will focus on addiction as one example, although note that others are relevant, e.g. schizophrenia.

Heightened risk-seeking during adolescence is hypothesised to underlie the high incidence of experimentation with addictive substances (alchohol, tobacco, illegal drugs) during adolescence, and in some cases this experimentation develops into addiction. While it should be noted that individuals who develop substance use disorders often show emotional abnormalities prior to adolescence (Maggs et al., 2008), it has been suggested that certain characteristics of adolescence predispose individuals to a risk of developing addiction. Specifically, a 'hypo-active' neural incentive processing system (e.g. ventral striatum) is hypothesised to result in a drive for more immediate, high risk and powerful rewards (Spear, 2000), while 'hyper-activity' of the system during reward consummation may mean that adolescents experience these rewards as more intensely pleasurable than do adults (Geier & Luna, 2009). In addition, continuing maturation within prefrontal cortex cognitive control systems is said to predispose adolescents to act on their reward-seeking urges (Casey et al., 2008). More evidence is needed in support of these hypotheses, but they are suggestive.

The transition from incentive-seeking and experimentation to full-blown addiction may be more rapid and insidious in adolescence. Evidence from a number of non-human animal studies suggests that adolescents may experience drug effects that are more pleasant or benign than those experienced by adults (for a review, see Spear, 2000). For example, adolescent rodents have been observed to experience reduced sensitivity to the motor impairing and sedative consequences of alcohol relative to adults (Hollstedt et al., 1980; Ernst et al., 1976). Greater biological tolerance to alcohol in adolescence may engender less unpleasant hang-overs per unit of alcohol consumed (York & Chan, 1993). Similar patterns have been reported with other addictive substances (Spear, 2000). These factors may partially account for the elevated rate of progression from causal use to substance dependence in adolescence (Spear, 2000). More research is needed on the neural and biochemical differences between adolescent and adult brains that mediate these differential effects, including the factors that mediate the transition from experimentation to addiction, and their interaction with environmental and social influences.

7.3.2.2 Social anxiety disorder

A rather different disorder that tends to arise during adolescence is social anxiety disorder (SAD), which is characterised by a chronic and exaggerated fear of negative social feedback. SAD has its peak incidence and mean age of onset in adolescence (with lifetime incidence of 11%; Banerjee, 2008; Beesdo et al., 2007), and results in an array of negative life consequences including unfulfilled economic potential (e.g. due to poor school attendance) and interference with normal social development (e.g. due to poor peer socialisation).

The cognitive-developmental basis of SAD is poorly understood. There is evidence that socially anxious children have specific social cognitive difficulties with understanding the links between mental states (Banerjee, 2008). However, mental state processing ability also shows protracted development throughout healthy adolescence (e.g. Dumontheil et al., 2009), and furthermore, a high but sub-clinical level of social anxiety may be a normative feature of adolescence (Sebastian et al., 2009). Research is needed on the cognitive components that differentiate normative adolescent social development from its pathological counterparts in SAD, in order for individuals at risk to be identified. Could adolescence itself be considered as a 'risk factor' for SAD, or is pathological social processing in SAD fundamentally different from typical adolescent self-consciousness and social awareness?

Individuals with SAD, or at risk of developing SAD, also show abnormalities within parts of the brain that undergo protracted structural development up to or during adolescence, including brain regions that are implicated in social cognition such as the rostral and anterior cingulate cortex (including arMPFC), the amygdala, and fronto-amygdalar white matter tracts (Phan et al., 2009; Milham et al., 2005; Blankenstein et al., 2009). The functional relevance of these abnormalities in SAD, and their relationship to typical adolescent neuroanatomical development, is a potentially fruitful avenue for future investigation.

7.4 Overall summary

This thesis combines the new and rapidly expanding fields of social cognitive neuroscience, and developmental cognitive neuroscience, to present novel evidence for development during adolescence of aspects of decision-making, emotion understanding and the neural correlates of social cognition. Much remains to be done. Future research could focus on (1) the mechanisms by which social and emotional factors influence decision-making during adolescence, especially risky decision-making; (2) possible relationships between pubertal development and neuroanatomical/cognitive development; (3) the extent to which neuroanatomical and/or cognitive development underlie changes in functional brain activity during adolescence; and (4) relationships to the development of psychiatric disorders.

