# Effects of Peer Influence in Adolescence

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## SIGNED DECLARATION

‘I, Laura Kathrin Anette Wolf, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.'

Laura Wolf

**Abstract**

Adolescence is a period in life that is characterised by substantial changes in the social environment. Compared to childhood, relationships with peers gain more importance and adolescents are particularly sensitive to peer influence. Adolescents, but not adults, show increased levels of risk-taking when in the presence of peers relative to when alone. Experimental studies suggest that heightened levels of risk-taking during adolescence might be specific to affective contexts (e.g. the presence of peers), while risk-taking in non-affective contexts remains stable or decreases. In **Chapter 2** of this thesis the development of the impact of two decision variables (risk and valence) on decision-making in a non-affective context during adolescence is investigated in a behavioural risk-taking task. **Chapter 3** employs a functional magnetic resonance imaging (fMRI) approach to examine the development of the neural correlates of social influence during adolescence.

Previous studies have focussed on peer influence on risk-taking and little is known about the neural mechanisms of peer influence. This thesis examines whether heightened levels of sensitivity to peer influence during adolescence extend to the influence of a peer audience on tasks with either high-level (reasoning) or low-level (perceptual) cognitive components (Chapters 4 and 5). **Chapter 4** investigates the effect of the presence of a peer audience on performance in a cognitively challenging task (relational reasoning), the development of this effect during adolescence and whether this effect is dependent on the identity of the audience (peer or non-peer). **Chapter 5** examines the effect of the presence of a peer audience on performance in a low-level perceptual task to test whether peer audience effects would also extend to a low-level cognitive task. **Chapter 6** investigates the modulation of brain activity during a high-level cognitive task (relational reasoning) by an evaluative peer audience in adolescents and adults.

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# Contents

## ABBREVIATIONS

- AAL automated anatomical labeling
- ACC anterior cingulate cortex
- ANOVA analysis of variance
- ATC anterior temporal cortex
- BA Brodmann area
- BART balloon analogue risk task
- BOLD blood-oxygen level dependent
- BPVS British Picture Vocabulary Scale
- dACC dorsal anterior cingulate cortex
- DLFPC dorsolateral prefrontal cortex
- dmPFC dorsomedial PFC
- DTI diffusion tensor imaging
- EEG electroencephalography
- ERN error-related negativity
- EV expected value
- FA fractional anisotropy
- FD framewise displacement
- fMRI functional magnetic resonance imaging
- FMRIB Functional Magnetic Resonance Imaging of the Brain (analysis group)
- FSL FMRIB software library
- FWHM full width at half maximum
- GLM general linear model
- ICBM International Consortium for Brain Mapping
- IFG inferior frontal gyrus
- IGT Iowa Gambling Task
- IPL inferior parietal lobule
- ITI inter-trial interval
- MarsBaR Marseille Boîte À Région d'Intérêt
- mBA 10 medial Brodmann area 10
- MD mean diffusivity
- MFQ-FF McGill friendship questionnaire–Friend's Function
- MNI Montreal Neurological Institute
- mPFC medial prefrontal cortex
- MRI magnetic resonance imaging
- NAcc nucleus accumbens
- NIRS near-infrared spectroscopy
- OFC orbitofrontal cortex
- P postnatal day
- PCC posterior cingulate cortex
- PFC prefrontal cortex
- preSMA pre-supplementary motor area
- pSTS posterior superior temporal sulcus
- RLPFC rostrolateral prefrontal cortex
- RMS root mean square
- RPI resistance to peer influence
- RPM Raven's Progressive Matrices
- RT response time

- SD standard deviation
- SPM statistical parametric mapping
- SPSS Statistical Package for the Social Sciences
- STS superior temporal sulcus
- SVC small volume correction
- TE echo time
- TPJ temporo-parietal junction
- TR repetition time
- vACC ventral anterior cingulate cortex
- vlPFC ventrolateral prefrontal cortex
- vmPFC ventromedial prefrontal cortex
- VS ventral striatum
- WASI Wechsler Abbreviated Scale of Intelligence
- WFU Wake Forest University
- WHO World Health Organisation

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# CHAPTER 1: INTRODUCTION

## 1.1 Definitions

### 1.1.1 Defining adolescence

Adolescence (meaning 'to grow up' from Latin 'adolescere') (Chambers, 1993) describes the developmental period between childhood and adulthood and is characterised by substantial physical, cognitive, social and affective changes (Lerner & Steinberg, 2004). Different definitions of adolescence have been used in the literature. The World Health Organisation defines adolescents as people aged between 10 and 19 years, so equivalent to the second decade of life ('WHO | Health for the world's adolescents,' 2014). In contrast, a much broader definition of adolescence has become widely accepted in the field of developmental cognitive neuroscience (see reviews by Blakemore & Mills, 2014; Crone & Dahl, 2012; Lerner & Steinberg, 2004; Somerville, 2013): the start of adolescence is characterised with the beginning of puberty and ends when an individual attains a stable independent role in society. Consequently, the start of adolescence is defined biologically, while the endpoint is defined socio-culturally. Puberty onset in girls is usually between 9 and 10 years on average and in boys between 10 and 12 years (Peper & Dahl, 2013), although these onsets can vary up to 4 - 5 years in normally-developing individuals (Parent et al., 2003). As the endpoint is characterised socio-culturally, this definition is strongly dependent upon the culture the adolescent lives in. In industrialized nations, many young people are in University education or vocational training and possibly living with their parents into their mid-twenties or even later. Thus, the definition employed by many researchers in the developmental cognitive literature includes the developmental period termed 'emerging adulthood', which was introduced by Arnett (2000) to define the time between 18 - 25 years as an additional developmental period between adolescence and young adulthood in industrialized societies. The introduction will consequently review literature with developmental research questions up to the mid-twenties. However, the experimental studies described in this thesis include adolescents between 10 and 17 years, as the majority of developmental studies comparing behaviour or neural correlates in adolescence and adulthood include this age range. In addition, young people are legally considered to be adults when they turn 18. Finally, this age range was used to maximise differences with an adult comparison group, which is why adult participants included in the studies in this thesis were at least 21 years and older.

### 1.1.2 Defining peers

Peers, derived from the Latin 'par' meaning equal (Chambers, 1993), describes individuals who are equals for instance in terms of their age, status or skills. In the adolescent literature the term peers usually refers to individuals in the same life stage, i.e. fellow adolescents (Brown & Larson, 2009). Developmental psychologists have identified three main levels at which peer interactions occur (Brown, 2004; Brown & Larson, 2009). At the smallest level are dyadic peer relationships, which are predominantly pairs of friends. With the appearance of romantic relationships during adolescence, dyadic relationships also include couples. Dyadic relationships exist in childhood long before adolescence and can already be found in toddlers. At the next level are smaller peer groups (also called cliques), whose members regularly meet and interact with each other and which are also existent prior to adolescence (Brown, 2004). At the highest level are crowds, which start to emerge during adolescence and are often so large that peers do not necessarily know each other personally (Brown, 2004; Brown & Larson, 2009; Rubin, Bukowski, & Parker, 2007). One major characteristic of crowds is that they can be relatively abstract without peers actually interacting with each other. Peer crowds affiliations are based on the joint identification with specific attitudes, shared values or lifestyles as well as shared features such as neighbourhood or ethnicity (Brown, 2004; Rubin et al., 2007). Studies on reputation-based crowds in predominantly White, American adolescents identified several reoccurring crowds, for instance, academically focused crowds ('Brains'), high-status crowds (‘Populars’ or ‘Preps’), athletically focussed crowds (‘Jocks’), deviant or anti-social crowds (‘Burnouts’ or ‘Dirts’) and adolescents without many peer affiliations (‘Loners’) (Prinstein & La Greca, 2002; Rubin et al., 2007). A British study found some overlap between American and British reputation-based crowds, although they differed in labelling (Thurlow, 2001). Adolescent relationships with their peers are very dynamic, meaning that peer relationships are not very stable and status within a group also changes frequently (Brechwald & Prinstein, 2011; Brown, 2004).

## 1.2 Structural brain development

Magnetic resonance imaging (MRI) studies of the developing human brain have demonstrated significant structural changes throughout childhood and adolescence (for reviews: Blakemore, 2012b; Mills & Tamnes, 2014). The spatial resolution currently achieved with typical MRI scanners is approximately 1 $mm^3$, consequently MRI allows to study the macroscopic structure of the brain (Mills & Tamnes, 2014). Insight into the structural development of the human brain on a cellular level is currently only available in post-mortem studies. Histological studies have demonstrated that after a period of synaptogenesis, synaptic density in the prefrontal cortex is significantly higher in late childhood than adulthood (Huttenlocher, 1979; Petanjek et al., 2011). Following this peak, synaptic density decreases throughout adolescence and early adulthood. Post-mortem studies have also revealed that myelination continues throughout the first and second decades of life (Benes, Turtle, Khan, & Farol, 1994; Miller et al., 2012).

In the following two sections I will summarize white matter changes (1.2.1) and grey matter changes (1.2.2) during adolescence, focussing predominantly on longitudinal studies when available, and discuss these macroscopic changes in light of microscopic evidence from post-mortem studies. Finally, the relationship between structural and functional developmental changes will be discussed (1.2.3).

### 1.2.1 White matter development

White matter is primarily comprised of myelinated axons, glial cells and extracellular space (Mills & Tamnes, 2014). A consistent pattern revealed by several longitudinal studies describes an increase in white matter volume throughout childhood and adolescence well into the twenties and even thirties (for a review see Mills & Tamnes, 2014). For example, Lebel and Beaulieu (2011) found a significant increase in white matter volume between 5 - 32 years, partly levelling off in the twenties with about 50% of participants between 22 - 32 years still demonstrating increases and the other 50% showing no change (see Figure 1.1). Similar results were found in another longitudinal study: white matter volume increased between 4.5 - 18.5 years, partly levelling off in females in later adolescence (Aubert-Broche et al., 2013). This increase in white matter volume follows very similar developmental trajectories in the frontal, temporal, parietal and occipital lobes; although the rates and timings of increase differ somewhat between lobes (Aubert-Broche et al., 2013; Lenroot et al., 2007).

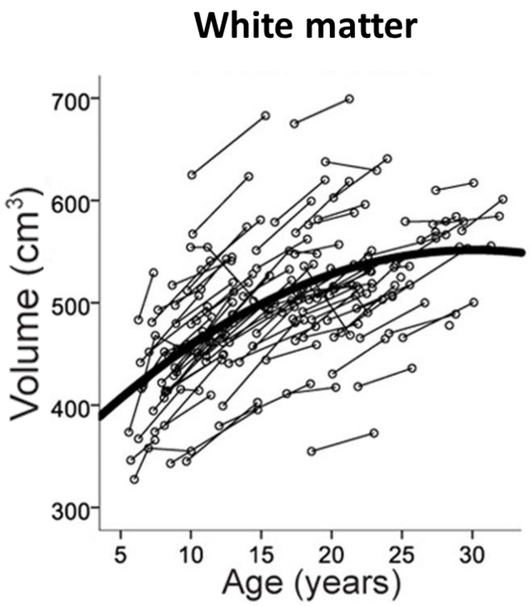


**Figure 1.1**: Longitudinal changes in white matter volume (Figure taken from Lebel & Beaulieu, 2011): across the age-range of the study (5 - 32 years) white matter volume significantly increased throughout adolescence well into the twenties.

These structural MRI findings, demonstrating white matter increases across adolescence, have been extended by diffusion tensor imaging (DTI) studies, which provided insight into the development of white matter microstructures. DTI measures the extent to which the diffusion of water molecules is restricted in biological tissues (Le Bihan & Johansen-Berg, 2012). Water diffusion in the white matter is mainly limited by axonal membranes as well as myelin and as such DTI measures are reflective of the white matter microstructure. The two most common DTI measures are mean diffusivity (MD), which describes the overall magnitude of diffusion, and fractional anisotropy (FA), which indicates the extent of directionality of diffusion, ranging from 0 (unlimited diffusion: isotropy) to 1 (diffusion limited to one direction: anisotropy) (Mills & Tamnes, 2014). Longitudinal studies investigating structural connectivity have shown that overall FA increases and MD decreases for many white matter tracts during adolescence (Bava et al., 2010; Lebel & Beaulieu, 2011). The developmental trajectories of FA and MD changes differ between white matter tracts with connections between the frontal and temporal lobes maturing at slower rates than other connections (Lebel & Beaulieu, 2011; Tamnes et al., 2010). The age-related changes in white matter volume and microstructure during childhood and adolescence have been linked to increasing axon diameters and continued myelination (Paus, 2010).

### 1.2.2 Grey matter development

Grey matter is comprised of neuronal cell bodies, dendrites, glial cells, extracellular space, capillaries and axons (Mills & Tamnes, 2014). The first large-scale, longitudinal study to describe changes in grey matter volume was conducted at the National Institute of Mental Health and included 145 participants aged between 4 - 22 years (Giedd et al., 1999). In this study, grey matter volume in the frontal, parietal and temporal lobes described an inverted U-shape, with an increase in grey matter volume during childhood, followed by a peak in late childhood/young adolescence and a subsequent decrease. Developmental trajectories differed between lobes, with the parietal lobe peaking first in young adolescence, followed by the frontal lobe and lastly the temporal lobe in late adolescence. More recent longitudinal studies employing other samples also report a decrease of grey matter volume (see Figure 1.2a) during adolescence into early adulthood (Aubert-Broche et al., 2013; Lebel & Beaulieu, 2011; Tamnes et al., 2013), however they do not necessarily replicate the precise peak found in earlier studies (Giedd et al., 1999; Lenroot et al., 2007). Grey matter development shows strong regional differences in developmental trajectories: in another longitudinal study (age range: 4 - 21 years) Gogtay et al. (2004) found that primary sensory and motor cortices matured earlier relative to later-maturing polymodal association cortices following a posterior-to-anterior developmental gradient. A recent longitudinal study (age range: 8 - 22 years) also showed a posterior-to-anterior gradient with higher rates of grey matter decreases at the youngest age in the parietal and lateral occipital lobes relative to higher rates of decreases at older ages in the frontal lobes and anterior temporal lobes (see Figure 1.2b, Tamnes et al., 2013).

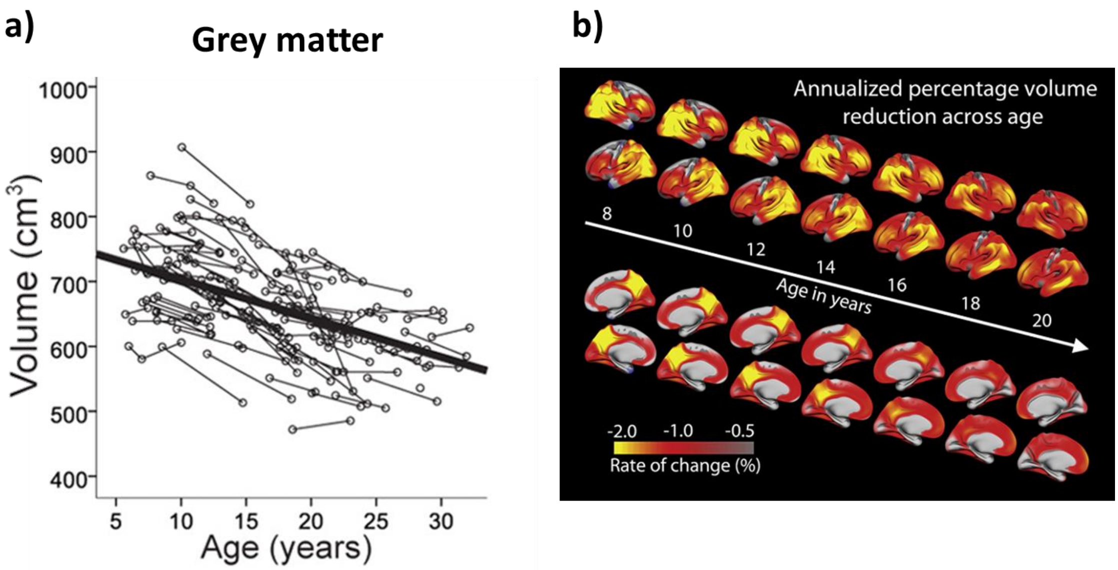


**Figure 1.2**: Developmental changes in grey matter volume: a) Grey matter volume was shown to decrease throughout adolescence and the twenties in a longitudinal study design (age range: 5 - 32 years; Figure taken from Lebel & Beaulieu, 2011). b) Region-specific grey matter volume reductions, plotted as annual percentage of volume change, in a longitudinal study followed a posterior-to-anterior gradient with age (age range: 8 - 22 years; Figure taken from Tamnes et al., 2013).

There are two main interpretations of this decrease in grey matter volume during adolescence and early adulthood. *Firstly*, the increase in white matter volume during adolescence – presumed to reflect continued myelination and expanding axonal diameters – might lead to a shift of tissue boundaries between grey and white matter and thus a relative reduction in grey matter volume (Blakemore, 2012b; Mills & Tamnes, 2014). *Second*, it has been proposed that the decrease of grey matter volume during adolescence might be partly related to the prolonged period of synaptic pruning during adolescence (Huttenlocher, 1979; Petanjek et al., 2011) - although this view has been challenged (Paus, Keshavan, & Giedd, 2008). Synaptic boutons only occupy a very small proportion of cortical volume (1.5% in monkeys; Bourgeois & Rakic, 1993); consequently changes in synaptic densities are unlikely to be the sole explanation for the relatively large cortical volume changes (average grey matter volume loss is estimated as 11% in humans; Mills & Tamnes, 2014). Changes in glia cells and other cellular structures including white matter changes are likely to contribute to changes in grey matter.

The majority of studies investigating grey matter maturation have focused on the development of cortical volume. On a macroscopic scale, cortical volume can also be described as a product of cortical thickness and surface area. Due to the development of surface-based cortical reconstruction tools (such as Freesurfer), recent studies have started to conduct more fine-grained analyses of grey matter maturation by tracing the development of cortical thickness, surface area and gyrification (Alemán-Gómez et al., 2013; Raznahan et al., 2011; Wierenga, Langen, Oranje, & Durston, 2014). Surface area can be quantified as the total area of the cortical surface, and cortical thickness is measured as the distance between the white matter/grey matter boundary and the grey matter/pia mater boundary (Mills & Tamnes, 2014). Cortical thickness has been found to decrease during adolescence with one study describing a linear decrease (age range: 7 - 23 years, Wierenga et al., 2014) and another study describing a cubic trajectory with a peak in cortical volume in late childhood followed by the decrease (age range: 3 - 30 years, Raznahan et al., 2011). Surface area also showed a cubic trajectory with age, showing a peak in late childhood/early adolescence and a decrease during adolescence and into the early twenties (Raznahan et al., 2011; Wierenga et al., 2014). The degree to which changes in surface area and cortical thickness contributed to changes in cortical volume was found to differ by age and gender (Raznahan et al., 2011). Finally, surface area itself is comprised of the area exposed on the cortical surface and the area buried in the sulci and, consequently, studies have also investigated changes in cortical gyrification. The gyrification index (i.e. the ratio between exposed cortical surface and total surface area) showed decreases throughout childhood and adolescence into the early twenties, while the area exposed on the cortical surface increased between late childhood and early adolescence (Raznahan et al., 2011). A similar decrease in the gyrification index was described in adolescents aged 11 to 17 years in another longitudinal study (Alemán-Gómez et al., 2013). This study further showed an overall flattening of the cortex, due to an increase in sulcal width in all lobes and additionally a decrease in sulcal depth in the frontal and occipital cortex. This increase in sulcal width was associated with a decrease in cortical thickness. In line with the theory that a decrease in cortical grey matter volume might be related to a shift of tissue boundaries as a result of an increase in white matter volume, the study also found that increases in gyral white matter thickness in the parietal, temporal and occipital lobes were associated with decreases in cortical thickness. Consequently, these studies suggest that macroscopic changes in grey matter maturation are a result of partly interrelated changes in cortical thickness, surface area, cortical folding and white matter thickness.