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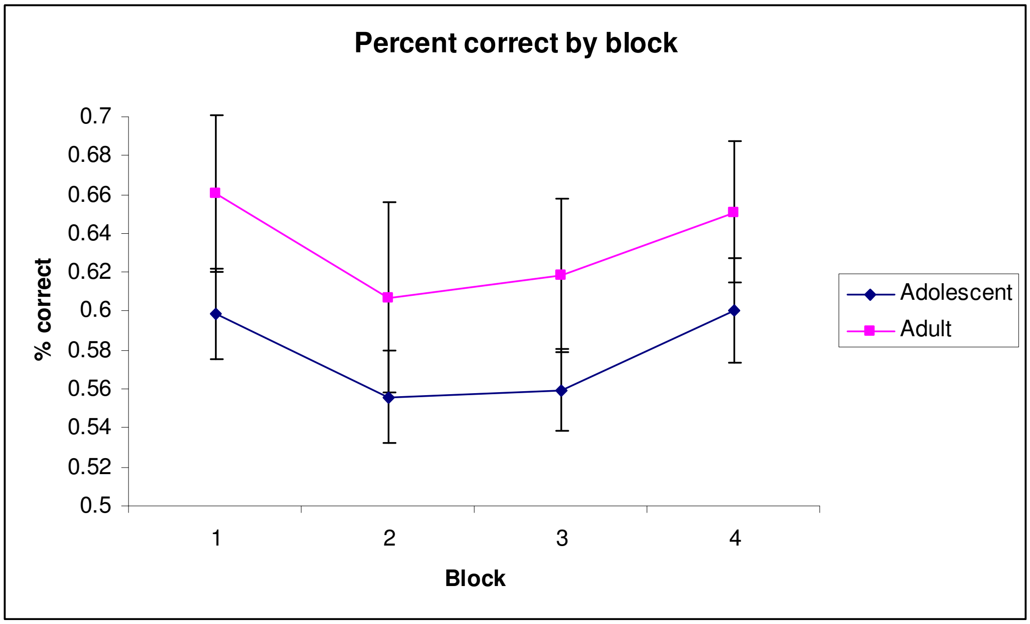
Appendix 2.1: Gambling task parameter structure

x1 and y1 are the two possible outcomes of lottery1, p(x1) is the probability of obtaining x1, outcome1 is the actual outome of lottery1, EV1 is the expected value of lottery1 and SD1 is the standard deviation for lottery1. Similarly q(x2), x2, y2, outcome2, EV2 and SD2 are the parameters for lottery2. dEV and dSD are the differences in expected values and standard deviation respectively between the two lotteries.

Trial	p(x1)	x1	y1	outcome1	EV1	SD1	q(y1)	x2	y2	outcome1	EV2	SD2	dEV	dSD
1	0.2	-50	-200	-200	-170	60	0.2	50	-50	-50	-30	40	-140	20
2	0.5	200	-50	-50	75	125	0.5	200	-200	200	0	200	75	-75
3	0.8	200	-200	200	120	160	0.5	200	50	50	125	75	-5	85
4	0.2	200	50	50	80	60	0.5	50	-200	-200	-75	125	155	-65
5	0.8	50	-200	50	0	100	0.2	50	-50	-50	-30	40	30	60
6	0.5	200	50	50	125	75	0.5	200	-200	200	0	200	125	-125
7	0.5	200	-200	-200	0	200	0.8	200	-50	200	150	100	-150	100
8	0.2	200	-200	200	-120	160	0.5	200	-50	-50	75	125	-195	35
9	0.2	50	-200	-200	-150	100	0.8	50	-50	50	30	40	-180	60
10	0.2	50	-50	-50	-30	40	0.2	50	-200	-200	-150	100	120	-60
11	0.2	200	-50	200	0	100	0.2	200	50	50	80	60	-80	40
12	0.8	200	-50	-50	150	100	0.5	200	-200	200	0	200	150	-100
13	0.8	50	-50	50	30	40	0.5	200	-200	-200	0	200	30	-160
14	0.2	-50	-200	-200	-170	60	0.8	-50	-200	-50	-80	60	-90	0
15	0.5	200	-50	-50	75	125	0.2	200	50	50	80	60	-5	65
16	0.8	200	-200	200	120	160	0.2	200	-50	-50	0	100	120	60
17	0.8	50	-200	50	0	100	0.2	200	-200	200	-120	160	120	-60
18	0.8	-50	-200	-50	-80	60	0.8	50	-200	50	0	100	-80	-40
19	0.5	-50	-200	-50	-125	75	0.2	200	-200	-200	-120	160	-5	-85
20	0.2	200	-200	-200	-120	160	0.8	50	-200	50	0	100	-120	60
21	0.2	200	-200	-200	-120	160	0.8	50	-200	50	0	100	-120	60
22	0.8	200	-50	200	150	100	0.8	200	-200	-200	120	160	30	-60
23	0.5	200	-50	-50	75	125	0.2	200	-200	200	-120	160	195	-35
24	0.5	200	-200	200	0	200	0.8	50	-50	50	30	40	-30	160
25	0.5	50	-200	50	-75	125	0.5	-50	-200	-50	-125	75	50	50
26	0.5	200	50	200	125	75	0.8	200	-50	-50	150	100	-25	-25
27	0.8	-50	-200	-50	-80	60	0.2	50	-200	-200	-150	100	70	-40
28	0.8	200	50	50	170	60	0.8	200	-200	200	120	160	50	-100
29	0.2	-50	-200	-200	-170	60	0.5	-50	-200	-50	-125	75	-45	-15
30	0.5	50	-200	50	-75	125	0.5	-50	-200	-200	-125	75	50	50

Appendix 3.1: The pattern across blocks of percent correct choices (w.r.t. ideal observer model) is highly similar between groups. This suggests that age group differences in performance are due to stable differences in strategy, not merely due to slower learning or familiarisation with the task in adolescents relative to adults.