### 1.2.3 Relating structural brain development to developmental changes in functional activation

Developmental changes in functional activation are often explained in terms of structural changes during development. However, as with the underlying cellular changes of macroscopic structural changes, it is currently only possible to speculate about the cellular changes underlying changes in functional activation (Blakemore, 2012b). Synaptic pruning reduces excess synapses. This has been proposed to improve the signal-to-noise-ratio and thus the 'efficiency' of neural processing – and might be reflected in improved performance. As such synaptic pruning might lead to decreased functional activation as fewer, but more efficient synapses are involved in the neural signalling (Blakemore, 2012b; Durston et al., 2006; Luna, Padmanabhan, & O'Hearn, 2010). However, it must be noted that the interpretation of decreases in functional activation as increased efficiency has been criticised, as this link makes several assumptions that remain to be tested (for example that the underlying cognitive processes are the same or that changes in synaptic density are directly reflected in functional activation; for reviews see Blakemore, 2008; Poldrack, 2015). Synaptic pruning may also lead to a specialisation of regions in the processing of specific tasks, particularly in complex cognitive processes. Consequently, increases in activation with increasing age may reflect greater specificity of a region as a result of synaptic pruning. Increased task-specific recruitment of regions is also thought to be supported by stronger long-range connections as a result of myelination (Dumontheil, 2014; Luna et al., 2010). It is currently not possible to study whether these supposed cellular changes underlie the observed changes in functional activation. However, a few studies have directly tested to what extent developmental changes in functional activation are related to macroscopic structural changes (Cohen Kadosh, Johnson, Dick, Cohen Kadosh, & Blakemore, 2013; Dumontheil, Houlton, Christoff, & Blakemore, 2010; Lu et al., 2009; van den Bos, Crone, & Güroğlu, 2012; Wendelken, O'Hare, Whitaker, Ferrer, & Bunge, 2011). In general, these studies found that some but not all developmental changes in functional activation can be accounted for by structural changes. For example, age-related increases in functional activation in the left frontal gyrus and right inferior temporal gyrus during a face processing task were associated with age-related increases in white matter volume in these regions and a quadratic relationship with grey matter volume in the frontal gyrus (participants aged 7 – 37 years; Cohen Kadosh et al., 2013). However, the age-related increase in functional activation in the left supramarginal gyrus during a different face processing task was not associated with structural changes. In another study, decreases in functional activation between adolescence and adulthood in the rostrolateral prefrontal cortex (RLPFC) and pre-supplementary motor area (presMA), but not in the anterior insula, during a relational reasoning task were accounted for by local structural changes (and partly by performance, Dumontheil, Houlton, et al., 2010). Consequently, future studies are required to further disentangle the relationship between functional and structural changes during adolescence.

## 1.3 Reward-related and risky decision making in adolescence

Adolescence is often characterised as a period of heightened risk-taking (Boyer, 2006; Steinberg, 2008). Increased risk-taking is likely to aid adolescents in their process of becoming independent by facilitating the approach of novel situations or social environments. However, the type of risk-taking that receives the majority of public attention is the engagement in actions with potential negative outcomes such as risky driving, drug abuse and aggressive as well as violent behaviour. These risk-taking behaviours are thought to contribute to the high number of deaths in adolescents caused by transport injuries (percentage of deaths among 10 - 24-year-old Americans: 30%), other unintentional injuries (16% of deaths) and homicide (16% of deaths; Eaton et al., 2010).

A prominent model in developmental cognitive neuroscience in recent years, proposed to explain heightened risk-taking and sensation-seeking during adolescence, is the so-called dual-systems or mismatch model (Casey, Jones, & Hare, 2008; Somerville, Jones, & Casey, 2010; Steinberg, 2008). According to this model, there is a developmental mismatch (see Figure 1.3) between the earlier maturation of subcortical regions such as the ventral striatum/nucleus accumbens (VS/NAcc) and the amygdala, involved in reward and emotion processing, and the protracted maturation of prefrontal regions, involved in cognitive control. This mismatch was suggested to be greatest during adolescence (Somerville et al., 2010). According to this model, in the face of salient incentives, signalling of the more mature subcortical regions is not sufficiently controlled by the less mature prefrontal systems. A recent analysis of longitudinal structural imaging data investigated the developmental trajectory of subcortical (NAcc and amygdala) relative to prefrontal maturation within individuals (Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). In most of the participants there was evidence for an earlier maturation of the NAcc and/or amygdala in relation to the prefrontal cortex (PFC), although there were significant inter-individual differences in the developmental trajectories of these regions. The study did not support a relationship between the presence of a mismatch and risk-taking behaviours during adolescence in retrospective self-reports (possibly due to the relatively small sample size (n = 33) and the fact that self-reports were retrospective).

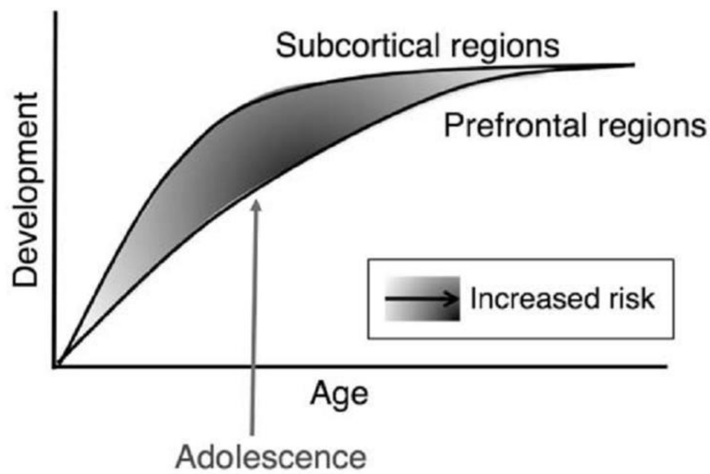


**Figure 1.3:** Dual-systems model (or developmental mismatch model; Figure taken from Somerville et al., 2010): This model proposes that affective-driven behaviours during adolescence are elevated due to an early maturation of subcortical regions (amygdala and VS) in relation to a prolonged maturation of the PFC.

Despite its popularity, the dual-systems model has been criticised as being too simplistic. Recent findings from functional imaging studies do not all match the predicted pattern of the dual-systems model and few studies have directly compared subcortical responses to rewards or emotions and prefrontal regulatory activity (Crone & Dahl, 2012; Pfeifer & Allen, 2012). Furthermore, there is also a lack of studies – particularly longitudinal studies - demonstrating that structural and/or functional changes in brain development are linked to real-world behaviours (Pfeifer & Allen, 2012). A recent meta-analysis of functional imaging studies investigating the development of cognitive control did not support the simple picture of prefrontal immaturity: while many studies report an increase in prefrontal activation in cognitive control tasks during childhood and adolescence, other studies report a decrease or a peak in activation (Crone & Dahl, 2012). Consequently, the authors suggested that the cognitive control systems do not just become increasingly more engaged during adolescence (as suggested by the dual-systems model), but instead that they are more flexibly recruited in dependence on the motivational salience of a context. The Crone and Dahl model of brain development proposes that this flexible recruitment is a result of the interaction of the gradually developing cognitive control processes and developmental changes in affective and social processing in subcortical regions, with a maximal influence of social-affective processes during mid-adolescence. These social-affective changes are thought to contribute to greater novelty, as well as sensation-seeking, and also to increase the motivational salience of social, particularly peer, contexts. Thus the recruitment of cognitive control processes is proposed to be dependent on the presence of peers, specific task instructions or the subjective value of performing or learning a task (Crone & Dahl, 2012). While this model of flexible cognitive control, may lead to increased engagements in health-risking and sensation-seeking activities in some contexts, it also enables flexible and quick learning and adaptation to new, particularly social, contexts during adolescence. Another recent review by Pfeifer and Allen (2012) criticized the view of the dual-systems model that greater subcortical activation is generally thought to be linked to vulnerabilities or engagement in activities with potential negative outcomes, while greater prefrontal activation is generally considered to be protective. For example, activation in the VS does not only exclusively respond to rewards nor is it solely associated with maladaptive behaviour (Pfeifer & Allen, 2012). Consequently, while the dual-systems model has provided an initial, compelling model of brain development, more recent reviews of adolescent development suggest that the dual-systems model may be too simplistic.

The literature on reward-based decision-making in adult participants is extensive and there has also been a large increase in developmental studies in this area in adolescence over the last ten years. The following sections will comprise a non-exhaustive review of studies that are relevant to the research questions investigated in **Chapters 2 and 3**. The first section will discuss behavioural evidence that heightened risk-taking in adolescence relative to childhood and adulthood is predominantly found when choices are made in affective contexts (1.3.1). Next, evidence from functional imaging studies supporting a heightened, adolescent reward-sensitivity will be reviewed (1.3.2) and finally the impact of valence on decision-making will be discussed (1.3.3).

### 1.3.1 Decision making in affective versus non-affective contexts

Only some of the experimental studies that have investigated risk-taking behaviour have found evidence for an adolescent peak in risk-taking in laboratory settings. It was suggested that the developmental pattern of risk-taking might be dependent on whether risky choices are made in a non-affective ('cold') or an affective ('hot') context, i.e. when emotions are at stake or peers are present (for the latter see section 1.6.2.1) (Blakemore & Robbins, 2012). Both affective and non-affective decision-making tasks that were employed to investigate developmental changes in risk-taking involved making choices about potential gains and/or losses. The terms affective versus non-affective here refer to the context that decisions were made in. Context is either manipulated as an integral part of choice, i.e. in the way that choices were made (e.g. dynamically increasing risk, Figner, Mackinlay, Wilkening, & Weber, 2009a, 2009b) and/or feedback was given (e.g. feedback inducing relief or regret, Burnett, Bault, Coricelli, & Blakemore, 2010) or externally (e.g. the presence of peers, Gardner & Steinberg, 2005) (for a review see Figner & Weber, 2011).

In affective contexts, there is evidence that risk-taking peaks in mid-adolescence. A peak in reward-sensitivity in mid- to late adolescence (14 - 21 years) was found on a modified version of the Iowa Gambling Task, one of the most widely used tasks to assess affective decision-making (IGT; Cauffman et al., 2010). Participants in the IGT choose among four packs of cards, each associated with different profiles of monetary gain and loss (Bechara, Damasio, Damasio, & Anderson, 1994). Two packs are apparently lucrative but eventually result in significant loss (disadvantageous packs). The other two packs are 'steady earners', with small wins hardly ever penalised by even smaller losses (advantageous packs). Adults tend to sample the disadvantageous packs initially but then settle on the advantageous options. Cauffman and colleagues (2010) designed a modified version of the IGT in which gambling decisions were made about a particular deck on each trial, which enabled assessment of decision-making in response to gains or losses. There appeared to be a linear, age-related increase in the tendency to avoid the disadvantageous packs over the course of the task. However, compared with younger adolescents and adults, mid- to late adolescents learned more quickly to play from the advantageous packs, suggesting that this age group shows a heightened sensitivity to approaching rewards (Cauffman et al., 2010).

In a study employing a gambling task designed to induce relief or regret (Burnett et al., 2010), a quadratic relationship emerged between age (9 - 35 years) and risk-taking, which peaked in mid-adolescence (around age 14). In a further study, adolescents (aged 14 - 19 years) and adults (aged 20 +) played a card game in which cards could be turned over as long as gains were encountered, but as soon as participants received a loss the trial terminated (Figner et al., 2009a). Compared with adults, adolescents exhibited suboptimal decision-making, failing to consider value and probability information when making decisions in an affective but not a non-affective version of the task. In a follow-up experiment, 10-year-olds performed at a level similar to adults, suggesting that risk-taking in affective contexts peaks in adolescence but does not change in a non-affective context (Figner et al., 2009b).

In other gambling tasks, where feedback is given but the context is non-affective, there was no evidence of a mid-adolescent peak in risk-taking; instead these tasks showed a gradual decrease in risk-taking or no developmental change (Paulsen, Platt, Huettel, & Brannon, 2011; Rakow & Rahim, 2010; Van Leijenhorst, Moor, et al., 2010). In a non-affective task in which participants aged 8 - 18 chose between a sure outcome and a gamble option (either high- or low-risk), risk-taking decreased across adolescence. Older adolescents chose low-risk gambles more frequently than high-risk gambles, and this difference was smaller in younger participants (Crone, Bullens, Van Der Plas, Kijkuit, & Zelazo, 2008). These studies suggest that risk-taking peaks in mid-adolescence in an affective context, while risk-taking remains stable or decreases in a non-affective context. However, it must be noted that the distinction between affective versus non-affective contexts is not always straightforward, which could lead to inconsistencies in the literature, especially because different studies employ different paradigms, age ranges, sample sizes, and measures of risk-taking.

### 1.3.2 Increased responsiveness of reward-related regions during adolescence

Evidence from functional neuroimaging studies has indicated that activation in reward-related brain regions describes a non-linear developmental pattern during adolescence (for reviews see Blakemore & Robbins, 2012; Galván, 2013). Many studies have demonstrated that adolescents show heightened VS activation in the response to reward compared to children and adults (Ernst et al., 2005; Galván, Hare, Voss, Glover, & Casey, 2006; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; Padmanabhan, Geier, Ordaz, Teslovich, & Luna, 2011; Van Leijenhorst, Moor, et al., 2010; Van Leijenhorst, Zanolie, et al., 2010). For instance, in one study, participants (aged 8 - 26 years) had to make choices between high- and low-risk gambles (Van Leijenhorst, Moor, et al., 2010). The neural response in the VS, when winning relative to not winning a monetary reward, described an inverted U-shape with age with adolescents having the greatest VS response to the delivery of rewards. Generally the majority of evidence points towards heightened reward-related VS activation during adolescence, however there is some evidence that adolescents activate the VS less than adults during reward anticipation (Bjork et al., 2004; Bjork, Smith, Chen, & Hommer, 2010) and reward assessment (Geier et al., 2010) and some studies have found no difference in VS activation between adolescents and adults during reward anticipation (Galván & McGlennen, 2013; Van Leijenhorst, Zanolie, et al., 2010) and reward outcome (Bjork et al., 2004, 2010). These inconsistencies in the literature might be due to differences in the developmental comparison groups, different experimental paradigms or trial phases analysed (reward anticipation versus reward outcome) (Crone & Dahl, 2012).

Many studies demonstrating an adolescent hypersensitivity to rewards have employed monetary rewards. From a neuroeconomical perspective, the use of real monetary incentives is crucial to allow extrapolation of experimental findings to 'real world' choice behaviour (Glimcher & Fehr, 2013; V. Smith, 1976). However, in the developmental literature the use of monetary rewards has been criticised, as the subjective value of money is likely to differ between age groups (Barkley-Levenson & Galván, 2014; Galván & McGlennen, 2013). This issue has been addressed in a recent study that demonstrated that adolescent (aged 13 - 17 years) choice behaviour was more strongly influenced by expected value (EV, i.e. the average value of potential outcomes weighted by their probabilities) in a mixed (gain/loss) gamble than adult choice behaviour (Barkley-Levenson & Galván, 2014). Crucially, this developmental effect remained when participants' income was controlled for. Adolescents also showed greater right VS activation to increasing EV relative to adults, even when adolescent and adult performance was matched with respect to subjective valuation (i.e. the number of accepted trials). In another task using primary rewards instead of monetary rewards, adolescents also demonstrated heightened bilateral VS activation when receiving an appetitive relative to a neutral stimulus (sugar water versus water) than adults, although this was only at a statistical trend level (Galván & McGlennen, 2013). Consequently, these two studies either controlling for subjective value in a monetary gamble or employing primary rewards replicate the finding of increased reward sensitivity in adolescence.

It was suggested that the exaggerated sensitivity of adolescents to rewards might partly stem from a heightened striatal reward prediction error to positive outcomes (J. R. Cohen et al., 2010). Reward prediction errors signal the difference between the expected value of an action and the actual outcome of the action and have been found to be encoded in midbrain dopaminergic neurons (Rescorla & Wagner, 1972; Schultz, Dayan, & Montague, 1997). In a learning paradigm, which separately modelled the neural signals of the decision value and of the prediction error, participants improved in both accuracy and response time (RT) with training (J. R. Cohen et al., 2010). However, only adolescents responded more quickly to stimuli predicting high reward relative to low reward. The neural positive prediction error signal in the striatum followed a quadratic age trend, indicating that adolescents showed heightened neural responses to unexpected reward relative to children and adults.

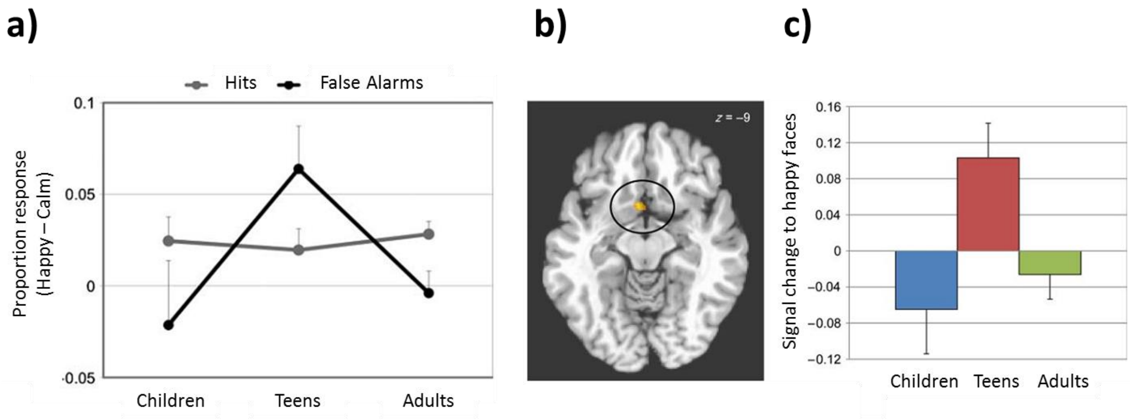


**Figure 1.4**: Heightened sensitivity to social appetitive cues during adolescence in a go/no-go task (Figures taken from Somerville et al., 2011). a) Behavioural performance difference in response to happy versus calm faces (y-axis) plotted as the proportion of correct hits (i.e. correct go-trials per total go-trials) and the proportion of false alarms (i.e. incorrect no-go trials per total no-go trials). The teenage group (aged 13 - 17 years) committed significantly more false alarms in trials with happy relative to calm faces in comparison to children (aged 6 - 12 years) and adults. b) and c) Activation in the VS in response to happy faces (collapsed across no-go and go trials) relative to rest: adolescent activation was significantly greater than activation in adults and children.

Heightened sensitivity to rewards in adolescence has also been demonstrated for social rewards in a developmental study investigating neural correlates of a social go/no-go task in adolescence (Somerville, Hare, & Casey, 2011). In this study, go and no-go stimuli were paired with happy (appetitive social stimuli) or calm (neutral social stimuli) faces (see Figure 1.4). Whereas performance in trials with neutral faces improved linearly with age, adolescents relative to both children and adults were particularly bad at inhibiting responses to happy faces. Adolescents also showed the greatest neural response in the VS to happy faces in comparison to both children and adults.

To sum up, the majority of functional imaging studies have found evidence for heightened reward-sensitivity in the VS during adolescence, which might, at least partly, underlie the observed pattern of increased risk-taking in adolescence in affective contexts (see 1.3.1). In addition, heightened sensitivity to social rewards might be related to increased sensitivity to social approval by peers (see 1.5.3) and developmental differences in social influence (see 1.7).

### 1.3.3 Influence of valence on adolescent decision-making

As reviewed above (1.3.1 and 1.3.2), the majority of studies have focussed on adolescent sensitivity to rewards, however less is known about adolescent sensitivity to losses or the relative impact of gains or losses on decision-making. Valence – whether potential outcomes entail rewards (e.g. monetary gains) or punishment (e.g. financial losses or painful electric shocks) – is known to impact on adult decision-making (De Martino, Kumaran, Seymour, & Dolan, 2006; Kahneman & Tversky, 1979; Tom, Fox, Trepel, & Poldrack, 2007). Few studies have investigated the development of the effect of valence on decision-making. In a key study, this was tested by examining responses to unexpected rewards and punishments in a probabilistic reversal learning task (van der Schaaf, Warmerdam, Crone, & Cools, 2011). Reversal learning performance in young adolescents (aged 10 - 11 years) was better following an unexpected punishment than following an unexpected reward. This effect of valence on reversal learning was found to decrease with increasing age during adolescence (from 10 to 17 years). This study suggests that the effect of valence on decision-making might decrease during adolescence.

Since the conception of the experimental study described in **Chapter 2**, new studies have been published that have investigated the effect of valence on decision-making in adolescence and developmental changes in loss aversion. A recent study, using a mixed gamble with monetary rewards and losses, found that both adolescent (aged 13 - 17 years) and adult choice behaviour was more strongly influenced by increasing losses than by increasing gains and that both age groups displayed a similar degree of behavioural loss aversion (Barkley-Levenson, Van Leijenhorst, & Galván, 2013). While behavioural loss aversion did not differ between the two age groups, adolescents activated the left caudate and bilateral frontal pole more strongly than adults when rejecting a mixed gamble relative to a baseline. In another study, which employed primary reinforcers in the form of appetitive (sugar water) or aversive liquids (salt water), adolescents (aged 13 - 17 years) rated both the appetitive stimuli as more appetitive and the aversive stimuli as more aversive (Galván & McGlennen, 2013). Adolescents also showed increased striatal activation relative to adults during the delivery of the appetitive stimulus relative to water (bilateral VS) and during the delivery of the aversive stimulus relative to water (left caudate). Consequently, there is mixed evidence for a developmental change in behavioural loss aversion between adolescents and adults; however adolescents showed heightened striatal activation in response to punishment suggesting that neural mechanisms processing punishment are changing between adolescence and adulthood.

## 1.4 Changes in social environment and social processing during adolescence

### 1.4.1 Changes in social environment

Experience-sampling studies in the USA have found that the amount of time adolescents spent with the family decreases by about a half between early and late adolescence (Larson & Richards, 1991; Larson, Richards, Moneta, Holmbeck, & Duckett, 1996). Adolescent girls spent more of this time with their friends and alone; while adolescent boys reported spending more time alone with increasing age (Larson & Richards, 1991). Including class time, American adolescents (aged 14 - 18 years) spend the majority of their waking time in the company of peers (52%), while they only spend about a fifth of their waking time with their family (Csikszentmihalyi & Larson, 1984).

Not only does the quantity of interaction with peers change during adolescence, but also the quality of peer interactions. It has been suggested that, in the process of becoming emotionally autonomous from their parents, adolescents become more reliant on their peers (Steinberg & Silverberg, 1986). While parents are perceived as the greatest source of support in late childhood (mean age 9 years), both same-sex friends as well as parents are described as equally supportive in young adolescence (mean age 12 years) and by mid-adolescence (mean age 15 years) same-sex friends become the greatest source of support (Furman & Buhrmester, 1992).

Relationships with peers become increasingly complex and hierarchical during adolescence (Brown, 2004). In late childhood, peer groups are still predominantly defined by shared activities or similar social behaviour (e.g. acting tough) (S. F. O'Brien & Bierman, 1988). In contrast, adolescents mainly characterize peer groups with respect to shared attitudes, similar appearances and more abstract group aspects such as status. Consequently, between childhood and adolescence, basic features of peer relationships change. Furthermore, adolescence is characterised by the appearance of a different type of peer relationship. As described in 1.1.2, peer crowds emerge as a third level of peer relationships during adolescence, in addition to dyadic relationships and peer groups, which already exist in childhood (Brown, 2004). Peer relationships also become more hierarchical during adolescence. Hierarchies can evolve within peer groups, for example, one member might become a leader of the group - but also between peer groups with some peer groups having higher statuses than others (Brown & Larson, 2009; Horn, 2006).

### 1.4.2 Changes in social processing and development of the social brain during adolescence

The period of adolescence is characterised by significant development of the social brain (Blakemore, 2008; Burnett & Blakemore, 2009). The social brain refers to a network of brain regions, including the medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), superior temporal sulcus (STS), the anterior cingulate cortex (ACC), amygdala, anterior insula and inferior frontal gyrus (IFG), that are associated with social cognition. Social cognition processes support interactions with others, such as the recognition of others via faces or body movements, communication with individuals, and making inferences about the mental states of others (mentalising) (Frith & Frith, 2007).

With new challenges facing adolescents in their social life, such as increasing complexity and hierarchical structures of peer relationships (Brown, 2004), the ability to infer others' mental states becomes more important, in order to correctly predict and interpret the behaviour of peers. Until recently, research on the development of mentalising has focussed on early childhood (Frith & Frith, 2007). This is probably due to the fact that children have been found to master relatively complex mentalising tasks by mid-childhood. However, there has also been a lack of paradigms to investigate mentalising beyond mid-childhood, as performance in many paradigms shows ceiling effects (Blakemore, 2012a; Blakemore & Mills, 2014).

One of the first developmental studies to demonstrate behavioural changes in social cognitive processing in adolescence showed that the ability to use another person's perspective to complete an executive task correctly is still developing from mid-adolescence into early adulthood (Dumontheil, Apperly, & Blakemore, 2010). In a computerized task, participants (aged 7 - 27 years) viewed some objects in a set of shelves, in which some of the shelves were hidden from a director's view. In order to correctly perform the task (move a specific item to a different slot), participants had to both listen to the director's instructions and take into account the director's perspective. While accuracy in a control task did not improve beyond mid-adolescence, performance in the director condition improved until early adulthood, suggesting that the ability to consider another person's perspective to choose an appropriate action is still developing after mid-adolescence.

As reviewed in 1.2, profound anatomical changes are taking place during adolescence, which include regions that are part of the social brain network. A recent study specifically investigated grey matter development in the mPFC (medial Brodmann area 10), TPJ, posterior STS (pSTS) and anterior temporal cortex (ATC), the regions (Figure 1.5) associated with mentalising (Mills et al., 2014). Grey matter volume in the mPFC, TPJ and pSTS peaked at late childhood, while grey matter volume in the ATC peaked in young adolescence. In all of these four regions, grey matter volume subsequently decreased throughout adolescence into the early to mid-twenties. This suggests that regions known to be involved in mentalising are structurally maturing throughout adolescence into early adulthood.

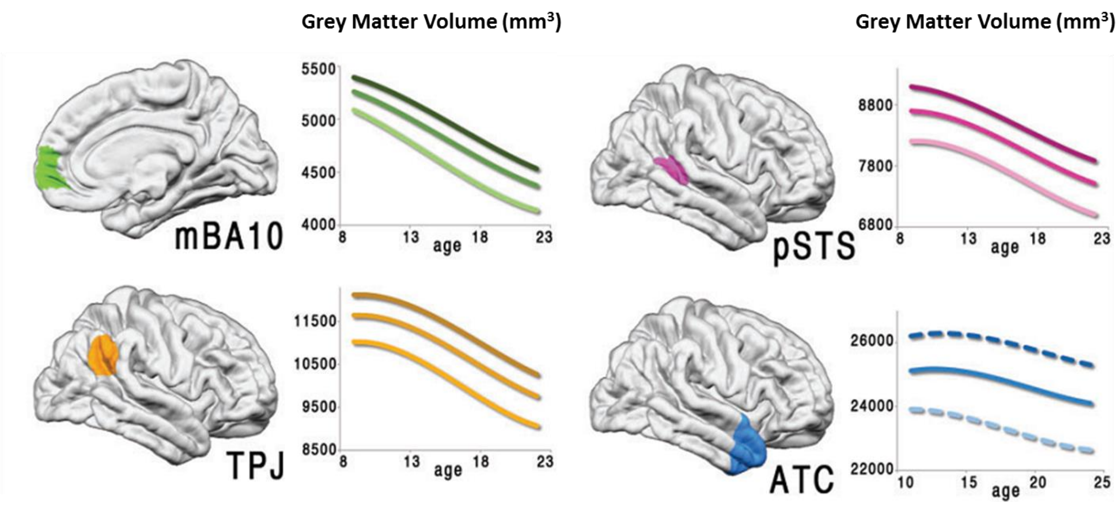


**Figure 1.5**: Fitted models of grey matter volume development in four regions (medial Brodmann area 10 (mBA 10), TPJ, pSTS and ATC) of the mentalising network (Figure taken from Mills et al., 2014). Lighter lines are fitted models for female participants and darker lines are fitted models for male participants (solid lines show significant model fits, while dashed lines are not significant). Grey matter volume in the mPFC (mBA 10), TPJ and pSTS peaked in late childhood and then decreased throughout adolescence into the early twenties, while grey matter volume in the ATC increased until young adolescence and then decreased into the mid-twenties.

Several functional magnetic resonance imaging (fMRI) studies have also demonstrated developmental changes in activation patterns in the regions of the social brain during adolescence. For example, in one study, adult and adolescent (aged 10 - 18 years) participants were asked to make judgements about 'basic' (e.g. fear or disgust) and 'social' (e.g. guilt or embarrassment) emotional scenarios; the latter requiring taking into account another person's mental states and emotions. When 'social' scenarios were contrasted with 'basic' scenarios, the adolescent group showed higher mPFC activation relative to adults (Burnett et al., 2009). This decrease in mPFC activation between young adolescence and adulthood is in line with several other fMRI studies that have employed a variety of different tasks, for example requiring participants to distinguish ironic from sincere statements (Wang, Lee, Sigman, & Dapretto, 2006), to think about the consequences of their own intentions (Blakemore, den Ouden, Choudhury, & Frith, 2007) or to understand emotions of cartoon characters (Sebastian et al., 2012). While adolescents showed increased activation in the mPFC relative to adults, some studies have also found elevated activation in more posterior regions of the mentalising network, such as the pSTS and ATC, in adults relative adolescents (right pSTS in Blakemore et al., 2007; left ATC in Burnett et al., 2009). This anterior to posterior shift in neural activation pattern within the mentalising network might indicate a change in neural strategy for mentalising between adolescence and adulthood (Blakemore, 2012a).

It is likely that mentalising abilities have an effect on individual levels of sensitivity to peer influence, as improvements in the ability to infer others' mental states will also make adolescents more aware that peers may be judging them. Thus, adolescents might be especially sensitive to peer evaluation as a consequence of the above-described behavioural and neural changes in mentalising.

## 1.5 Heightened sensitivity to peer contexts during adolescence

### 1.5.1. Heightened salience of social evaluative contexts during adolescence

The idea that adolescents are particularly concerned about what others think about them has been a topic of interest in developmental psychology for a long time (Somerville, 2013). It has been suggested that adolescents believe they are constantly being observed and evaluated by others; a phenomenon termed the 'imaginary audience' (Elkind, 1967). In a study employing hypothetical social scenarios, adolescents visiting the 8th grade of an American school (mean age 13.8 years) were more likely to choose an option that allowed them to avoid facing a potential evaluation by an audience, than did younger (6th grade; mean age 11.8 years) or older adolescents (12th grade; mean age 17.7 years; Elkind & Bowen, 1979). These findings were interpreted as adolescents perceiving themselves to be in the constant focus of others' attention, i.e. having an imaginary audience (being overly concerned about what others' might think about them), although note that some studies cast doubt on the existence of the imaginary audience phenomenon (Vartanian, 1999). Public self-consciousness, i.e. the awareness of aspects of the self that are apparent to others, was also found to be elevated in younger relative to older adolescents (aged 13 - 18 years) and to be higher in girls relative to boys (Rankin, Lane, Gibbons, & Gerrard, 2004). Consequently, there is some evidence from questionnaire-based studies to support the notion that adolescence, particularly young to mid-adolescence, is period of heightened self-consciousness.

In a recent study, Somerville et al. (2013) demonstrated that adolescents show heightened sensitivity to alleged peer observation in a minimal experimental peer presence manipulation. Under the pretence of testing new camera equipment, participants were asked to observe the status of a camera (attached to the head coil in the fMRI scanner) on a screen in an otherwise passive task. Participants (aged 8 - 22 years) were told that a similar-aged, same-sex peer was observing the video-stream and would see their face when the camera was on. Adolescents reported to feel more embarrassed when being watched by the peer than children. Activation in the mPFC (a key region of the mentalising network see 1.4.2), when being observed relative to being alone, was also elevated in adolescence relative to late childhood and partly levelling off in adulthood. Finally, autonomic arousal, measured by skin conductance, was increased relative to both children and adults (Somerville et al., 2013). These findings indicate that minimal peer evaluative contexts – even in the absence of interaction and feedback from peers - might be particularly salient during adolescence.

### 1.5.2 Sensitivity to social exclusion

During adolescence, peers become one, if not the most, important part of the social environment (see 1.4). Consequently, adolescents naturally worry about being excluded by their peers for certain behaviours or attitudes or being rejected from a peer group. Evidence for this was found in a questionnaire-based study, which demonstrated that, while fear of punishment (e.g. 'Getting punished by my father', 'Being called on by the teacher') was decreasing from late childhood (8 - 11 years) to adolescence (12 - 18 years), fear of social evaluation (e.g. 'Having to wear clothes different form others', 'Looking foolish') was elevated in mid- to late adolescence (15 - 18 years) relative to late childhood and young adolescence (8 - 14 years; Westenberg, Drewes, Goedhart, Siebelink, & Treffers, 2004). Questionnaire-based studies have also suggested that adolescent girls are more afraid of negative evaluation by their peers than are boys (La Greca & Lopez, 1998; La Greca & Stone, 1993; Rudolph & Conley, 2005).

Social exclusion in laboratory settings is often studied using a paradigm called 'Cyberball' (see Figure 1.6a), an online ball playing game, in which participants play 'catch' with two other alleged players over the Internet (Williams, Cheung, & Choi, 2000). The actions of the two other players are pre-programmed to either include or exclude the participant. In this task, adult participants, who have been excluded from the ball playing game in the experiment, reported higher negative affect, lower self-esteem and feelings of belonging, than participants that have been included (Williams et al., 2000). Similarly, adolescents experiencing social exclusion in the Cyberball game also showed negative affective responses (for a review see Platt, Kadosh, & Lau, 2013). There is some behavioural evidence that adolescents may be more sensitive to social exclusion than children or adults (Abrams, Weick, Thomas, Colbe, & Franklin, 2011; Sebastian et al., 2011; Sebastian, Viding, Williams, & Blakemore, 2010). After experimentally induced social exclusion, adolescents' (aged 11 - 15 years) mood was lower than adults' mood (Sebastian et al., 2010). Young adolescents (aged 11 - 13 years) - but not mid-adolescents (aged 14 - 15 years) or adults - also reported greater anxiety after exclusion relative to inclusion. Social exclusion evoked greater social distress in adolescents (aged 14 - 16 years) than adults (Sebastian et al., 2011) and had a stronger impact on adolescents' feelings (aged 13 - 14 years) of belonging than on children's (aged 8 - 9 years; Abrams et al., 2011).