<u>Appendix 4.1:</u> Physical development questionnaire

Responses to this questionnaire were used to assign participants to one of three puberty groups: Pre-puberty, Mid-puberty and Post-puberty. We assigned participants to the Pre-puberty group if they answered ‘no’ to question 6 and also circled option ‘a’ in response to questions 3, 7 and 8. We assigned participants to the Post-puberty group if they answered ‘yes’ to question 6 and also circled options ‘c’ and ‘d’ in response to questions 3, 7 and 8. Participants who did not fit either of these criteria were assigned to the Mid-puberty group.

Development Questionnaire

This is a standard questionnaire that is used to look at development during childhood and adolescence.

This questionnaire may be completed by:

*The parent(s)
*The parent(s) and pupil
*The pupil

*Please place a tick against the option chosen.

The questions are about physical changes that normally happen to young people at different ages. As we are researching development during childhood and adolescence, it is important for us to know at approximately what stage each child/young person is in terms of physical development. We would therefore like to ask you to do your best to answer these questions carefully.

If you do not understand a question or do not know the answer, try to answer as best as you can or leave it blank. If you don't feel comfortable answering a question, please just leave it blank and move on to the next one.

1. What is your date of birth?

2. How tall are you?

3. How would you describe any recent growth in height?
    a. I have not yet had a growth spurt (a "spurt" means a sudden increase in height)
    b. A growth spurt seems to have just begun
    c. I have noticed a definite growth spurt taking place
    d. I have finished having a growth spurt and have barely grown at all recently

4. How much have you grown in height in the last 6 months?

5. How much do you weigh?

6. Have you started having periods yet?
    a. Yes
    b. No

If 'yes', at what age did they start?

7. Would you say that your bodily hair (e.g. under your arms):
    a. Has not yet started growing
    b. Has only just begun to grow
    c. Has been increasing for some time
    d. Is no longer increasing – it seems to have stopped growing

8. Have you noticed any skin changes on your face or neck, especially spots?
    a. I have not noticed any changes
    b. I have begun to notice small changes
    c. I am definitely noticing a lot of changes at the moment

d. The changes seemed to have finished happening

9. Do you think any changes in your physical development have been happening any earlier or later than most other girls your age?
    a. much earlier
    b. a little earlier
    c. at about the same time
    d. a little later
    e. much later

Appendix 4.2: Scenarios used in the emotion questionnaire

Anger

1. One day you went to the park. Somebody had hurt a baby bird.
2. You saw your brother in your bedroom. He took something of yours withou asking.
3. You asked your friend to hand in your homework. She forgot, and you got int trouble.
4. You were standing in the dinner queue. Someone pushed in front of you.
5. You got a new CD for your birthday. You lent it to your brother and he broke it.
6. You saw someone walk by the window. They threw rubbish into your garden.
7. You told your friend a secret. He told everyone about it.
8. You tried really hard on a maths test. Your teacher thought you had cheated.

Fear

1. You were riding your bike down a steep hill. Suddenly, your brakes stoppe working.
2. You were watching the news on TV. You heard that a poisonous bee wa invading Britain.
3. It was a very dark and windy night. Suddenly, all the lights went out in the house
4. You felt something on your neck. It was a huge spider crawling on you.
5. You were climbing a very tall tree. You realized the branch you were standing o was going to break.
6. Your mum was driving you to school. The road was very icy and the car kep skidding.
7. Your friend was being bullied at school. The bully threatened to hurt you too.
8. You were watching TV at night. Suddenly, a loud noise made you jump.

Embarrassment

1. At the dinner table, someone told a funny joke. While laughing, you burpe loudly.
2. You were eating lunch at school. You realised you had food stuck in your teeth.
3. You ate too many sweets at a party. You threw up in front of your friends.
4. You were wearing your school jumper inside out. Everyone was laughing at you.
5. You dressed as a mouse for a fancy dress party. When you got there, no one els was dressed up.
6. You made a joke about your best friend. Then you realized she was standing righ behind you.
7. You were nasty about a girl in your class. Your friend said that she was his ne girlfriend.
8. While shopping, you broke a cup. You tried to leave quietly, but the manag shouted for you to stop.

Guilt

1. You were running down the corridor at school. You bumped into your friend an she fell over.
2. You were meant to be looking after your little brother but you went out. Whe you got back, he was crying.
3. You told your friend you would meet her after school, but you forgot. She wa waiting in the playground by herself.
4. Your little sister asked you to help tie her shoe laces, but you didn’t. She fell ove and hurt herself.
5. You took your dog to the park. While you were talking to your friend, your do got lost.
6. Your Mum bought you a hamster. You didn’t look after it properly and it died.
7. You were looking at your Mum’s jewellery but you were not careful and yo broke it. You knew she would be upset.
8. You were running around the living room. You accidentally knocked over th television.