In another study, using the 'Social Judgment Task' (see Figure 1.6b), participants were asked to anticipate whether unfamiliar peers would like them or not on the basis of their photo (Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010). Young adolescents (aged 12 - 14 years) expected fewer positive peer evaluations than adults, while older adolescent ratings (aged 16 - 17 years) did not differ from adult ratings. Adolescent sensitivity to peer feedback has also been investigated in the 'Chatroom Task' (see Figure 1.6c): on a first visit participants viewed photos of unfamiliar peers and rated how interested they were in chatting to them (Guyer et al., 2008; Guyer, McClure-Tone, Shiffrin, Pine, & Nelson, 2009). Participants also had their photo taken for the peers to allegedly evaluate them in turn. On the second visit, participants received feedback about whether the peers, who were classified as high-interest or low-interest on the basis of the participant's ratings at the first visit, were interested in chatting with them afterwards. When receiving rejection feedback from a high-interest peer, participants reported lower mood than after acceptance feedback, while mood

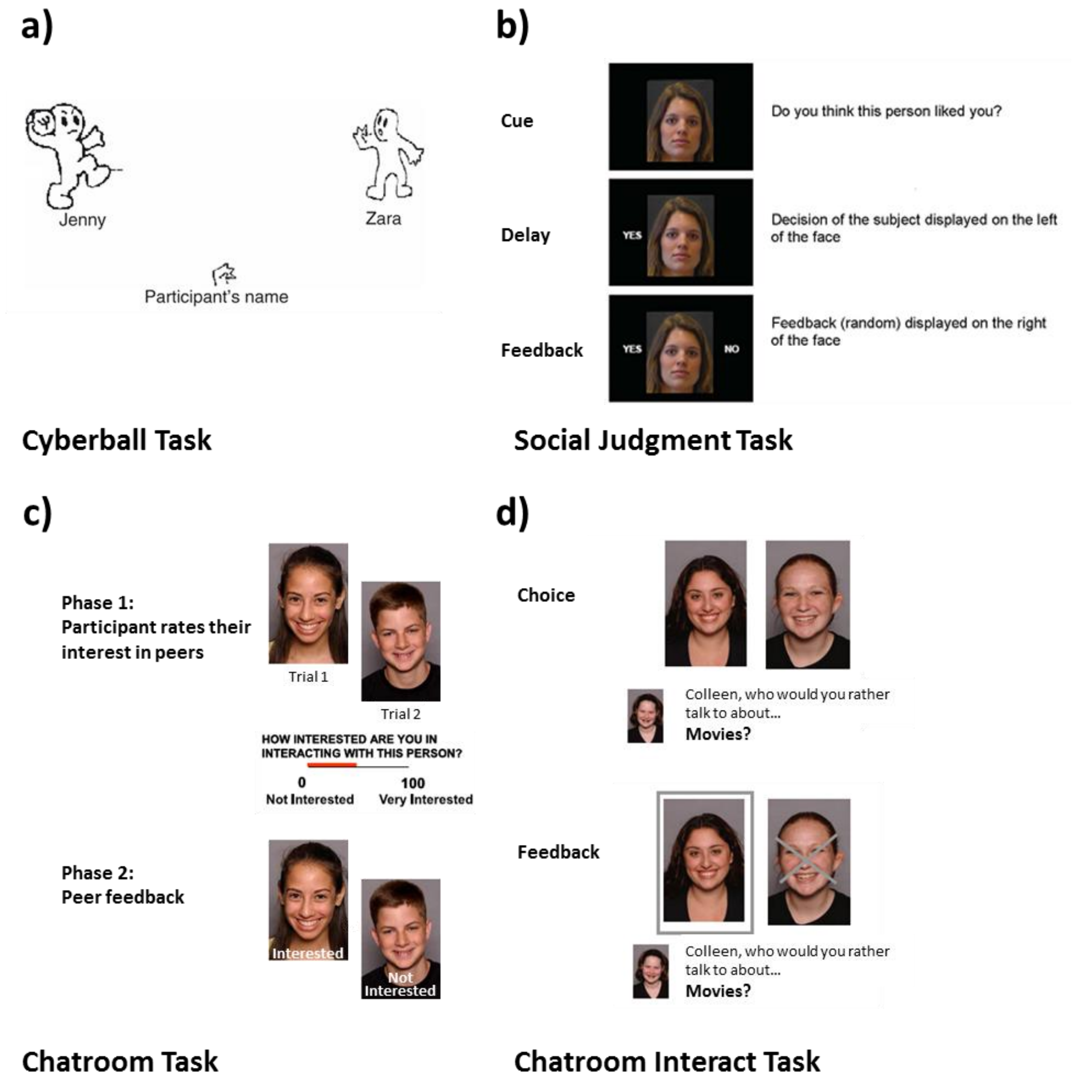


**Figure 1.6**: Paradigms employed to investigate adolescent sensitivity to social exclusion and peer evaluation. a) The Cyberball task: The participant (represented by the hand on the bottom of the screen) plays an online ball game with two other alleged players, who are represented by two cartoons. In the inclusion condition the participant receives the ball equally often as the other two players. In the ostracism condition the other two players stop throwing to the participant (Figure taken from Sebastian et al., 2010). b) The Social Judgment Task: In an alleged study on first impressions the participant is asked to predict whether the peer, shown on the photo, would like or dislike them on the basis of their photo. Afterwards the participant receives feedback whether the peer liked or did not like them (Figure adapted from Moor et al., 2010). c) The Chatroom Task: In the first phase, participants rate how interested they are in interacting with peers on the basis of their photographs. In the second phase, participants receive feedback on whether these peers are interested in chatting to them after the experiment on the basis of the participant's photograph (Figure adapted from Guyer et al., 2009). d) The Chatroom Interact Task: The participant allegedly plays an online chat game with two peers (peer A and B) and receives feedback about whether one of the other peers (e.g. peer A) prefers or does not prefer them to the other peer (peer B) to chat about a specific topic (Figure adapted from Silk et al., 2012).

was not differentially affected by feedback type from low-interest peers (Guyer, Choate, Pine, & Nelson, 2012; Lau et al., 2012).

In the ‘Chatroom Interact task’ (see Figure 1.6d), participants received feedback whether an alleged chat partner preferred them (i.e. acceptance feedback) or another peer (i.e. rejection feedback) to talk about specific topics, e.g. ‘Who would you rather talk to about movies?’ (Silk et al., 2012). Responses to peer feedback were studied with pupillary responses, which are an index for emotional arousal. Children and adolescent participants (9 - 17 years) demonstrated greater pupillary responses when the chat partner chose the other peer over them and this pupillary response to negative peer feedback increased with age. This study suggests that being rejected by a peer is more salient in older adolescents (Silk et al., 2012), which is consistent with the idea that sensitivity to social rejection is changing during adolescence. However, it is not clear whether sensitivity to peer rejection might be greater in early or later adolescence, with the behavioural evidence from Sebastian et al. (2010) suggesting early adolescence was the most sensitive period and Silk et al. (2012) suggesting late adolescence.

Evidence from fMRI studies is also indicating that the neural processing of rejection feedback is changing during adolescence. In an fMRI study of the Cyberball Task, both adolescents and adults showed greater activation in ventral anterior cingulate cortex (vACC), mPFC and ventrolateral PFC (vlFPC) during exclusion relative to inclusion (Sebastian et al., 2011). However, adolescents showed reduced right vlPFC activation during exclusion relative to inclusion compared to adults. It was suggested that adolescents’ sensitivity to social exclusion might derive from a protracted maturation of the neural regulatory response to negative social feedback.

To sum up this section, growing evidence from behavioural and imaging studies characterizes adolescence as a period of hypersensitivity to social exclusion. Fear of social rejection is likely to impact on adolescent behaviour in the presence of their peers resulting in adolescents engaging in behaviours that their peers will approve of.

### 1.5.3 Sensitivity to social approval

While heightened sensitivity to social exclusion might influence adolescent behaviour in the presence of peers, it is equally likely that adolescents might adapt their attitudes and behaviours in order to gain social approval by their peers. Evidence from questionnaire-based studies suggests that adolescent girls are most worried about being accepted by their peers at 15/16 years, while these worries decline in later adolescence (Kloep, 1999). Being accepted by one's peers becomes increasingly important for self-esteem between late childhood and adolescence (aged 10 - 17 years) and the importance of peer approval for self-esteem is greater in girls than in boys (S. F. O'Brien & Bierman, 1988).

The **behavioural results** of anticipating and receiving peer feedback in fMRI studies, which employed the 'Chatroom Task' and the 'Social Judgment Task', have been reviewed in the previous section (see 1.5.2 and Figure 1.6; Guyer et al., 2009; Moor et al., 2010). The **fMRI results** of these studies are informative with respect to the neural correlates of anticipating and receiving positive peer feedback (approval) and will be described in the following. The 'Chatroom Task' found that girls (9 - 17 years) showed greater BOLD activity in the NAcc and insula – regions that have been implicated in reward and emotion processing - with age when predicting whether high-interest versus low-interest peers would like to chat to them, whereas activation in boys either did not change (NAcc) or decreased (insula) with age (Guyer et al., 2009). The 'Social Judgement Task' examined the neural activation when anticipating to be liked or disliked by unfamiliar peers and during peer feedback (Moor et al., 2010). With age (between 8 - 25 years) participants showed greater activity in the ventromedial PFC (vmPFC) and striatum (among other regions) when expecting to be liked by peers, whereas when this positive anticipation was followed by positive feedback, vmPFC and striatal activation was similar across age. This suggests that neural response patterns to positive social feedback might mature relatively early on, whereas neural correlates in anticipation of positive social feedback might still be developing during adolescence.

A different set of studies (Jankowski, Moore, Merchant, Kahn, & Pfeifer, 2014; Pfeifer et al., 2013) investigated the development of the neural correlates of self-evaluations, particularly about social features such as popularity. In the longitudinal study of Pfeifer et al. (2013), participants made judgements about either themselves or a highly familiar fictional character (Harry Potter). The study found an increase in vmPFC activation between late childhood (mean age 10.1 years) and young adolescence (mean age 13.1 years) when participants were making self-judgements (e.g. 'I am popular', 'I wish I had more friends') relative to judging the fictional character. Activation in this vmPFC cluster was positively correlated with pubertal development, but only when judgements were made about social characteristics and not for academic judgements. In another study, adolescents (aged 11 - 14 years) but not adults, showed an interaction between the domain of evaluation (academic, physical or social) and the perspective of evaluation (self, other or reflected from their best friend's view) in the bilateral VS (Jankowski et al., 2014). When adolescents were thinking about how their best friend would evaluate them on a social trait they activated the VS more relative to when thinking about an academic or physical characteristic.

Consequently, both self-reported sensitivity to peer acceptance and neural correlates of positive peer evaluation have been found to increase during adolescence with some evidence for self-reported sensitivity to peer acceptance to decrease in late adolescence. Studies on the anticipation of peer evaluation reveal activations of brain regions that are typically associated with reward-related and emotional processing.

## 1.6 Peer Influence

### 1.6.1 Peer influence

Adolescents tend to associate with peers who share similar behaviours, preferences and attitudes including academic aspiration, music taste, political opinion, fashion style or preferred leisure activities (Brechwald & Prinstein, 2011). This homophily in adolescence has been attributed to two processes: adolescents initially choose peers with similar attitudes and preferences (selection effects), but also become more similar to their peers over time (socialization effects; Kandel, 1978). Until recently, the majority of studies on the effects of peer influence were observational or based on questionnaire-measures (Brechwald & Prinstein, 2011; Brown, 2004). In order to study an effect of peer influence on measures such as alcohol use or deviant behaviour, studies often controlled for baseline levels and selection effects. However, due to the correlational nature of this data, it was not possible to establish causal relationships between peer influence and behavioural changes in these studies. In the last decade, studies have started to investigate effects of peer influence on behavioural measures of risk-taking, risk attitudes and associated brain activations in controlled experimental conditions (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; G. L. Cohen & Prinstein, 2006; Gardner & Steinberg, 2005).

It has been suggested that adolescents might adopt attitudes or engage in behaviours that they perceive to be endorsed by popular peers (Brechwald & Prinstein, 2011). Two different constructs of popularity have emerged in the literature (Cillessen & Rose, 2005; Parkhurst & Hopmeyer, 1998). *Sociometric* popularity is measured on the basis of peer nominations as being liked or disliked as a friend. *Perceived* popularity is assessed based on how adolescents perceive their own or others' popularity. After an initial sociometric popularity assessment of all students in the 11$^{th}$ grade of an American school (aged 16 - 17 years), the effect of popularity on peer influence was investigated in a chatroom paradigm (this task will be referred to as Cohen's Chatroom Paradigm to avoid confusion with the Chatroom Task described in 1.5; G. L. Cohen & Prinstein, 2006). In this task, averagely popular participants interacted with three anonymised, alleged peers from their school, whose popularity was experimentally manipulated. Participants and the alleged peers were asked to indicate how they would behave in hypothetical scenarios, which involved aggressive or health-risking actions, with the participant always responding last. Adolescent boys (aged 16 - 17 years) were more likely to choose aggressive or risky behaviours when popular peers had endorsed those behaviours compare to when unpopular peers had endorsed them.

### 1.6.2 Domains of peer influence

#### *1.6.2.1 Peer influence on anti-social and risk-taking behaviours*

The following two sections will review peer influence effects on anti-social and risk-taking behaviours. The first section will focus on observational, questionnaire-based or epidemiological studies investigating peer influence on attitudes towards and engagement in health-risking and anti-social behaviours. This section only intends to give a short overview of this very large literature (for reviews Brechwald & Prinstein, 2011; Dishion & Tipsord, 2011). In addition, this section will include some more recent studies that have investigated peer influence effects on risk perception and attitudes in experimental manipulations. The second section will concentrate on peer influence effects on experimental measures of risky as well as reward-related decision-making.

##### *1.6.2.1.1 Observational, questionnaire-based and epidemiological measures of peer influence on anti-social and health-risking behaviours and risk-perception*

The majority of observational and questionnaire-based studies have focussed on peer influence effects on health-risking and anti-social behaviours. These studies consistently find peer influence effects on alcohol and tobacco consumption, anti-social, aggressive and criminal behaviours, but also on internalizing behaviours (for reviews Brechwald & Prinstein, 2011; Dishion & Tipsord, 2011).

An exhaustive review of peer influence effects on health-risking and anti-social behaviours would be beyond the scope of this introduction; instead these effects will be illustrated with examples of peer influence effects on attitudes towards and engagement in alcohol consumption, which have been very well researched. A recent longitudinal study investigated the role of selection and socialization processes on alcohol use in young adolescents (aged 11 - 12 years) over the course of four school years (from 6$^{th}$ - 9$^{th}$ grade American school; Osgood et al., 2013). This study found strong evidence for a role of socialization processes on alcohol use in young adolescence; adolescents adjusted their behaviour to match their alcohol use to that of their friends. In addition, adolescents chose friends with similar alcohol consumption patterns (selection processes). Both selection and socialization effects have also been found for smoking; adolescent smokers chose friends who were smokers and non-smokers who were befriended by smokers were more likely to start smoking than those without smoking friends (Kobus, 2003; Simons-Morton & Farhat, 2010).

Peer influence on alcohol consumption attitudes has also been demonstrated in experimental paradigms. Adolescents (aged 13 - 15 years) who had viewed alleged Facebook profiles of older peers consuming alcohol and thus perceived alcohol use as normative (see also 1.7.2), reported more positive attitudes towards alcohol consumers and the consequences of consumption as well as a higher propensity to drink alcohol than adolescents who viewed Facebook profiles in which alcohol use was not normative (Litt & Stock, 2011). In a version of Cohen’s Chatroom Paradigm (see 1.6.1, G. L. Cohen & Prinstein, 2006), adolescent boys (aged 14 - 15 years) reported their willingness to consume alcohol in hypothetical scenarios after viewing the responses of three alleged peers, who were either more or less willing to drink alcohol than the average student from their school (Teunissen et al., 2012). In both conditions, adolescents conformed to their peers' attitudes towards alcohol; in addition, they were more influenced by supposedly popular relative to unpopular peers.

A recent study assessed whether peer influence effects on alcohol consumption could also be found in mice (Logue, Chein, Gould, Holliday, & Steinberg, 2014). Peer effects on alcohol consumption were tested in the C57BL/6J mouse strain that voluntarily drinks ethanol solutions. Juvenile mice (postnatal day (P)28 - P30), which were raised in same-sex triads, consumed more alcohol in a novel environment in the presence of their cage-mates than when alone, while drinking behaviour was not affected by the presence of the cage-mates in adult mice (P84 - P86). However, this study did not employ a control to test whether these peer effects in mice were actually specific to alcohol or could also be found for instance for water. Thus, the presence of cage-mates might just increase foraging behaviours, even though the experimental set-up aimed to minimize competition. However, if this peer effect was specific to alcohol, this would suggest that even mice show peer influence effects on drug consumption, indicating that at least some peer influence processes might be mediated by lower-level arousal effects.

Observational studies that mostly control for selection effects and/or initial levels of aggression, have found that adolescents with peers who engage in anti-social or criminal behaviours are more likely to also engage in anti-social or criminal acts (Dishion & Tipsord, 2011). For instance, adolescents chose friends with similar levels of relational aggression (manipulating social relationships or status, for example by bullying) and being befriended with relationally aggressive peers led to an increase in relationally aggressive behaviour over the period of a year (Sijtsema et al., 2009). A recent longitudinal study in a sample of high-risk male students (aged 12 - 15 years, $7^{th}$ - $9^{th}$ grade American school at the first time point) from low socio-economic status schools found that being befriended by peers who carried weapons was related to a greater likelihood of carrying a weapon over the course of a year; controlling for selection effects (Dijkstra et al., 2010). The authors suggested that carrying a weapon might be a status symbol in this sample. Supporting this hypothesis, the study demonstrated that carrying a weapon was associated with a higher number of friendship nominations. Observational studies have described that one way peers exert negative influence is via ‘deviancy training’ during which deviant attitudes and behaviours are encouraged by peers via positive feedback such as laughter and stories of past deviant behaviour (Dishion & Tipsord, 2011).

Peers do not only influence the current attitudes and behaviours in adolescence, but also have long-lasting effects into adulthood. A recent longitudinal questionnaire-based study demonstrated that being more resistant to peer influence in adolescence (across the ages of 13 - 15 years) was associated with lower levels of alcohol use as well as fewer alcohol and substance-abuse related problems in adulthood (21 - 23 years); controlling for participants’ and peers’ alcohol use in adolescence (Allen, Chango, & Szwedo, 2014). Being resistant to peer influence in adolescence was also predictive of lower levels of criminal behaviour in adulthood, controlling for externalizing behaviours in adolescence (Allen et al., 2014).

##### *1.6.2.1.2 Peer influence on experimental measures of risky and reward-related decision-making*

One of the first studies to examine peer influence effects on risk-taking behaviour in a controlled experimental setting, employed a computerised, car-driving simulation (see Figure 1.7a) in adolescents in the presence of two same-sex peers (Gardner & Steinberg, 2005). Participants drove up a car to a traffic light, which turned from green to amber, and consequently had to decide whether to stop or to move further. Moving further would win points, but at the same time, it risked crashing into a wall and losing all points if the light turned red. The two peers were instructed to call out advice to the participant whether to continue moving the car or to stop. When adolescents (aged 13 - 16 years) played the game in the presence of two peers, they took more risks than when they played on their own, whereas adult (24 years and older) risk-taking behaviour did not differ when alone or with peers (Gardner & Steinberg, 2005).

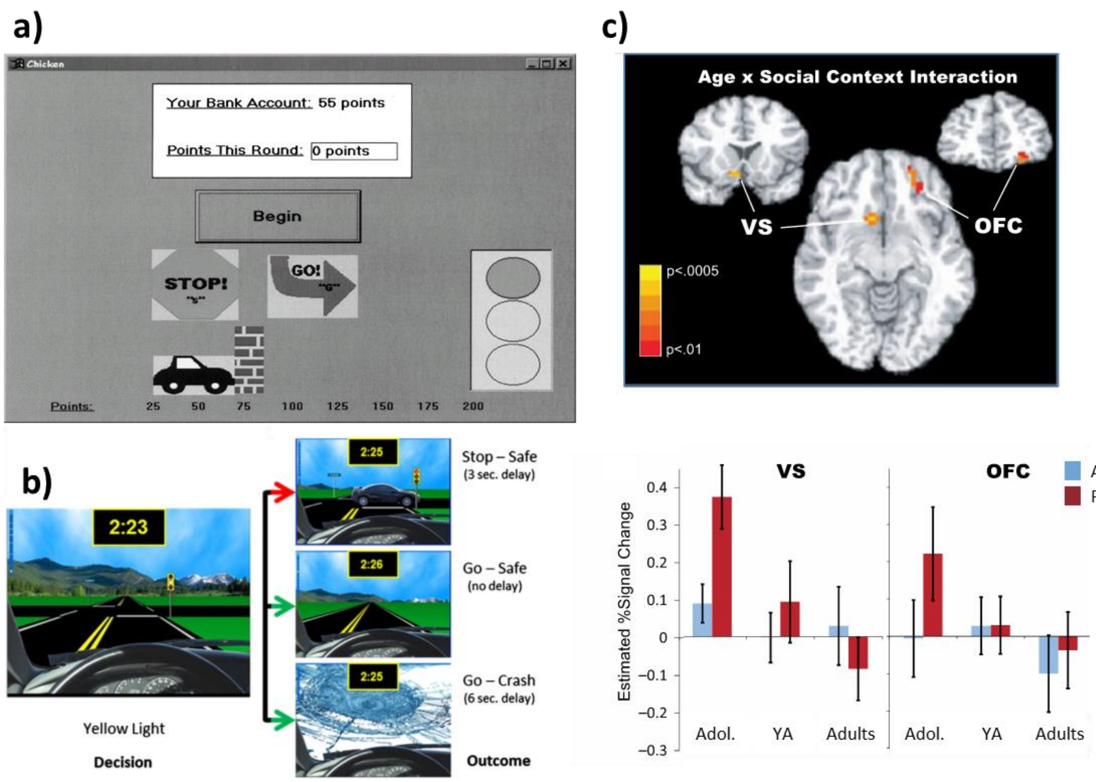


**Figure 1.7**: The Stoplight Task as a measure of risk-taking behaviour in the presence of peers. a) 'Stoplight Task' (Chicken Task) to assess behavioural risk-taking in a car-driving simulation: Participants are asked to make choices at amber traffic lights whether to stop the car (and securing already gained points) or to move further (and gaining more points, but also risking to lose all points if the light turned red). Here, the traffic light has turned red, resulting in a crash and the loss of the points (Figure taken from Gardner & Steinberg, 2005). b) FMRI version of the 'Stoplight Task' employed to assess neural activation when making decisions at the amber traffic light (Figure taken from Peake et al., 2013). c) Regions (VS and OFC) showing an age (adolescents (Adol.: 14 - 18 years), young adults (YA: 19 - 22 years) and adults (24 - 29 years)) x social context (peer versus alone) interaction in the decision-period of the Stoplight Task (Figure adapted from Chein et al., 2011).

In the decision-period of an fMRI version of this task (see Figure 1.7b), adolescents (aged 14 - 18 years) showed increased activation in the VS and orbitofrontal cortex (OFC; see Figure 1.7c) in the peer-present relative to the alone condition (peers were observing but not interacting during the task; Chein et al., 2011). In contrast, activation patterns in young adults (aged 19 - 22 years) in these regions were not significantly affected by peer presence. Risk-taking behaviour in adolescents was associated with greater activity in the VS and OFC during

Go versus Stop trials. These findings indicate that the presence of peers might render adolescents more sensitive to potential rewards.

In the study of Gardner and Steinberg (2005), familiar peers were instructed to advise the participant during the risk-taking task. A recent study found that adolescents (aged 15 - 17 years) also showed increased levels of risk-taking in a wheel-of-fortune type gamble when being told that an unfamiliar, same-sex peer was observing them via a camera to make predictions about their performance without having met them (A. R. Smith, Chein, & Steinberg, 2014). In another recent study employing a wheel-of-fortune task, adolescents (aged 11 - 18 years) took more risks than adults in high-risk gambles when being told that their choices were observed by three alleged, unfamiliar, same-sex peers, while risk-taking did not differ between adolescents and adults when choices were made unobserved (Haddad, Harrison, Norman, & Lau, 2014). When peers advised participants to choose the risky option, both adolescents and adults took more risks than when making choices unobserved, however adults took on this risky advice more than adolescents in this condition. Another study investigated peer influence effects in the balloon analogue risk task (BART task; Lejuez et al., 2002), in which participants decide whether to inflate a balloon to accumulate more money, at the risk of the bursting the balloon, or to stop inflating and bank the money (Reynolds, MacPherson, Schwartz, Fox, & Lejuez, 2013). This study also reported peer influence effects on risk-taking behaviour in 18 - 20-year-olds. An increase in risk-taking was however only found when peers had been instructed to encourage risk-taking and their payment depended on the participant's level of risk-taking (this instruction was unknown to the participant). There was no difference in risk-taking in the peer relative to the alone condition if peers did not receive this instruction. Consequently, more studies and replications are needed to determine whether explicit encouragement by peers is required or whether the mere presence of peers is sufficient to elicit heightened risk-taking in adolescence. Furthermore, it remains to be determined what role familiarity and physical presence of peers play in peer influence effects.

This is particularly important in light of the different tasks and age groups employed by the studies that have reported these different results.

Increased levels of risk-taking in adolescence in the presence of peers have been linked to a modulation of reward sensitivity by peers (Chein et al., 2011) and evidence from studies using delay-discounting paradigms have been supporting this hypothesis (L. O'Brien, Albert, Chein, & Steinberg, 2011; Weigard, Chein, Albert, Smith, & Steinberg, 2014). For example, when in the presence of peers relative to when alone, 18 - 20-year-olds demonstrated greater preferences for immediate rewards (such as $ 600 immediately rather than $ 1000 in one year; L. O'Brien et al., 2011). Similar results were found when 18 - 22-year-olds were simply told that an unfamiliar peer was observing them from an adjacent room (Weigard et al., 2014). This and other studies suggest that physical presence is not necessary to produce peer influence effects (see also e.g. Guyer et al., 2009; Haddad et al., 2014; Moor et al., 2010; Silk et al., 2012). A recent developmental study investigated peer-induced modulation of activation in a reward-processing task that did not involve risky decisions (A. R. Smith, Steinberg, Strang, & Chein, 2014). This study provided preliminary evidence that adolescents (aged 14 - 19 years) relative to adults show heightened activation during the receipt of rewards in the NAcc when peers were observing them, while there was no developmental difference when participants were alone. These studies suggest that the presence of peers influences adolescent choice behaviour in reward-related decisions and neural activation in reward-related regions.

Recent studies have also provided experimental evidence that fear of social exclusion might play a role in peer influence effects. Adolescents (aged 14 - 17 years) played a car-driving simulation twice (see Figure 1.7b), while allegedly being observed by two peers over the Internet (Peake, Dishion, Stormshak, Moore, & Pfeifer, 2013). However, prior to the second round of the car-driving simulation, the participant was ostracised by the two peers in the Cyberball task (see 1.5.2). Following social exclusion participants showed a trend for heightened risk-taking and this increase in risk-taking was greater in adolescents who reported lower resistance to peer influence in a questionnaire. Activation in the right TPJ (a region implicated in mentalising; see 1.4.2), when making risky choices, mediated the relationship between resistance to peer influence scores and elevated risk-taking. In another study, participants played the Cyberball game one week prior to the car-driving simulation (Falk et al., 2014). Activation during exclusion relative to inclusion in a network of regions previously implicated in social exclusion (subgenual ACC and anterior insula) and a network of regions associated with mentalising (dorsomedial PFC (dmPFC), right TPJ and posterior cingulate cortex (PCC) see 1.4.2) was extracted to predict peer influence effects on risk-taking. Both activations in the social exclusion and the mentalising network were positively associated with the difference in risk-taking between the peer-present and the alone condition. These two studies suggest that in addition to a modulation of activation in reward-related regions, peer influence is associated with activation of regions in the mentalising network and areas typically activated during social exclusion.

#### *1.6.2.2 Beneficial peer influence*

Interactions with peers are important for adolescents to learn how to navigate in different social environments and adapt their interaction patterns depending on the social group they are with. With the increasing emergence of peer groups and crowds during adolescence (Brown, 2004), adolescents can practice to 'play different roles' depending on which peers are present. A longitudinal questionnaire-based and observational study demonstrated that being liked and accepted by peers in adolescence (across the ages of 13 - 15 years) was predictive of greater competence in young adulthood to have positive relationships with close friends and romantic partners (Allen et al., 2014). In contrast, higher levels of resistance to peer influence were associated with lower levels of competence to have well-functioning relationships with close friends (Allen et al., 2014).

The majority of research revealing beneficial peer influence effects has been observational or questionnaire-based. Ryan (2001) demonstrated in a questionnaire-based approach that, during the course of a school year, young adolescents (aged 12 - 13 years, 7$^{th}$ grade American school) who spent time with motivated and academically high achieving peers were more likely to show improvements in their academic performance and enhanced motivation than students who spent time with unmotivated peers. In addition to academic performance, peers also positively influence prosocial behaviour (showing interest in the welfare of others and voluntary engagement in actions with the aim to benefit others; Eisenberg and Sheffield Morris 2004). Being befriended by a peer, who initially had a higher level of prosocial behaviour than the adolescent (aged 11 - 12 years, 6$^{th}$ grade American school), had a beneficial impact on the adolescent's prosocial behaviour over a period of two school years (Wentzel et al., 2004). A follow-up study further found that friendship quality moderated the effect of a friend's prosocial behaviour on adolescent's motivation to act prosocially (Barry & Wentzel, 2006). In another study, Walker et al., (2000) demonstrated differential impacts of parents or friends on adolescent moral development in a 4-year longitudinal study in 10 - 15-year-olds. For instance, in discussions about moral dilemmas (both hypothetical and real-life conflicts), having a friend challenge a participant's moral reasoning was associated with higher levels of moral development (assessed with Kohlberg's Moral Judgment Interview; Colby and Kohlberg 1987), whereas parents challenging reasoning led to slower maturation of moral reasoning.

In addition to positive peer influence effects on prosocial behaviour, academic motivation and moral development, peers were also found to have the potential to exert beneficial influence on health-risking behaviour (Pfeffer & Hunter, 2012). Transport injuries are the most frequent cause of death in adolescents (see 1.3, Eaton et al., 2010). In the light of this, a recent study investigated whether peers influenced adolescents' (aged 16 - 18 years) evaluations of road-crossing safety from a pedestrian perspective in video-clips (Pfeffer & Hunter, 2012). When in the presence of peers who had been briefed to encourage safe road crossing behaviour, more crossings were correctly identified as dangerous relative to when peers were exerting negative influence or no peers were present.

Health advertising campaigns have also recognized the powerful influence of peers, and many peer-led prevention and intervention programmes have been developed to reduce adolescent smoking, to educate on sexual health or to prevent drug abuse (Cuijpers, 2002; C. R. Kim & Free, 2008; Parkin & McKeganey, 2000; Stephenson et al., 2004). For example, the ASSIST intervention (A Stop Smoking in Schools Trial) is a school-based peer-led intervention programme, targeted at students aged 12 - 13 years (Campbell et al., 2008). Influential peers are identified on the basis of peer-nominations and then trained to be peer supporters to intervene in everyday situations and discourage smoking. This intervention led to a 22% decrease in the odds of being a regular smoker relative to control schools.

### 1.6.3 Heightened sensitivity to peer influence during adolescence

Questionnaire-based studies that have investigated developmental changes in sensitivity to peer influence usually employ hypothetical scenarios in which the participant needs to choose between an option that a peer suggests and an option that the participant would personally prefer to do (Berndt, 1979; Steinberg & Monahan, 2007; Steinberg & Silverberg, 1986). Earlier studies found a peak in sensitivity to peer influence during adolescence (around 14 - 15 years); however this peak was only reliably found for situations in which peers suggested anti-social behaviours (for example, stealing, cheating or trespassing; Berndt, 1979; Steinberg & Silverberg, 1986). A more recent questionnaire-measure, called resistance to peer influence (RPI), does not focus on anti-social behaviours and avoids socially desirable answers (Steinberg & Monahan, 2007). Employing this measure, a linear increase in the resistance to peer influence was found during adolescence. However this increase was most profound in adolescents aged 14 - 18 years, while there was no significant change during young adolescence (aged 10 - 14 years), thus supporting the notion that young adolescence is a period of heightened sensitivity to peer influence.

As described in 1.6.2.1.2, there is some experimental evidence for heightened sensitivity to peer influence in adolescence relative to adulthood, with adolescents taking more risks and showing increased activation in reward-related regions when in the presence of peers relative to when alone, while this was not found for adults (Chein et al., 2011; Gardner & Steinberg, 2005; A. R. Smith, Steinberg, et al., 2014). Studies investigating car crashes in the USA found that death rates in adolescents (aged 16 - 17 years) were elevated when they were transporting passengers – particularly when transporting passengers aged 13 - 29 years - while death rates in adult drivers (aged 30 - 59 years) were decreased when transporting passengers (Chen, Baker, Braver, & Li, 2000). Epidemiological studies have also found evidence for a role of peers on the likelihood of committing criminal acts in adolescence (Erickson & Jensen, 1977; Zimring, 1998). These studies showed that adolescents mostly perpetrate crimes such as drug abuse, vandalism, burglary, robbery or homicide when they are in company of one or more peers, whereas adults tend to be alone when committing a crime.

## 1.7 Social Influence

### 1.7.1 Social influence and conformity

A phenomenon that demonstrates the powerful impact of the social environment on individual's behaviour is social influence. A large social psychology literature in adults has reported the effects of social influence and conformity, demonstrating that individuals adjust their attitudes and/or behaviours in order to conform with those of others (see Cialdini and Goldstein 2004 for a review). One of the best-known studies to measure conformity assessed this in an alleged visual discrimination task (see Figure 1.8), in which participants had to match a target line with one of three differently long lines, after a group of confederates had responded (Asch, 1956). Conformity was measured by the number of times participants chose a wrong answer because the confederates unanimously had chosen it. Participants were influenced in their choices by wrong answers of the confederates showing on average 37% incorrect responses, whereas the control group (no social influence) responded wrong on 1% of trials only.

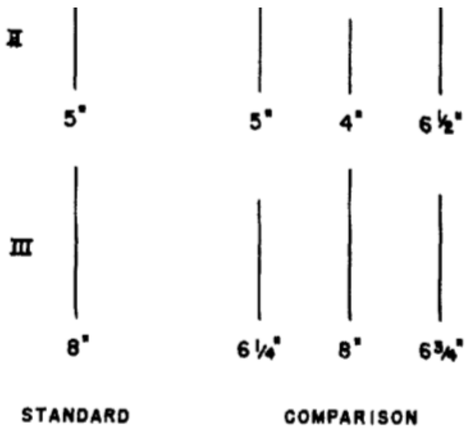


**Figure 1.8**: Asch's line paradigm to measure behavioural conformity: Participants believed to take part in a visual discrimination task, which required them to match a target line ('Standard') with one of three 'Comparison' lines. When participants responded after having been exposed to the unanimous and wrong response of a group of confederates, participants made more incorrect responses relative to a control condition (Figure taken from Asch, 1956).

The social psychology literature differentiates between two types of social influence: normative influence and informational influence (Deutsch & Gerard, 1955). In the case of ***normative influence,*** individuals' motivation to comply is thought to derive from the drive to obtain social approval and/or avoid social rejection (i.e. the motivation to be 'liked'). Individuals will adjust their behaviour in order to meet the expectations of others, thus publicly complying; however their private preferences might not be affected (Cialdini & Goldstein, 2004; Deutsch & Gerard, 1955). For instance, when eating out with a group of vegetarian friends, an individual might order a vegetarian dish, despite craving for a steak, in order to avoid disapproval from the friends. Williams et al. (2000) demonstrated that participants who had been ostracised in the Cyberball task (see section 1.5.2), subsequently conformed more frequently when making visual judgements than participants who were included. This increase in conformity after the experience of social exclusion suggests that conformity might be partly driven by the avoidance of social exclusion.

In contrast, ***informational influence*** describes the phenomenon that others' attitudes and behaviours can serve as a source of information about the environment to guide behaviour, which individuals might privately accept and thus adjust their own preferences (Cialdini & Goldstein, 2004; Deutsch & Gerard, 1955). For informational influence, the motivation to conform is thought to stem from the goal to be accurate (i.e. the motivation to be 'right'). Informational influence often occurs when individuals are uncertain about a choice and greater conformity was found when stimuli were ambiguous (R. Bond & Smith, 1996). For example when choosing a restaurant on holiday, an individual might be more likely to pick the restaurant that is filled with guests over an empty restaurant.

Informational and normative influence can both contribute to a change in behaviour and public compliance to opinions might be followed by private acceptance. It is difficult to disentangle the two types of influence in experimental settings as both results in conforming behaviour. Deutsch and Gerard (1955) suggested that the level of normative influence is dependent on whether participants' choices can be seen by the group and found that participants conformed less when making anonymous judgements in Asch's line paradigm (Asch, 1951) than when feeling observed by the rest of the group (although note that a meta-analysis of studies using Asch's line paradigm did not find a significant difference between public versus private judgements; R. Bond & Smith, 1996).

The following sections will first review studies on developmental changes of conformity (1.7.2), then briefly describe the similarity of social and non-social reward and punishment processing (1.7.3), and finally review functional imaging studies investigating social influence in adults (1.7.4) and adolescents (1.7.5).

### 1.7.2 Development of social influence and conformity

A number of recent developmental studies have investigated children's (aged 4 - 6 years) sensitivity to social influence (Haun & Tomasello, 2011; Over & Carpenter, 2009). In a child-friendly version of Asch's line paradigm, 4-year-olds conformed to the unanimous, but wrong judgment of a majority of peers and crucially showed stronger conformity when responding publicly (verbal response) compared to privately (pointing response; Haun & Tomasello, 2011). Studies in young childhood have also investigated imitation and have found that children over-imitate a model, i.e. imitate unnecessary actions to complete a task, in some social contexts (Over & Carpenter, 2013). For instance, after children (aged 4 - 6 years) observed an animation of shapes being ostracised, they subsequently imitated the actions of an adult model more faithfully than did children who had watched a control animation (Over & Carpenter, 2009).

As reviewed in 1.6.3, conformity to peers in hypothetical scenarios was found to follow an inverted U-shape during adolescence (peaking around 14 - 15 years), when peers suggested anti-social behaviours, while conformity was found to decrease linearly between 14 - 18 years when the hypothetical scenarios did not focus on anti-social behaviours (Berndt, 1979; Steinberg & Monahan, 2007; Steinberg & Silverberg, 1986). A few studies have investigated the development of conforming behaviour in Asch's line paradigm during adolescence. Costanzo et al. (1966) found that young adolescents (aged 11 - 13 years) showed greater conforming behaviour in a variant of Asch's line paradigm (employing ambiguous stimuli) relative to children (aged 7 - 9 years), older adolescents (aged 17 - 19 years) and young adults. In contrast, Walker and Andrade (1996) described a decrease in conformity between 3 - 17 years in a version of Asch's line paradigm using unambiguous stimuli. However, there were only two critical trials, in which participants were confronted with a wrong unanimous majority judgement of same-aged peers acting as confederates. In addition, the ability of 3-year-olds to act as confederates is questionable and difficult to compare with the effects of adolescent confederates. Differences in developmental trajectories might also be due to the differences in the ambiguity of the stimuli: similar to what has been shown in adults (R. Bond & Smith, 1996), studies in children and adolescents have also found greater conformity if the stimuli are ambiguous (Haun, van Leeuwen, & Edelson, 2013; M. B. Walker & Andrade, 1996).