Appendix 5.1

fMRI study of social emotion: Sentences used in the scanner

Disgust

Self

Someone did a massive sneeze and snot flew in your face.

You saw a big hairy fly laying eggs on your friend's lunch.

Your dad told you that the fridge was infested with maggots

You saw dried green vomit stuck to the inside of your friend's sink.

You were in your friend's garden and you put your hand in slimy cat poo.

You saw a pile of rotting guts near the dustbin at your friend's house.

A dirty child picked its nose with its fingers and wiped it on you.

You and your friend saw a dead pig's head in an alleyway.

Someone had left the toilet seat dirty and you sat on it by mistake.

You saw your friend's dog eating its own vomit in the garden.

You took a big gulp of your friend's milk but it had gone off.

You found a sandwich under your friend's bed with ants crawling on it.

You saw flies and stinking fish in your friend's kitchen bin.

You were with your friend and you slipped on some wet dog poo.

Someone on the bus did a big snotty sneeze in your face.

You saw a big hairy fly crawling all over your friend's lunch.

Your friend was vomiting next to you and you could smell it.

You saw a pile of rotten fish guts by the sink in your friend's kitchen.

Other

Snot flew all over your Mum's face when someone sneezed.

Your Mum saw a big hairy fly laying eggs on her friend's lunch.

Your Mum's friend said that the fridge was infested with maggots.

Your Mum saw dried green vomit stuck inside her friend's sink.

Your Mum put her hand in slimy cat poo in her friend's garden.

Your Mum saw a pile of rotting guts near the dustbin at her friend's house.

A dirty child picked its nose and wiped it on your Mum.

Your Mum and her friend saw a dead pig's head in an alleyway.

Someone had left the toilet seat dirty and your Mum sat on it.

Your Mum saw her friend's dog eating its own vomit.
Your Mum took a big gulp of her friend's milk but it had gone off.
Your Mum found a sandwich under her friend's bed with ants crawling on it.
Your Mum saw flies and stinking fish in her friend's kitchen bin.
Your Mum was with a friend and she slipped on wet dog poo.
Someone did a big snotty sneeze in your Mum's face.
Your Mum saw a big hairy fly crawling on her friend's lunch.
Your Mum's friend was vomiting next to her and she could smell it.
Your Mum saw some rotten fish guts by the sink in her friend's kitchen.

Fear

Self

A strange man's face appeared at your window in the night.
An angry dog was barking and running towards you and your friend.
You suddenly woke up as someone screamed by your bed.
You thought that someone was following you in the dark.
A man on a motorbike suddenly swerved and almost hit you.
Your dad slammed on the brakes as a lorry hurtled towards you.
You were with your friend and a creature ran up your neck.
A dog was growling and trying to bite you and your friend.
You and your friend were alone in the dark and there were funny noises.
You were with your friend and a spider ran across your bare feet.
Your friend said there was a hairy spider crawling on your neck.
You were watching horror movies with your friend and a loud noise made you jump.
You felt something tickling your neck and your friend screamed that it was a huge spider.
The old cupboard door slammed and you and your friend were locked in.
Your friend screamed that there was a wasp inside your jumper.
You imagined that a scary face appeared at your window in the night.
You were about to cross the road when a motorcyclist swerved in front of you.
You suddenly woke up as a face appeared at your window.

Other

A face appeared at your Mum's window in the night.
An angry barking dog was running towards your Mum and her friend.

Your Mum suddenly awoke as someone screamed by her bed.

Your Mum thought someone was following her in the dark.

A man on a motorbike swerved and almost hit your Mum.

Your Mum slammed on the brakes as a lorry driver almost hit her.

Your Mum was with her friend and a creature ran up her neck.

An angry dog was trying to bite your Mum and her friend.

Your mum and her friend were alone in the dark and there were funny noises.

Your Mum was with her friend and a spider ran across her bare feet.

Your Mum's friend said there was a hairy spider on her neck.

Your Mum was watching horror movies with her friend and a loud noise made her jump.

Something tickled your Mum's neck and her friend screamed that it was a huge spider.

The old cupboard door slammed and your Mum and her friend were locked in.

Someone screamed that there was a wasp inside your Mum's jumper.

Your Mum imagined a scary face looking into her window at night.

Your Mum was about to cross the road when a motorcyclist swerved in front of her.

Your Mum suddenly woke up as a face appeared at her window.

Embarrassment

Self

You did a squeaky fart in front of a boy you fancied.

Your friend said you had a wet patch on your bum all the way home.

You couldn't stop blushing in front of a boy you liked.

Your friend told you that you had really bad breath.

You were quietly picking your nose but your friend saw you.

You were eating with your friend and spinach got stuck in your teeth.

You sneezed in front of someone and snot flew out of your nose.

You fell asleep on the bus with your head on someone's shoulder.

Food flew out of your mouth while you were eating with your friend.

You were eating with your friend and you dribbled down your top.

You tripped over in front of a boy you liked.

You were at the cinema with your friend and you got loud hiccups.

You fell asleep on the train and dribbled on the person next to you.

Your dad started doing rock 'n' roll dances in the supermarket.

You farted loudly in front of your friend's big brother.

You sneezed on the bus and snot flew onto someone sitting next to you.

Your friend said you had baked beans down your top all day.

Your dad was singing loudly in a silly voice in the street.

Other

Your Mum did a squeaky fart in front of her boss.

Your Mum's friend said she had a wet patch on her bum all the way home.

You Mum couldn't stop blushing in front of her work friend.

Your Mum's friend told her she had really bad breath.

Your Mum was quietly picking her nose but her friend saw.

Your Mum was eating with her friend and spinach got stuck in her teeth.

Your Mum sneezed in front of someone and snot flew from her nose.

Your Mum fell asleep on the bus with her head on someone's shoulder.

Food flew from your Mum's mouth while she was eating with her friend.

Your Mum dribbled down her top while eating with her friend.

Your Mum tripped in front of her boss at work.

Your Mum was at the cinema with her friend and got loud hiccups.

Your Mum fell asleep on the train and dribbled on the person next to her.

Your Mum's friend started doing a silly dance in the supermarket.

Your Mum farted loudly in front of her friend's husband.

Your Mum sneezed on the bus and snot flew onto someone next to her.

Your Mum's friend said she had baked beans down her top all day.

Your Mum's friend was singing loudly in a silly voice in the street.

Guilt

Self

You laughed at a quiet girl you know and it made her sad.

You sent a horrible text message to your friend when you were angry.

You laughed when your friend told you she was feeling really upset.

You forgot to feed your friend's cat while she was on holiday.

You got really cross one day and swore at a little child.

You joined in when people were laughing at your best friend.

You completely forgot about your best friend's birthday and she was upset.

You spread gossip about your best friend and she found out.

You pretended to be sick so you didn’t have to go and visit your gran.

Your gran asked you to post an important letter but you lost it.

You didn't help your little brother with his work and he was crying with frustration.

You accidentally laughed when your friend tripped over and hurt herself.

You found some money in your friend's house and kept it for yourself.

You forgot to meet your friend and she was waiting in the cold by herself.

You lied to your dad when you wanted to go out with your friend.

You kept some money that a little old lady had dropped in the street.

You wrote a horrible email to your friend when you were angry.

You joined in when people were gossiping behind your best friend's back.

Other

Your Mum laughed at a quiet lady at work and it made her sad.

Your Mum sent a horrible text message to her friend when she was angry.

Your Mum laughed when her friend said she was feeling upset.

Your Mum forgot to feed her friend's cat while she was away.

Your Mum got cross and swore at her friend's baby.

Your Mum joined in when people laughed at her best friend.

Your Mum forgot about her best friend's birthday and she was upset.

Your Mum spread gossip about her best friend and she found out.

Your Mum pretended to be sick so that she didn’t have to visit her friend.

Your Mum's friend gave her an important letter to post and she lost it.

Your Mum didn't help your little brother and he was crying with frustration.

Your Mum laughed when her friend tripped over and hurt herself.

Your Mum found some money in her friend's house and kept it.

Your Mum forgot to meet her friend and she was waiting in the cold.

Your Mum lied to her friend when she didn't want to see her.

Your Mum kept some money that an old lady had dropped in the street.

Your Mum wrote a horrible email to her friend when she was angry.

Your Mum joined in when people were gossiping about her best friend.

Happy[16]

You finished all of your exams and had a party.

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[16] Happy sentences were shown at the end of the scanning session in order to counteract possible negative emotional carry-over effects from the emotion stimuli.

You won an iPod in a competition.

You were about to go on a summer holiday.

You won tickets to the cinema for you and your friends.

You went out for a special meal with your family.

You were looking forward to your birthday celebrations.

Appendix 5.2

fMRI study of social emotion: Pilot questionnaire

An example questionnaire which was distributed to child pilot participants is shown overleaf. There were eight different versions of the questionnaire, with the order of the four emotions fully counterbalanced and the order of the specific sentences reversed within each emotion.

Emotion questionnaire 11

In this questionnaire, you will be answering questions about the **emotions** you feel in different situations. The emotions you will be asked about are:

> **Disgust:** you might feel *disgusted* if you smell rotting rubbish in the street outside your house.
>
> **Embarrassment:** you might feel *embarrassed* if you have to go to school with food stains down your clothes.
>
> **Fear:** you might feel *afraid* if there is an angry dog running towards you in the park.
>
> **Guilt**: you might feel *guilty* if you forgot about your friend's birthday and she was sad.
>
> **Happiness:** you might feel *happy* if you won a pair of cinema tickets for you and your friend.

For each sentence you read, you should *imagine* that the situation described is happening to you, and circle one of the numbers from 1 to 4 to show how much of the emotion you would feel.

1 = I would not feel the emotion at all
2 = I would feel the emotion a little bit
3 = I would feel the emotion quite a bit
4 = I would really feel the emotion a lot

Then, circle one of the numbers from 1 to 4 to show how sure you feel about this.