In an experimental study, adolescents aged 12 - 17 years listened to short music clips from Myspace and rated how much they liked the song (Berns, Capra, Moore, & Noussair, 2010). In a second round of ratings, after participants had viewed the overall popularity of the song on Myspace, participants' ratings conformed to these popularity ratings and younger adolescents conformed more strongly than did older adolescents. To summarize, there is evidence from questionnaire-based and experimental studies that the tendency to conform to others changes during adolescence, however some findings support a peak in conformity during young- to mid-adolescence while others suggest a decrease of conformity during adolescence.

Adolescents, but not adults, showed increased risk-taking in a car-driving simulation in the presence of peers relative when alone (for details see 1.6.2.1.2, Gardner & Steinberg, 2005). A recent study suggested this effect is dependent on whether a confederate, who posed as a peer, was perceived to endorse risk-avoidant or risk-seeking norms prior to the car-driving simulation (Simons-Morton et al., 2014). Male adolescents aged 16- 17 years took more risks during driving when with a supposedly risk-seeking peer relative to when alone, while risk-taking in the presence of a supposedly risk-avoidant peer was not elevated (the participant and the peer were not allowed to interact). This suggests that conformity to social norms might contribute to peer-influence effects on risk-taking in driving situations in adolescence.

Recently, studies investigating adolescent conformity to peers aimed to disentangle public compliance from private acceptance. As described in 1.6.1, Cohen and Prinstein (2006) found that adolescent boys were more likely to publicly comply in a Chatroom paradigm to high-status than low-status peers who endorsed aggressive and health-risking behaviours. Participants also responded to the same hypothetical scenarios in the absence of the alleged peers. In this private session, adolescent boys also showed higher private acceptance of aggressive or health-risking attitudes after interacting with the high-status peers compared to the low-status peers. These findings suggest that adolescents do not only comply with their peers in public, but also internalize their peers' attitudes. In a follow-up study in adolescent boys (aged 14 - 15 years), described in 1.6.2.1.1, participants had also privately adjusted their willingness to drink alcohol after being exposed to responses of peers who were less willing to consume alcohol; however this effect was not found when they viewed attitudes of peers with a greater willingness to consume alcohol (Teunissen et al., 2012). These studies indicate that adolescents conform to their peers' norms. There is also some evidence suggesting that adolescents privately accept those norms.

### 1.7.3 Social reward and punishment

As reviewed in 1.7.1, conforming behaviour is in part motivated by the prospect of obtaining social approval by others and the desire to affiliate (Cialdini & Goldstein, 2004). The rewarding value of social approval might reinforce behaviour that is consistent with social norms (Falk, Way, & Jasinska, 2012). A large number of neuroimaging studies in adults have described the role of the VS and the OFC in the processing of primary (e.g. food and water) and secondary (monetary) rewards (Haber & Knutson, 2010; Montague, King-Casas, & Cohen, 2006; Rangel, Camerer, & Montague, 2008). Recent studies demonstrated that these regions are also involved in the processing of social rewards (Bhanji & Delgado, 2014; Davey, Allen, Harrison, Dwyer, & Yücel, 2010; Fareri & Delgado, 2014; Lieberman & Eisenberger, 2009). For example, being described by others with positive relative to neutral trait adjectives activated similar regions in the striatum as receiving monetary rewards (Izuma, Saito, & Sadato, 2008). Anticipation of positive social feedback (happy face expressions) and monetary gains both activated reward-related regions including the VS/NAcc, with greater activity for cues predicting greater social or monetary rewards (Rademacher et al., 2010; Spreckelmeyer et al., 2009), indicating that similar brain areas are involved in processing of monetary and social rewards. Engaging in social interactions also activates reward-related regions: perceiving that another participant was controlling a virtual agent in a gaze-based interaction paradigm activated the VS and OFC relative to perceived computer-controlled agents (Pfeiffer et al., 2014).

In addition to the pursuit of social approval, normative social influence is thought to be motivated by the avoidance of social exclusion, i.e. individuals will adjust their behaviour to match social norms to prevent becoming the target of others' disapproval (Cialdini & Goldstein, 2004). Neuroimaging studies in adults have suggested that the affective component of physical pain and the 'pain' of being social excluded are both processed by similar brain regions, including the ACC and insula (Lieberman & Eisenberger, 2009; Rotge et al., 2014; Shackman et al., 2011). The first fMRI study to assess the neural correlates of ostracism, contrasting social exclusion relative to the inclusion conditions of the Cyberball task (see 1.5.2 for details about the task), revealed greater activation in the dorsal ACC (dACC) and anterior insula (Eisenberger, Lieberman, & Williams, 2003). Self-reported distress during exclusion was positively correlated with activation in the dACC during exclusion relative to inclusion. Activation in the dACC, when viewing disapproving facial emotions relative to fixation, correlated positively with individual sensitivity to rejection (Burklund, Eisenberger, & Lieberman, 2007). Additionally two recent meta-analyses showed that both social exclusion and physical pain activate the anterior part of the dACC (Rotge et al., 2014; Shackman et al., 2011; although see 1.7.4 for a discussion of a role of the dACC in monitoring response conflict). Both pain and social exclusion can act as negative feedback to reinforce behaviour and functional imaging studies in adults indicate that the same brain regions might process the affective components of physical pain and social exclusion.

A recent study in adults provided further insight in the way that peer feedback might affect behaviour via social reinforcement learning (Jones et al., 2011). The study employed a learning task, in which participants responded to cues of three alleged peers, who differed in their likelihood of giving positive feedback (i.e. their frequency of providing notes that displayed interest in personal information that participants recorded on video before the experiment). Participants became quicker over the course of the experiment in responding to peers who were more likely to provide positive feedback relative to those who gave less positive feedback, and also rated those peers who interacted more frequently with them as more likeable. Similarities between social and non-social reinforcement learning suggest that positive and negative social feedback might reinforce behaviour that is consistent with social norms. Activity in the vACC, VS, anterior insula and OFC correlated positively with the prediction error signal. These areas are also known to be involved in reinforcement learning of non-social primary or secondary reinforcers (Montague et al., 2006).

To summarize, with normative influence being mediated by the pursuit of social approval and the avoidance of social exclusion, developmental differences in the sensitivity to social rewards and/or social exclusion might be related to changes in the susceptibility to social influence.

### 1.7.4 Neural correlates of social influence

As reviewed in 1.7.1, the reasons why individuals conform to others' attitudes or preferences are thought to be twofold: an aim to be accurate, i.e. using others' opinions as a source of information (**informational influence**) and an aim to obtain social approval from others and to avoid social exclusion (**normative influence**), i.e. conforming to meet others' expectations. In the recent years, functional imaging studies in adults have aimed to unravel the neural mechanisms of social conformity.

Supporting the idea that social rewards activate similar regions as non-social rewards, studies have demonstrated that agreeing with others activates typical reward-related regions. Agreeing with two music experts on song choice activated similar areas in the VS as receiving a token for the favoured song (see Figure 1.9a; Campbell-Meiklejohn, Bach, Roepstorff, Dolan, & Frith, 2010). Similarly, activation in the NAcc was greater when agreeing relative to disagreeing with the ratings of a group on the attractiveness of faces (Klucharev, Hytönen, Rijpkema, Smidts, & Fernández, 2009). Therefore, regions associated with the processing of primary or monetary rewards also seem to be activated when matching preferences with others. However, this effect appears to be only true when agreeing with a liked group; in the case of a disliked group activation in the VS was elevated when disagreeing relative to agreeing with them (Izuma & Adolphs, 2013).

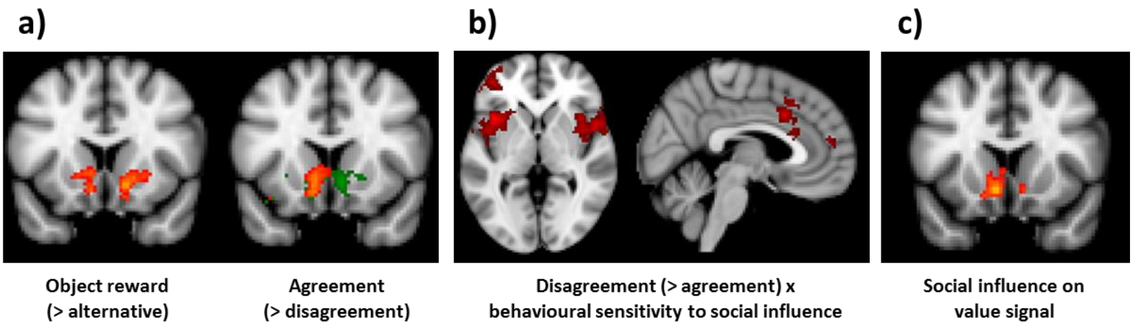


**Figure 1.9**: Neural activation in a social influence task (Figures adapted from Campbell-Meiklejohn et al., 2010). Green maps shows activation at reduced cluster defining threshold (orange: Z > 2.3; green: Z > 2.0). a) Agreeing (versus disagreeing) with music experts on song choice activated similar regions in the VS as receiving a token for the preferred song (versus the alternative song). b) Activation in the anterior insula/frontal operculum and dACC when disagreeing with the music experts relative to when agreeing correlated positively with the behavioural tendency to conform to the music experts. c) Social influence on the value signal when receiving a token for the music song.

When conforming to others' opinions, individuals will maintain their opinions if they match those of others, and in the case when they do not match, individuals will adjust their opinions towards the others' opinions (Berns et al., 2010; Campbell-Meiklejohn et al., 2010; Cialdini & Goldstein, 2004; Klucharev et al., 2009; Zaki, Schirmer, & Mitchell, 2011). In the study of Campbell-Meiklejohn et al. (2010), the behavioural metric $B_{inf}$ was employed as a measure of sensitivity to social influence indicating how much participants adjusted their song ratings at the second time of judging towards the opinions of the music experts. Higher $B_{inf}$ values (i.e. greater sensitivity to social influence) were associated with greater activation in the dACC and anterior insula when disagreeing relative agreeing with the music experts (see Figure 1.9b, Campbell-Meiklejohn et al., 2010). Similarly, Klucharev et al. (2009) found increased activation in the dACC and insula when participants' facial attractiveness ratings disagreed with the group norms. Activation in the dACC and insula are also typically found during social exclusion. The dACC has however also been implicated in the detection of response conflicts and errors (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). A recent meta-analysis of functional imaging studies demonstrated that physical pain, negative affect and cognitive control activate an overlapping area in the anterior region of the dACC (Shackman et al., 2011). This meta-analysis integrated these findings in the adaptive control hypothesis, which suggests a role of the dACC in processing information about punishment across domains to control aversively motivated actions. The activation pattern during disagreement relative to agreement described by Klucharev et al. (2009), i.e. increased activation in the dACC and decreased activation in the striatum, is similar to the neural prediction error signal found in reinforcement learning and also predicted the level of behavioural conformity. This activation pattern might thus signal the need to decrease the conflict between one's own and others' preferences. Speculatively, social norms might reinforce behaviour similarly to non-social rewards or punishments. However, note that it is not possible to infer the involvement of a specific cognitive process on the basis of the activation of a certain brain region (see 7.2.3 for a discussion of reverse inference).

In the case of informational influence, individuals do not only comply in public, but also change their own values and opinions (Cialdini & Goldstein, 2004). It has been suggested that private acceptance of social norms might be reflected in a change of the value signal of an object or stimulus (Zaki et al., 2011). In one experiment studying social influence on perceived facial attractiveness, participants showed greater VS and OFC activation at the second time of rating, when peers had judged the faces initially as more attractive relative to faces judged as less attractive (Zaki et al., 2011). Likewise, when participants received a token for a song, the value signal for the token in the VS was affected by music experts' preferences in dependence on the behavioural magnitude of preference changes (see Figure 1.9c, Campbell-Meiklejohn et al., 2010). This suggests that changes in behavioural preferences in response to deviating judgements of others are also reflected in an adjustment of the neural value signal of this object.

To summarize, agreeing with others' preferences activates typical reward-related regions (VS and OFC), while disagreeing with others' preferences activates regions (insula and dACC) typically found during social exclusion. There is also evidence that social norms might mediate conformity similar to neural mechanisms of reinforcement learning. Finally, the value signal of an object is modulated by social influence.

### 1.7.5 Developmental changes of the neural correlates of social influence

Adolescence is a period of heightened reward sensitivity as well as heightened sensitivity to social exclusion (see 1.3 and 1.5.2). Adult findings show activations in reward-related regions when agreeing with others' preferences and activations in regions typically found during social exclusion (dACC and insula) when disagreeing with others' preferences. Consequently, developmental changes in the neural correlates of sensitivity to social reward or exclusion during adolescence might be associated with developmental changes of social influence. Studies examining the development of the neural correlates of social influence are scarce. One study investigating adolescent conformity of music preferences to popularity ratings (see 1.7.2) found that individual differences in conformity were positively correlated with activity in the dACC and anterior insula at the second time of rating when participants (aged 12 - 17 years) had viewed popularity ratings after their first rating (Berns et al., 2010). Thus, similar to what has been reported in adult social influence studies, conflicts between one's own and others' preferences in adolescence elicit activity in areas also associated with social exclusion (Eisenberger et al., 2003; Masten et al., 2009; Sebastian et al., 2011).

Studies on peer influence have demonstrated that adolescents', but not adults' risk-taking, is elevated in the presence of peers relative to when alone (Gardner & Steinberg, 2005, see 1.6.2.1.2 for details). However, risky decision-making in adolescence seems to be adaptive depending on the social context in which the choices are made. When making choices between a sure gain and a lottery, risk-averse advice by an adult economics expert affected adolescents' (aged 12 - 17 years) choices more than adults' choices (Engelmann, Moore, Capra, & Berns, 2012). In young adolescents (aged 12 - 14 years) this behavioural effect seemed to be mediated by a greater positive correlation between activation in the dorsolateral prefrontal cortex (DLPFC) and the magnitude of the sure option in the presence of advice relative when no advice was given. The authors suggested that the presence of an adult expert might modulate the activation of regions typically associated with cognitive control (DLPFC). This study cannot determine how adolescents would adjust their choice behaviour to risk-seeking advice of an adult or risk-averse advice by a peer because these conditions were not included.

## 1.8 Social facilitation and the audience effect

### 1.8.1 What is social facilitation?

There has been a long history of research on social facilitation in adults (Triplett, 1898), which describes the phenomena of *co-actor effects* (individuals performing the same task as the participant) or *audience effects* on task performance. The term social facilitation stemmed from early studies (Guerin, 1993) showing that participants were faster in a competitive motor task (Triplett, 1898) and generated more words in a word association task (Allport, 1920) when performing along co-actors compared to when alone. Performance improvements were also found in the presence of an audience; for example, in tasks testing motor coordination (Travis, 1925) or vigilance (Bergum & Lehr, 1963). In contrast, Pessin (1933) showed that participants required more trials to learn a list of nonsense syllables in the presence of an audience compared to when learning on their own. However, when recalling these syllables after several days, performance was better in the presence of an audience. Zajonc (1965) put these apparently inconsistent findings into a theoretical framework proposing that improved performance in the presence of others is usually found for simple or well-learned tasks, whereas an impairment of performance is reported for complex or learning tasks. Even though both improvements and impairments of performance have been reported, the somewhat misleading term social facilitation continues to be used (Aiello & Douthitt, 2001; Guerin, 1993).

A meta-analysis of 241 co-actor and audience effect studies (C. F. Bond & Titus, 1983) generally supports Zajonc's framework: participants perform quicker (RT or response rate) in simple tasks and slower in complex tasks when in the presence of others. Similarly, the presence of others leads to a decrease in accuracy in complex tasks and an increase in accuracy in simple tasks. However, the mean effect size of this improvement in accuracy is fairly small (mean d = 0.11), which might be a result of ceiling effects or a publication bias towards findings that are consistent with the framework.

Due to the variety of tasks that have been used to study social facilitation (C. F. Bond & Titus, 1983; Guerin, 1993; Zajonc, 1965), it is challenging to generate a comprehensive classification system as to what constitutes a simple task versus a complex task. An example of this challenge can be seen in the Bond & Titus (1983) meta-analysis, which, instead of classifying tasks used in different studies as simple or complex based on a consistent rule, labelled tasks according to their classifications in the original papers. This lack of a consistent classification system might have also contributed to the small effect size of the improvement in accuracy in simple tasks: while 60% of the effects in simple tasks were an improvement in accuracy with an audience, 40% were *impairments* in accuracy, suggesting that some of these tasks might actually be complex or the theory is wrong. In addition, only about a sixth of the studies in the Bond & Titus meta-analysis (1983) manipulated task difficulty within a single experiment.

Only a few studies have considered how individual differences might contribute to the direction of social facilitation effects. A task that is simple for one participant might be complex for another and consequently individual differences might play a role as to whether a participant's performance improves or decreases in the presence of others. A recent meta-analysis on individual differences (Uziel, 2007) showed that personality also modulates the effect of the presence of others on task performance. This meta-analysis showed that, for the small number of social facilitation studies (14 studies) that collected personality variables, positively oriented individuals performed better and negatively oriented individuals performed worse in the presence of others.

Experimental peer influence studies in adolescents have so far mostly focused on the effect of the presence of peers on risky or reward-related decision-making (see 1.6.2.1). Few developmental studies have investigated the effect of the presence of others – in particular peers - on task performance. While peers might play a special role in both audience effects and co-actor effects during adolescence, it is difficult to disentangle effects of competition or rivalry from other co-actor effects; consequently I will now narrow the review to audience effects. The next section (1.8.2) will summarize the most relevant theories of audience effects and link these to the special role of peers during adolescence. Subsequently, developmental studies on audience effects (1.8.3) and neural correlates of audience effects (1.8.4) will be reviewed.

### 1.8.2 Theories for the audience effect

In addition to providing a framework to explain the directionality of audience effects in dependence on task difficulty or mastery, Zajonc also developed the 'drive theory' to explain the framework. According to his theory, the mere presence of others increases drive levels (arousal), which enhances the production of dominant responses. He asserted that in simple or well-learnt tasks the 'dominant' (habitual) response would be a correct response, while in complex or learning tasks it would be incorrect and consequently leading to performance improvements in simple tasks and performance impairments in complex tasks (Zajonc, 1965; Zajonc & Sales, 1966). In the following decades, the drive theory of mere presence was challenged and many new theories evolved; in fact by 1993 seventeen different theories had been developed (Guerin, 1993). I will now briefly summarize the three most relevant theories in light of potential peer audience effects in adolescence.