1 = I am not at all sure
2 = I feel a bit unsure
3 = I am quite sure
4 = I am definitely sure

For example,

DISGUST	**How DISGUSTED?**	**How sure ar you abou this?**
You saw a dustbin spilling its rubbish into the street.	1 2 [✓ 3] 4	1 2 3 [✓ 4]

Thank you! ☺

DISGUST	**How DISGUSTED?**	**How sure ar you about this?**
1. You saw flies and stinking fish in your friend's kitche bin.	1 2 3 4	1 2 3 4
2. You saw dried green vomit stuck to the inside of you friend's sink.	1 2 3 4	1 2 3 4
3. You saw a big hairy fly laying eggs on your friend's lunch.	1 2 3 4	1 2 3 4
4. You were with your friend and you slipped on some wet dog poo.	1 2 3 4	1 2 3 4

EMBARRASSMENT	**How EMBARRASSED?**	**How sure are you about this?**
1. You did a squeaky fart when you were with a boy.	1 2 3 4	1 2 3 4
2. Your dad started doing rock 'n' roll dances in the supermarket.	1 2 3 4	1 2 3 4
3. Your friend said you had a wet patch on your bum all the way home.	1 2 3 4	1 2 3 4
4. You couldn't stop blushing in front of a boy in your class.	1 2 3 4	1 2 3 4

FEAR	**How AFRAID?**	**How sure ar you about this?**
1. You were with your friend and something furry ran down your neck.	1 2 3 4	1 2 3 4
2. Someone jumped out at you in the dark.	1 2 3 4	1 2 3 4
3. The old cupboard door slammed and you and your friend were locked in.	1 2 3 4	1 2 3 4
4. You were with your friend and a furry creature ran across your bare feet.	1 2 3 4	1 2 3 4

GUILT	**How GUILTY?**	**How sure ar you about this?**
1. Your mum was sad when you completely forgot about Mothers' Day.	1 2 3 4	1 2 3 4
2. You spread gossip about your best friend and she found out.	1 2 3 4	1 2 3 4
3. You laughed when your friend told you she was feeling upset.	1 2 3 4	1 2 3 4
4. Your little sister’s rabbit died because you didn't look after it properly.	1 2 3 4	1 2 3 4

DISGUST	**How DISGUSTED?**	**How sure ar you about this?**
5. You opened your brother's lunchbox and it was full o mould	1 2 3 4	1 2 3 4
6. Your friend was turning her eyelids inside out on the bus.	1 2 3 4	1 2 3 4
7. You were in your friend's garden and you put your hand in slimy cat poo.	1 2 3 4	1 2 3 4
8. You saw a pile of rotting guts near the dustbin at you friend's house.	1 2 3 4	1 2 3 4

EMBARRASSMENT	**How EMBARRASSED?**	**How sure are you about this?**
5. Your friend told you that you had really bad breath.	1 2 3 4	1 2 3 4
6. You were quietly picking your nose but your friend saw you.	1 2 3 4	1 2 3 4
7. You were eating with your friend and spinach was stuck in your teeth.	1 2 3 4	1 2 3 4
8. Your dad was singing loudly in a silly voice in the street.	1 2 3 4	1 2 3 4

FEAR	**How AFRAID?**	**How sure ar you about this?**
5. You thought someone was following you in the dark.	1 2 3 4	1 2 3 4
6. A man on a motorbike suddenly swerved and almost hit you.	1 2 3 4	1 2 3 4
7. Your friend told you there was a wasp crawling insid your jumper.	1 2 3 4	1 2 3 4
8. You got stuck in your friend's basement and you thought you couldn't breathe.	1 2 3 4	1 2 3 4

GUILT	**How GUILTY?**	**How sure ar you about this?**
5. You couldn't be bothered to help your friend with her work and she failed.	1 2 3 4	1 2 3 4
6. You found some money in your friend's house and kept it for yourself.	1 2 3 4	1 2 3 4
7. You were messing around with your friend and you broke her parents' wedding photos.	1 2 3 4	1 2 3 4
8. You kept some money that a little old lady had dropped in the street.	1 2 3 4	1 2 3 4

DISGUST	**How DISGUSTED?**	**How sure ar you about this?**
9. A dirty child picked his nose with his fingers and wiped it on you.	1 2 3 4	1 2 3 4
10. You saw your friend's dog eating its own vomit in the garden.	1 2 3 4	1 2 3 4
11. You found an old sandwich under your friend's bed with ants crawling on it.	1 2 3 4	1 2 3 4
12. Your dad told you to put the bin bags out and they were all slimy.	1 2 3 4	1 2 3 4

EMBARRASSMENT	**How EMBARR ASSED?**	**How sure are you about this?**
9. Your friend told you that you snore loudly at sleep-overs.	1 2 3 4	1 2 3 4
10. Your mum made you go and buy loads of loo roll from the corner shop.	1 2 3 4	1 2 3 4
11. You sneezed in front of someone and snot flew out of your nose.	1 2 3 4	1 2 3 4
12. You fell asleep on the bus with your head on someone's shoulder.	1 2 3 4	1 2 3 4