*First*, in the *evaluation apprehension theory*, Cottrell (1972) asserted that the presence of others would only result in audience effects if individuals were concerned about how others evaluate their performance. Cottrell suggested that increased arousal in the presence of others results from the anticipation of positive or negative evaluations of their performance. For example, while the presence of an evaluative audience affected performance in recalling well-practiced relative to rarely-practiced non-sense syllables, there was no difference between the alone condition and a blindfolded audience (Cottrell, Wack, Sekerak, & Rittle, 1968). As reviewed in 1.5, adolescents are particularly concerned about and sensitive to peer evaluation (Kloep, 1999; Moor et al., 2010; Sebastian et al., 2011, 2010; Westenberg et al., 2004) and also showed heightened autonomic arousal when being observed by a peer relative to both children and adults (Somerville et al., 2013). Thus, adolescents might excessively worry about their performance in the presence of peers and demonstrate greater peer audience effects than adults.

*Second*, Duval and Wicklund proposed in their *objective self-awareness theory* (Duval & Wicklund, 1972) that the presence of an audience leads to increases in self-awareness, causing individuals to think about how others evaluate their performance. As a consequence, individuals are thought to become more aware of potential discrepancies between their present and perfect performance, which is an aversive state that motivates individuals to reduce this discrepancy. In simple tasks this increased effort to do well would lead to performance improvements, while in complex tasks excessive effort would cause performance impairments (Duval & Wicklund, 1972). Similarly to the evaluation apprehension theory, heightened concerns about being judged by peers might lead to greater audience effects in the presence of peers during adolescence. In order to avoid looking 'stupid' in front of their peer, adolescents might try particularly hard to perform well when being observed by a peer. In simple tasks this is likely to be successful, however in difficult tasks cognitive resources taken up by excessive task monitoring might lead to performance impairments. The idea of limited cognitive resources was also discussed in the *third* theory, the *distraction-conflict theory,* implicating attentional conflicts between an audience and the task in performance differences in the presence of an audience (Baron, 1986).

### 1.8.3 Developmental audience effect studies

Few developmental studies have investigated the effect of the presence of an audience on task performance. In a young sample, it was found that children aged 4 - 5 years performed more quickly on a simple motor task in the presence of a visible experimenter relative to an invisible one (Meddock, Parsons, & Hill, 1971). Another developmental study compared performance in the assembly of a jigsaw puzzle in children aged 5, 8 and 11 years (Newman, Dickstein, & Gargan, 1978). Only the oldest group showed performance impairments in the presence of a passive observer (same-aged participant waiting for the experimenter in the same room) relative to being alone. This suggests that as children get older their performance becomes more sensitive to the presence of a peer. In another study, poorer performance in the digit-span task was found when adolescents (aged 13 - 14 years, 8$^{th}$ grade American school) were observed by two unfamiliar teachers relative to when being unobserved (Quarter & Marcus, 1971). A decrease in performance on a relational reasoning task was also found in a sample of 9 - 14-year-olds with behavioural problems when solving relational reasoning problems in the presence of a classmate (Bevington & Wishart, 1999), although it is difficult to disentangle peer audience effects from distractions by disruptive behaviour in this sample.

To summarize, these developmental studies have demonstrated firstly the presence of audience effects in children and adolescents, secondly that performance is enhanced in a motor task and impaired in more cognitively challenging tasks and thirdly that there is limited evidence for increasing sensitivity to peer audience effects in children between 5 and 11 years of age. However, developmental studies have not yet investigated whether sensitivity to peer audience effects changes during adolescence or whether it differs between adolescents and adults. In addition, existing studies have not addressed whether adolescents might be particularly sensitive to the presence of peers in comparison to the presence of non-peers.

### 1.8.4 Neural correlates of the audience effect

Studies investigating the neural correlates of the audience effect are very limited. In a developmental electroencephalography (EEG) study, peer audience effects on error-related negativity (ERN; a negative deflection in the event-related potential occurring shortly after an error has been committed) in a go/no-go task were investigated in 7 - 11-year-old children (E. Y. Kim, Iwaki, Uno, & Fujita, 2005). This study found no difference in performance when being observed by the friend relative to when alone, possibly due to the relatively small sample size. However, in the presence of the friend the ERN amplitude was increased relative to when alone, suggesting that error signal processing is modulated by the presence of peers in 7 - 11-year-old children.

In a near-infrared spectroscopy study (NIRS) in adult participants, autonomic arousal and prefrontal activation during an N-back working memory task were compared when being observed and evaluated by two experimenters in a competitive scenario relative to an alone condition (Ito et al., 2011). Autonomic arousal (measured with skin temperature and blood volume pulse) was increased for all three task difficulty levels (1-back, 2-back and 3-back) in the presence of the audience relative to when alone. In contrast, the error rate was only significantly affected by an audience in the most difficult (3-back) working memory condition.

Activation in bilateral PFC when performing the working memory task relative to a control task was also only elevated in the presence of the audience relative to being alone in the 3-back condition. This increase in activation in the left PFC was associated with the increase in error rate in the 3-back condition, while there was no correlation between arousal and error rates. This data suggests that changes in arousal in the presence of an audience might at least not directly mediate performance changes. Increased PFC activation in the complex condition may be related to increased cognitive load in the presence of an audience. In the two simple conditions (1-back and 2-back) accuracy when alone was at a very high level (> 95%), consequently participants might have had sufficient cognitive resources to excel in the task even when being in the presence of an audience exerting pressure. In contrast, in the 3-back condition performance might have suffered from additional cognitive load by an audience.

## 1.9 Summary of experimental chapters

While epidemiological studies describe adolescence as a period of heightened engagement in risky behaviours such as dangerous driving, consuming drugs, or risky sexual behaviour (Boyer, 2006; Eaton et al., 2010; Steinberg, 2008), experimental studies have found mixed evidence for a peak in risk-taking during adolescence. When assessed in an affective context, the developmental trajectory of risk-taking appears to describe a peak during adolescence, while in non-affective contexts risk-taking decreases or is stable across adolescence (Blakemore & Robbins, 2012). The developmental mismatch theory proposed that increased levels of risk-taking might be linked to a hyper-responsiveness of the reward system during adolescence (Casey et al., 2008; Somerville et al., 2010; Steinberg, 2008). This is thought to result from a prolonged maturation of the prefrontal control system in relation to earlier maturation of subcortical reward-related regions; although this model has recently been criticised as being too simplistic (Crone & Dahl, 2012; Pfeifer & Allen, 2012).

In light of this developmental literature, **Chapters 2 and 3** examine two distinct aspects of the development of risk-taking and the neural correlates of reward-processing in adolescence. **Chapter 2** describes a study that examined the developmental changes of the impacts of risk and valence on decision-making in a non-affective context during young to mid-adolescence. This behavioural study employed a non-affective gambling task to assess the developmental patterns of the impacts of risk and valence. With recent evidence in adults suggesting that risk and valence independently influence decision-making, it was hypothesized that they might also follow different developmental patterns. **Chapter 3** examines the development of the neural basis of social influence on music song valuation. This chapter compares the neural correlates of agreeing with similar-aged music-experts on song choice and the modulation of value-related signals by social influence in female mid-adolescents and adults. Similarly to receiving non-social rewards, it was predicted that matching preferences with others would elicit reward-related activation and that others' preferences might modulate value-related activation in the VS. On the basis of studies suggesting increased responsiveness of reward-related regions during adolescence (for reviews see Blakemore & Robbins, 2012; Galván, 2013), it was hypothesised that there might be developmental changes in these neural correlates.

Adolescence is a period of profound changes in the social environment. The opinions and judgments of peers become especially important during adolescence and adolescents are particularly sensitive to peer influence. Previous experimental studies have demonstrated that the presence of peers affects risky and reward-related decision-making in adolescents and modulates activation in reward-related regions. **Chapters 4 to 6** examine whether sensitivity to peer influence in adolescence extends to peer audience effects on tasks with either high-level (reasoning) or low-level (perceptual) cognitive components and across different levels of task difficulty. **Chapter 4** investigates the effect of an audience on performance in a relational reasoning task and whether this audience effect is dependent on the identity of the audience (peer versus non-peer). Participants performed a relational reasoning task while being observed and evaluated by a friend (peer), by an experimenter (non-peer) or while being alone. The development of this peer audience effect on relational reasoning performance was compared in a group of young adolescent, mid-adolescent and adult female participants. It was hypothesized that adolescents' relational reasoning performance might be more sensitive to peer audience observation than adults' performance. Developmental changes were also examined between the young and mid-adolescents. **Chapter 5** investigates whether adolescent sensitivity to peer audience observation is specific to a high-level cognitive task or whether these peer audience effects also extend to the performance in a low-level perceptual task. Finally, **Chapter 6** examines peer audience effects on the neural correlates of relational reasoning in a group of female mid-adolescents and adults. This study employed a minimal, virtual peer observation manipulation (Somerville et al., 2013) to examine the modulation of activation in the fronto-parietal relational reasoning network. Developmental changes in the effect of peer audience observation on the recruitment of the fronto-parietal network were assessed.

This thesis will investigate these research questions exclusively in female participants. This approach was chosen to reduce noise in the sample due to potential sex differences. Previous questionnaire-based studies have indicated that there are gender differences in resistance to peer influence (Berndt, 1979; Steinberg & Silverberg, 1986). Adolescent girls also reported higher levels of public self-consciousness (Rankin et al., 2004), greater importance of peer approval for self-esteem (S. F. O'Brien & Bierman, 1988) and greater fear of negative evaluation by peers (La Greca & Lopez, 1998; La Greca & Stone, 1993; Rudolph & Conley, 2005), than boys. Furthermore, adolescent boys and girls show differences in their peer relationships (for a review Rose & Rudolph, 2006). FMRI studies have also suggested developmental differences in functional activation patterns during the anticipation of peer evaluation in female and male adolescents (see 1.5.3; Guyer et al., 2009). Finally, developmental trajectories in structural brain development have also shown sex differences (Herting, Maxwell, Irvine, & Nagel, 2012; Mills et al., 2014; Raznahan et al., 2011). Consequently, in order to reduce noise in the sample due to potential sex differences, this thesis will only include female participants to maximise sample homogeneity. This approach means that the results obtained in this thesis are specific to females only.

Most of the adolescent participants recruited for the studies in this thesis attended academically selective secondary schools. In order to ensure that adolescent and adult participants were matched in terms of educational background, the majority of adult participants were university students or graduates, resulting in relatively high IQ samples. While this recruitment approach limits the generalizability of the findings to a population with a wider range of general cognitive abilities, it maximises sample homogeneity and thus the ability to detect developmental changes.

The majority of developmental studies in adolescence have defined adolescent groups by chronological age and not by puberty status. This approach was also chosen for the studies in this thesis due to several reasons. *Firstly*, this approach allowed an easier comparison of the results of this thesis to the literature. *Second*, age can be easily and reliably quantified with a high validity, allowing a simple comparison across different studies. In contrast, puberty can be measured by different, often categorical measures, such as Tanner staging, hormonal assays or self-report questionnaires, which are more difficult to validate (Blakemore, Burnett, & Dahl, 2010). *Third*, apart from **Chapter 2**, the studies in this thesis aimed to compare adolescents to an adult group of participants. While puberty defines the start of adolescence, the end of adolescence in the developmental cognitive neuroscience literature is defined as the state when an individual attains a stable, independent role in society (Blakemore & Mills, 2014; Crone & Dahl, 2012; Lerner & Steinberg, 2004; Somerville, 2013). This definition of adulthood includes developmental changes that are occurring after the end of puberty, which could not be investigated using puberty as the main developmental measure. While it would be interesting to disentangle the effects of puberty from the effects of chronological age, this approach requires large numbers of participants and was not the focus of this thesis. *Fourth*, particularly in educational contexts, peers are more likely to be grouped by age than by pubertal status. Consequently, pairs of similar-aged peers rather than peers of similar pubertal status were invited to the studies investigating peer audience effects in this thesis (**Chapters 4 and 5**).

The experimental chapters (i.e. **Chapters 2 to 6**) investigated developmental changes in behavioural or functional correlates during adolescence. In general, assessing developmental changes with age as a continuous variable provides a more sensitive measurement of age and allows tracing both linear and non-linear changes with age. Furthermore, this avoids having to make arbitrary age groupings, particularly as no consistent classification of age grouping in adolescence exists in the literature. Thus, developmental changes during adolescence would ideally have been studied with age as a continuous variable. In order to use age as a continuous variable the sample needs to be sufficiently large and should not have gaps in the age sampling. In addition, the properties of the experimental design can limit the use of continuous age analyses. Firstly, simple experimental designs (i.e. few experimental factors and levels) work best for a continuous age analysis. This is because the interpretation of interaction effects in complex experimental designs is not straightforward in a continuous age analysis. Second, if the experimental design requires counterbalancing of critical experimental factors, individual values might be less meaningful than average group values. Due to these restrictions, most of the chapters of this thesis (**Chapters 3 to 6**), with the exception of **Chapter 2**, employed age groups to investigate developmental changes. In addition to these study-imposed restrictions, the analysis of age as age groups or as a continuous variable was also motivated by the type of age analysis in key previous studies, in order to allow better comparisons between the results of the studies in this thesis and previous findings.

# CHAPTER 2: DEVELOPMENTAL CHANGES IN EFFECTS OF RISK AND VALENCE

*Recent research on risky decision-making in adults has shown that both the risk in potential outcomes and their valence (i.e. whether those outcomes involve gains or losses) exert dissociable influences on decisions. Previous developmental studies have shown different developmental trajectories during adolescence for affective (i.e. when choices are made in the presence of peers or when emotions are at stake) and non-affective tasks. The current chapter investigates the development of the influences of these two decision variables - risk and valence - on decision-making in a non-affective context during adolescence. Sixty-one female adolescents aged 11 - 16 years completed a risk-taking paradigm, which provides precise metrics for the impacts of risk and valence on decisions. Decision-making was influenced by both risk and valence, and the impacts of risk and valence on decisions were independent of each other. The influences of risk and valence followed different developmental patterns during adolescence: the impact of valence on decisions showed a reduction with age, while there was an absence of developmental change in the impact of risk overall.*

## 2.1 Introduction

Value-based decision-making involves an agent choosing from several alternatives based on the subjective values of available options. Two powerful influences on such decisions are *risk* in potential outcomes (Harrison & Rutstroem, 2008; Kacelnik & Bateson, 1996) and whether those outcomes involve gains or losses i.e. their *valence* (Dayan & Seymour, 2008; Kahneman & Tversky, 1979). Risk in the Neuroeconomics literature is defined as a state in which the decision-maker lacks precise knowledge about which outcome will follow from a decision – there is uncertainty. Individuals may be risk-averse (preferring lower risk options when comparing options with identical expected value (EV)), risk-neutral or risk-seeking (preferring higher to lower risk options). Valence is defined as whether the potential outcomes under consideration entail either punishment (e.g. financial losses or painful electric shocks) or rewards (e.g. financial gains or tasty foods). The aim of the present study was to investigate the development of responses to these two crucial decision variables, risk and valence; from young to mid-adolescence (aged 11 - 16 years).

### 2.1.1 The effect of valence on decisions in adolescence

Of particular interest in this study was the development of the impact of valence on decision-making, prompted in part by a recent study that investigated valence-dependent reversal learning in response to unexpected reward and punishment in adolescence (van der Schaaf et al., 2011). Younger adolescents (aged 10 - 11 years) displayed better reversal learning scores following a punishment than following a reward, and this difference in performance decreased with age across adolescence (from 10 to 17 years). The current study investigated whether there is a similar development in the effect of valence on risky decision-making in young to mid-adolescence.

### 2.1.2 Development of risk-taking in adolescence

Previous studies have suggested that different aspects of risky decision-making show different developmental patterns (Blakemore & Robbins, 2012). Developmental trajectories of risk-taking behaviour differ depending on whether decisions are made in an affective or 'hot' experimental context (e.g., when emotions are involved or peers are present) or a non-affective or 'cold' context. As reviewed in detail in 1.3.1, evidence is suggesting that risk-taking peaks in mid-adolescence, when decisions are made in an affective context. This peak in reward-sensitivity in mid- to late adolescence (aged 14 - 21 years) was for instance demonstrated in a modified version of the Iowa Gambling Task (Cauffman et al., 2010). Similarly, risk-taking in a gambling task, designed to evoke relief or regret, peaked in mid-adolescence (around 14) (Burnett et al., 2010).

In studies with a non-affective context, the developmental pattern of risk-taking does not describe an inverted U-curve in adolescence, but instead there is a gradual decrease in risk-taking or no developmental change (Crone et al., 2008; Paulsen et al., 2011; Rakow & Rahim, 2010; Van Leijenhorst, Moor, et al., 2010). Studies manipulating the affective context of a risk-taking task demonstrated that adolescents make more suboptimal decisions relative to both children and adults when playing an affective version of a card game but not when playing a non-affective version of the task (Figner et al., 2009a, 2009b). While the affective context of decision-making tasks has been modulated in previous developmental studies, one aspect of decision-making that has not yet been examined is the differential impact of valence and risk. The current study used a non-affective task to isolate the effects of risk and valence on decisions (and developmental change in those effects), without studying how they interact with emotion.

### 2.1.3 Independent effects of valence and risk on decision-making in adults

The proposal that the impacts of risk and valence might have different developmental patterns is predicated on recent research in adults that suggests that risk and valence have independent effects on decision-making (Wright et al., 2012). The prevailing view in psychology and economics has been that risk and valence are related in a specific fashion, with risk-aversion for gains and risk-seeking for losses, given medium to high probabilities for gain and loss outcomes (Kahneman & Tversky, 1979). An alternative hypothesis is that valence and risk exert independent influences on decisions in gambling tasks (Wright et al., 2012). This alternative hypothesis was motivated by evidence that multiple, interacting neural valuation systems influence decisions (Dayan, 2008), with the processing of risk and valence by distinct neural systems being consistent with independent, rather than linked, behavioural effects. Behavioural and neurobiological evidence for a dissociation between the influences of risk and valence on decisions has been derived from studies that employed a financial gambling task that separately manipulated risk and valence (Wright et al., 2012).

### 2.1.4 The present study

The current study adapted the financial gambling task (Wright et al., 2012) to obtain precise metrics for the impacts of risk and valence on decisions and to study developmental changes captured by these metrics during adolescence (aged 11 - 16 years). First, the study aimed to investigate whether similar to adult decision-making adolescent decision-making would be influenced by both risk and valence and whether these influences are independent of one another. The study then examined whether the influences of risk and valence on decision-making show different developmental patterns during adolescence. Developmental change was possible in the impact of either risk or valence, or of both, on decisions in this non-affective risk-taking task.

## 2.2 Methods

### 2.2.1 Participants

Sixty-four female adolescents (mean age 13.9 years, range 11.5 – 16.5 years) took part. Data from three participants were excluded (two were unable to complete the task and one confused the buttons). All were recruited from the same academically selective secondary school in North London and were well matched for educational background and socioeconomic status. Participants were individually tested in a quiet classroom at their school.