FEAR	**How AFRAID?**	**How sure are you about this?**
9. A dog was growling and trying to bite you and your friend.	1 2 3 4	1 2 3 4
10. Your friend said there was a hairy spider crawling on your neck.	1 2 3 4	1 2 3 4
11. You and your friend were alone in the park at night.	1 2 3 4	1 2 3 4
12. There was a huge snake slithering towards you and your friend on holiday.	1 2 3 4	1 2 3 4

GUILT	**How GUILTY?**	**How sure are you about this?**
9. You forgot to meet your friend and she was waiting in the cold by herself.	1 2 3 4	1 2 3 4
10. You lied to your mum about where you went with your friends.	1 2 3 4	1 2 3 4
11. You wrote a horrible email to your friend when you were angry.	1 2 3 4	1 2 3 4
12. You laughed at your friend’s new haircut and she started crying.	1 2 3 4	1 2 3 4

DISGUST	**How DISGUSTED?**	**How sure ar you about this?**
13. You and your friend saw a dead pig's head in an alleyway.	1 2 3 4	1 2 3 4
14. You and your friend walked past a smelly dustbin i the street.	1 2 3 4	1 2 3 4
15. Somebody had left the toilet seat dirty and you sat on it by mistake.	1 2 3 4	1 2 3 4
16. Somebody did a massive sneeze and snot flew in your face.	1 2 3 4	1 2 3 4

EMBARRASSMENT	**How EMBARR ASSED?**	**How sure are you about this?**
13. Your friend told you your t-shirt had been inside out all day.	1 2 3 4	1 2 3 4
14. Food flew out of your mouth while you were eating with your friend.	1 2 3 4	1 2 3 4
15. You were eating with your friend and you dribbled down your top.	1 2 3 4	1 2 3 4
16. You had loo roll stuck to your shoe as you left the toilets with your friend.	1 2 3 4	1 2 3 4

FEAR	**How AFRAID?**	**How sure ar you about this?**
13. You and your friend were alone in the dark and there were funny noises.	1 2 3 4	1 2 3 4
14. You were in a storm with your friend and there was lightning all around.	1 2 3 4	1 2 3 4
15. You were watching a horror movie at night with you friend and a loud noise made you jump.	1 2 3 4	1 2 3 4
16. You felt something tickling your neck and your frien screamed that it was a huge spider.	1 2 3 4	1 2 3 4

GUILT	**How GUILTY?**	**How sure ar you about this?**
13. You told white lies to your mum to get out of doing the housework.	1 2 3 4	1 2 3 4
14. You let people think you did some work that your friend had spent ages on.	1 2 3 4	1 2 3 4
15. You pretend to be sick so you don’t have to go and visit your gran.	1 2 3 4	1 2 3 4
16. Your gran asked you to post an important letter but you lost it.	1 2 3 4	1 2 3 4

DISGUST	**How DISGUSTED?**	**How sure ar you about this?**
17. Your friend was vomiting and you could smell it.	1 2 3 4	1 2 3 4
18. You and your friend saw a filthy rat with fleas jumping on it.	1 2 3 4	1 2 3 4
19. You put something in your friend's bin and flies buzzed out in your face.	1 2 3 4	1 2 3 4
20. You took a big gulp of your friend's milk but it had gone off.	1 2 3 4	1 2 3 4

EMBARRASSMENT	**How EMBARR ASSED?**	**How sure are you about this?**
17. You were doing a pop dance in your room and your brother was spying on you.	1 2 3 4	1 2 3 4
18. You tripped over in front of a boy you liked.	1 2 3 4	1 2 3 4
19. You were at the cinema with your friend and you go loud hiccups.	1 2 3 4	1 2 3 4
20. You fell asleep on the train and dribbled on the person next to you.	1 2 3 4	1 2 3 4

FEAR	**How AFRAID?**	**How sure ar you about this?**
17. The lift got stuck and you and your friend were trapped.	1 2 3 4	1 2 3 4
18. An angry dog was barking and running towards you and your friend.	1 2 3 4	1 2 3 4
19. Your dad slammed on the brakes as a lorry hurtled towards you.	1 2 3 4	1 2 3 4
20. You imagined someone was creeping up behind you in the dark.	1 2 3 4	1 2 3 4

GUILT	**How GUILTY?**	**How sure ar you about this?**
17. You didn't help your little brother with his work and he was crying with frustration.	1 2 3 4	1 2 3 4
18. You accidentally laughed when your friend tripped over and hurt herself.	1 2 3 4	1 2 3 4
19. Your best friend was upset because you forgot it was her birthday.	1 2 3 4	1 2 3 4
20. You forgot to feed your friend's cat while she was o holiday.	1 2 3 4	1 2 3 4

DISGUST	**How DISGUSTED?**	**How sure ar you about this?**
21. You and your friend saw some flies buzzing all ove a dead rat.	1 2 3 4	1 2 3 4
22. You bit into your friend's brown rotten apple by mistake.	1 2 3 4	1 2 3 4
23. Your friend said she saw a fly crawling on your lunch.	1 2 3 4	1 2 3 4
24. Your dad told you that the fridge was infested with maggots.	1 2 3 4	1 2 3 4

GUILT	**How GUILTY?**	**How sure ar you about this?**
21. You got really cross and swore at a little child.	1 2 3 4	1 2 3 4
22. You joined in when people were laughing at your best friend.	1 2 3 4	1 2 3 4
23. You made fun of a quiet girl you know and it made her cry.	1 2 3 4	1 2 3 4
24. You sent a horrible text message to your friend when you were angry.	1 2 3 4	1 2 3 4

HAPPINESS	**How HAPPY?**	**How sure ar you about this?**
1. You won an iPod in a competition.	1 2 3 4	1 2 3 4
2. You were about to go on your summer holiday.	1 2 3 4	1 2 3 4
3. You thought your cat was lost but it came back.	1 2 3 4	1 2 3 4
4. You got a beautiful new pair of shoes.	1 2 3 4	1 2 3 4

HAPPINESS	**How HAPPY?**	**How sure ar you about this?**
5. You went out for a special meal with your family.	1 2 3 4	1 2 3 4
6. You were singing along to your favourite song.	1 2 3 4	1 2 3 4
7. You were looking forward to your birthday celebrations.	1 2 3 4	1 2 3 4
8. You finished all of your exams.	1 2 3 4	1 2 3 4

Appendix 5.3

Regression analysis: brain regions for which activity to other > self correlates with perceived dissimilarity of (m)other to self

Of interest was the effect of perceived self-mother difference (PSMD) on the neural processing of emotion sentences from the (m)other perspective. It was predicted that participants with high PSMD scores (those who perceived their mother to be dissimilar to self) would show stronger activity within dorsal MPFC during other > self, while participants with low PSMD scores (those who perceived their mother to be similar to themselves) would show stronger activity within ventral MPFC other > self (e.g. Mitchell et al. 2006), or perhaps no difference (if subjects were simply treating self and other as the same).

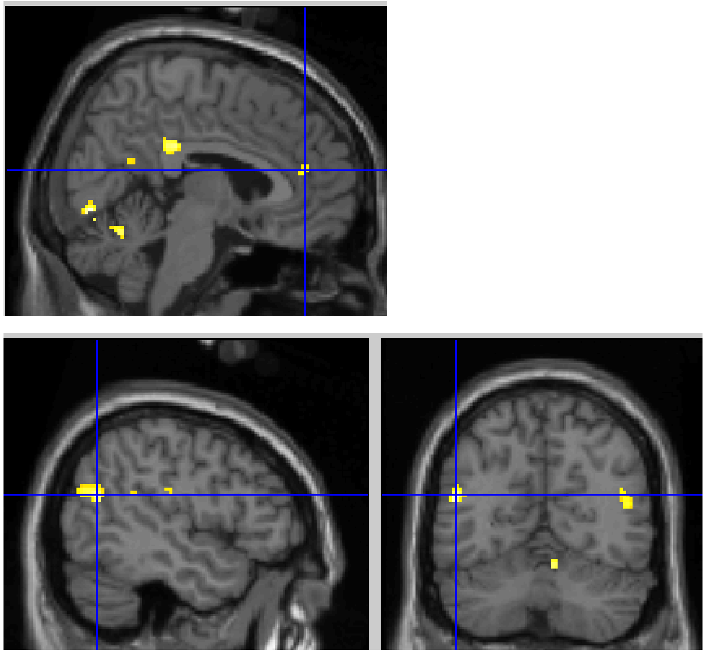
Linear regression analysis was therefore conducted at the second (group) level in SPM, using single-subject PSMD scores (from both age groups) as a regressor. Brain regions were identified for which activity in other > self correlated with the degree of perceived dissimilarity of mother to self.

Results showed that the dorsal MPFC ([6 42 16], $P < 0.001$ uncorrected; size in voxels = 26), left TPJ ([-48 -62 20], $P < 0.001$ uncorrected; size in voxels =108) and right TPJ ([48 -60 16], $P < 0.001$ uncorrected; size in voxels = 84 with a secondary peak at [44 -58 24], $P < 0.001$) were more active during other > self in participants with high PSMD scores, that is, participants who perceived the other (their mother) to be more dissimilar to self.

No brain regions showed a negative correlation with PSMD scores during other > self, that is, for subjects who perceived the other (their mother) to be similar to self, there were no differences in activation between self and other sentences.

Figure

PSMD-correlated activation in dorsal anterior rostral MPFC [6 42 16] (top), left TPJ [-48 -62 20] (bottom left and right) and right TPJ [48 -60 16] (bottom right, right hand activation shown without crosshair) during other > self. These brain regions were more active during other > self for participants who perceived the other (their mother) to be more dissimilar to self. Shown at $P < 0.001$ uncorrected (minimum voxel extent = 4).



Reference

Mitchell JP, Macrae CN, Banaji MR (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. Neuron, 50(4), 655-63.