Verbal IQ was assessed with the British Picture Vocabulary Scale (BPVS II; Dunn, Dunn, Whetton, & Burley, 1997) for all but seven participants (whose verbal IQ could not be assessed due to time limitations at the school). Verbal IQ was not associated with age (mean ± standard deviation (SD) = 114.3 ± 13.4; $\beta = 0.002$, $r^2 < 0.001$, $p > 0.9$) and covarying verbal IQ did not affect any of the experimental results.

### 2.2.2 Pre-test of stimulus understanding

Before the task, a validity check was employed to ensure that participants understood the basic information displayed in pie-chart stimuli. Participants saw eight printed pairs of pie-charts, and for each pair were told they should try to win as many points as possible (in the gain trials) or lose as few points as possible (in the loss trials) by choosing one of two pie-charts. An understanding of gains and losses (four pairs of pie-charts contained only gains and four only losses); magnitudes (in four pairs, probabilities were identical and magnitudes differed between the two pie-charts), and probabilities (magnitudes were identical and probabilities differed) was tested. Previous work has shown that children from age 5 understand simple probabilities (Schlottmann, 2001), and from age 8 children understand how risk and reward outcome contribute to a gamble's EV (Van Leijenhorst, Westenberg & Crone, 2008). As expected, all participants met the inclusion criterion of over 75% accuracy (mean correct pie-charts = 96.7% ± 6.4).

### 2.2.3 The gambling task

Participants completed a computer-based financial gambling task based on the 'accept/reject' task used by Wright et al. (2012). In the 'accept/reject' task used here (Figure 2.1), participants performed 112 trials presented in random order, of which 56 were Gain trials (all possible outcomes ≥ 0, Figure 2.1a) and 56 were Loss trials (all outcomes ≤ 0, Figure 2.1b). In each trial, participants chose to accept or reject a lottery (with three possible outcomes), compared to a sure option (a gain of 4 points in Gain trials, and a loss of 4 points in Loss trials). Each trial began with a fixation cross presented for 1 - 2 s (mean = 1.5 s), followed by a display of the options for 5 s. Finally, a black square appeared to signal that participants had 2 s to indicate their decision by pressing a button (the black square turned white when they chose). Participants were informed that non-responses resulted in the worst possible outcome, corresponding to 0 points in the Gain trials and loss of 8 points in the Loss trials. *No feedback* was given after the trials. The full 112 trials were split into two blocks of 56 trials, with each block lasting approximately 8 min. Stimuli were presented with Cogent 2000 (www.vislab.ucl.ac.uk/Cogent/index.html) implemented in Matlab R2010b (Mathworks Inc., Sherborn, MA).

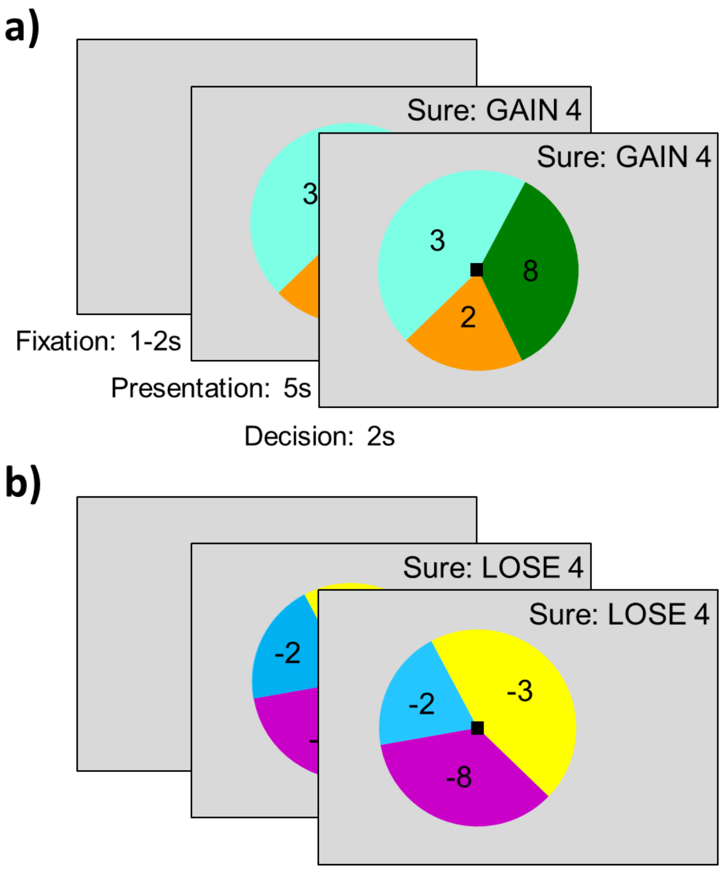


**Figure 2.1** Experimental design. In each trial, participants were instructed to choose between a lottery and sure option. The lottery was represented by a pie-chart with three segments corresponding to the three possible outcomes, with the size of each segment corresponding to the probability of that outcome occurring. The sure option was indicated on the upper right side of the screen. Half the trials involved winning points ('Gain' trials) and half involved losing points ('Loss' trials). a) In each 'Gain trial' participants chose either to accept a lottery (three varying possible outcomes, all ≥ 0) or reject it in favour of the sure option and so receive 4 points for certain. b) In each 'Loss trial' participants chose either to accept a lottery (three varying possible outcomes, all ≤ 0) or reject it in favour of the sure option and so lose 4 points for certain.

The decision variables of interest were risk and valence. Risk was manipulated by using a set of 56 lotteries (three possible outcomes, all ≥ 0), in which the degree of risk (eight levels; note this is variance as commonly defined in finance; Bossaerts, 2010; Markowitz, 1952) and EV (seven levels) were parametrically and orthogonally varied. Half the lotteries had an EV above the sure amount, and half were below it. Each lottery was presented in this set once to give 56 Gain trials. To manipulate valence, all outcome amounts were multiplied by -1 to give 56 Loss trials (i.e. all outcomes ≤ 0, and a sure option of -4 points). This created a set of Gain trials and a set of matched Loss trials.

Participants were told to treat the points as a currency, at an exchange rate of one point equal to 50 pence. Participants began the testing session with an endowment of eight points. After the experiment, one Gain trial and one Loss trial were picked at random, and their outcomes were added to this endowment to determine a final payment. Participants could receive between 0 - 16 points, which at the end of the experiment were converted into GBP (i.e. £0 - 8). Participants also received £1 for participation.

### 2.2.4 Stimulus sets

A set of 56 lotteries was generated by orthogonally manipulating the variance (8 levels; mean = 7.5; range = 0.9 - 14.4) and EV (7 levels; mean = 4.0; range = 2.2 - 5.8) of the lottery. This stimulus set was created in two stages. First, a list of every possible trial within the following constraints was generated: each lottery had three outcomes (i.e. three pie-chart segments); outcomes were between 0 and 8 points; the smallest allowable probability was 0.1 (to militate against possible probability distortion); and the smallest allowable probability increment was 0.05. Next, a set of 56 trials was selected that were the closest match to the desired 8 levels of variance and 7 levels of EV.

### 2.2.5 Data analysis

The majority of previous studies (see 1.3) that have investigated developmental changes in risky decision-making in adolescence have employed designs in which age was studied continuously. To be able to compare the results of the current study better to those of previous studies, in addition to the simple design and the relatively large number of adolescent participants in this sample, this study investigated the effect of age continuously (see also 1.9 for a discussion of age analyses).

The EV of half the lotteries was above the sure amount and half below (mean EV across all 56 trials was equal to the sure option in both the Gain and Loss trials). Thus, the proportion of riskier decisions was used as a metric of participants' *risk preference* (*PropRisk*; risk-neutral = 0.5; risk-averse < 0.5; risk-seeking > 0.5). To derive an individual measure for the effect of valence on decisions, the *impact of valence* was calculated as difference in proportion of riskier decisions between Gain and Loss trials ($ImpValence = PropRisk_{gain} - PropRisk_{loss}$). Wright et al. (2012) used identical metrics for risk and valence.

These participant-derived parameters were used in two separate analyses. *First*, the study assessed whether adolescent decision-making is influenced by both risk and valence. To examine whether risk influenced decisions, a one-sample t-test was employed to assess whether overall *PropRisk* ($PropRisk_{all}$ i.e. collapsed across Gains and Losses) was significantly different from 0.5 (i.e. participants being risk-neutral). To examine whether valence influenced decisions, a one-sample t-test was employed to assess whether *ImpValence* was significantly different from 0 (i.e. participants' decisions not being influenced by valence). *Second*, a regression analyses was employed to determine whether these influences are independent of one another and whether the influences of risk and valence on decision-making have different developmental patterns during adolescence. To examine whether the effect of age on valence was distinct from the effect of age on risk, a forced entry multiple regression was performed with age and $PropRisk_{all}$ (the proportion of riskier decisions collapsed across Gain and Loss trials) as predictors and *ImpValence* (the difference in the proportion of riskier decisions between Gain and Loss trials) as the dependent variable. Statistical tests were carried out in the Statistical Package for the Social Sciences (SPSS) 19.0 (Armonk, NY: IBM Corp.); reported p-values are two-tailed.

## 2.3 Results

### 2.3.1 Task performance

Participants performed the task well, with non-response rates (total 2.1% ± 2.8; Gains 1.6% ± 2.9; Losses 2.6% ± 3.2) similar to levels previously reported in adults (Wright et al., 2012), and not associated with age ($\beta$ = 0.007; $r^2 < 0.001$; $p > 0.9$).

### 2.3.2 Influence of risk and valence on decisions

The first aim of the study was to show that both risk and valence influenced decisions. Half the lotteries had an EV above the sure amount and half below (mean EV across all 56 trials was equal to the sure option with both Gains and Losses), which provided a simple metric of risk preference for each participant indexed as the proportion of riskier decisions made (*PropRisk*; risk-neutral = 0.5; risk-averse < 0.5; risk-seeking > 0.5). Risk influenced decisions, with individuals on average being significantly averse to risk ($PropRisk_{all}$ = 0.44 ± 0.10) as opposed to risk-neutral ($t(60) = -4.9$; $p < 0.001$, Figure 2.2a).

For each participant a simple metric for the impact of valence was extracted as the difference in riskier decisions between Gain and Loss trials ($ImpValence = PropRisk_{gain} - PropRisk_{loss}$). Individuals were also sensitive to valence (*ImpValence* = 0.12 ± 0.13) as opposed to valence having no impact on decisions ($t(60) = 7.3$; $p < 0.001$; Figure 2.2a). Individuals selected the riskier option more frequently in Gain trials than in Loss trials ($PropRisk_{gain}$ = 0.50 ± 0.12; $PropRisk_{loss}$ = 0.38 ± 0.12; $t(60) = 7.3$; $p < 0.001$), being risk-neutral with Gains ($PropRisk_{gain}$; $t(60) = -0.04$, $p > 0.9$) and risk-averse with Losses ($PropRisk_{loss}$; $t(60) = -8.0$; $p < 0.001$). In sum, both risk and valence influence decisions, as has previously been demonstrated with adults (Wright et al., 2012).

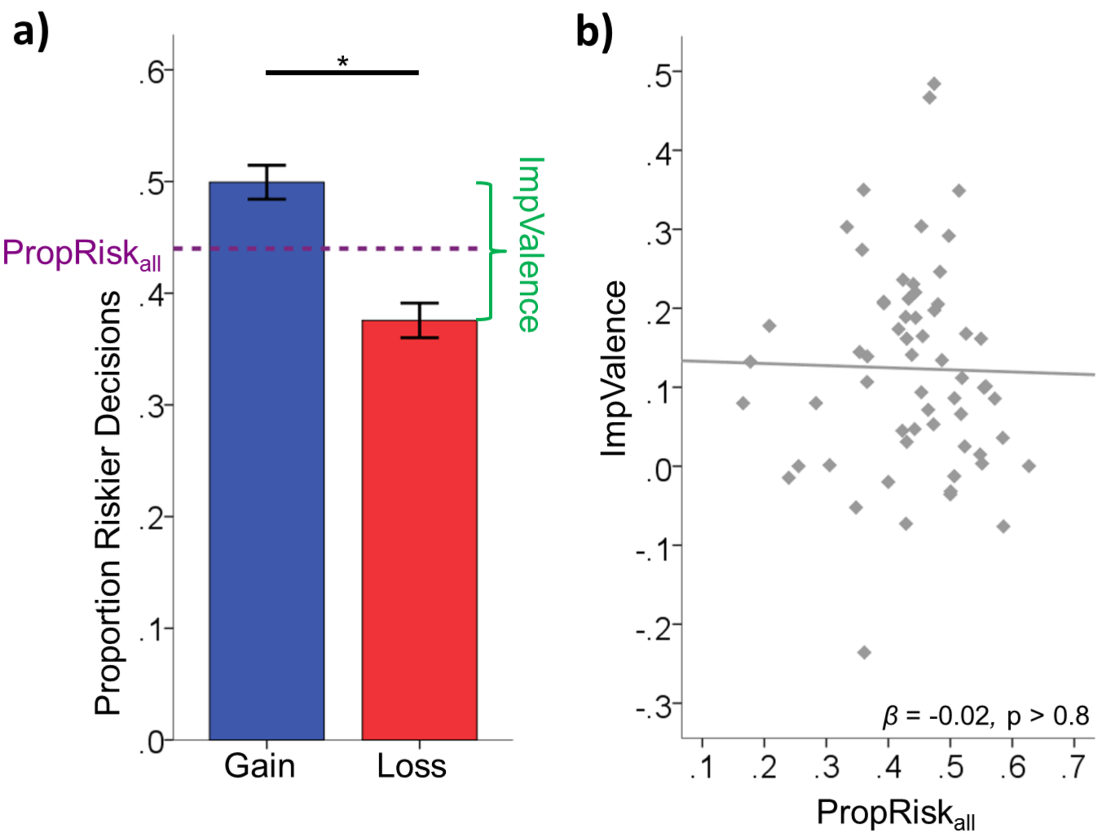


**Figure 2.2** Risk and valence both influenced decisions, and individuals' preferences for both were not associated. a) Individuals were significantly risk-averse overall (i.e. $PropRisk_{all}$ < 0.5) as opposed to risk-neutral. Valence ($ImpValence = PropRisk_{gain} - PropRisk_{loss}$) also significantly influenced decisions, with more gambling for Gains than Losses. b) Individuals' preferences related to risk ($PropRisk_{all}$) and valence (*ImpValence*) were not associated. Error bars indicate standard error. Significant differences are represented by * ($p < 0.05$).

Having shown that adolescent decision-making is influenced by both risk and valence, the study next investigated whether each of these variables had independent impacts on decisions using regression analysis. Consistent with previous adult data (Wright et al., 2012), the impacts of risk ($PropRisk_{all}$) and valence (*ImpValence*) were not associated with each other ($\beta = -0.02$; $r^2 < 0.001$; $p > 0.8$, Figure 2.2b).

### 2.3.3 Development of the influences of risk and valence on decisions

Finally, the study examined how the metrics for the impacts of risk ($PropRisk_{all}$) and valence (*ImpValence*) on decisions changed with age. The data revealed that the influences of risk and valence on decisions have different developmental patterns (Figure 2.3). The influence of risk on decisions did not change with age ($\beta$ = -0.04; $r^2$ = 0.001; p > 0.7, Figure 2.3a). In contrast, the impact of valence on decision-making decreased with age ($\beta$ = -0.30; $r^2$ = 0.09; p = 0.02, Figure 2.3b).

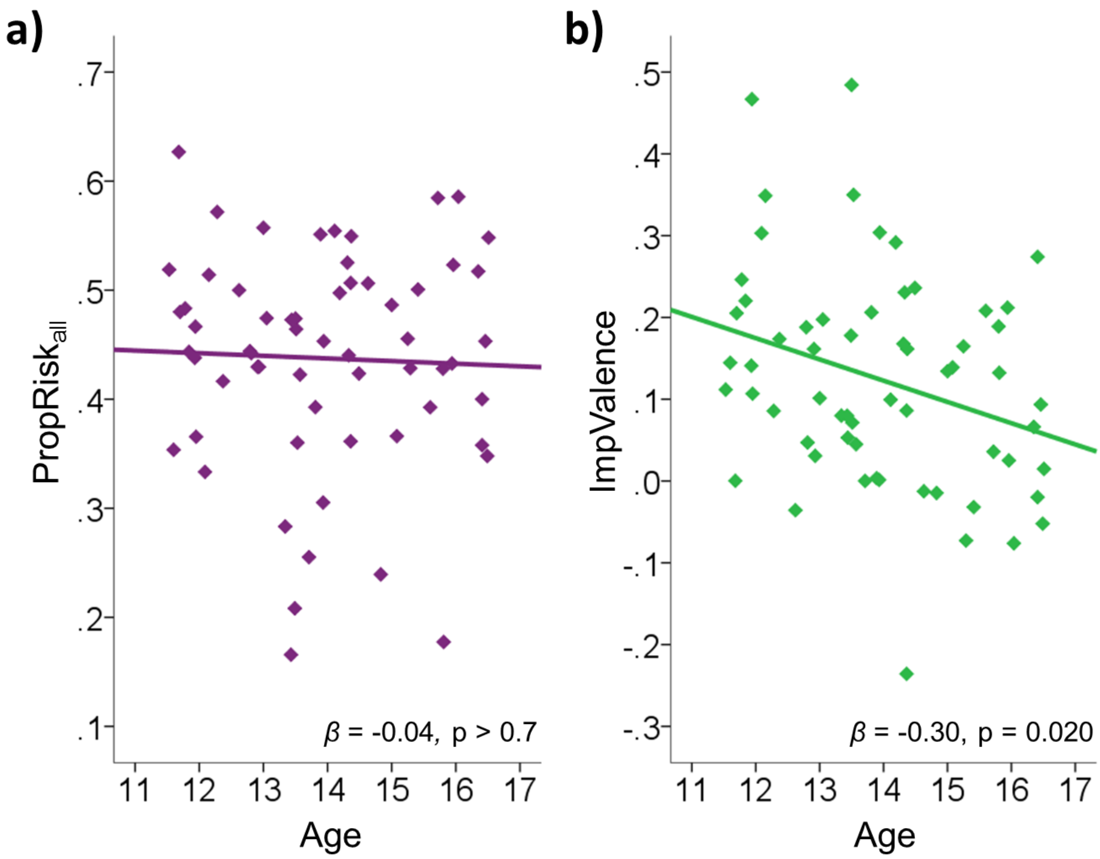


**Figure 2.3** The impacts of risk and valence have different developmental patterns. The study examined how the impacts of risk ($PropRisk_{all}$) and valence (ImpValence) on decisions changed with age. a) The influence of risk overall on decisions ($PropRisk_{all}$) did not change with age. b) In contrast, the impact of valence (ImpValence) on decisions decreased significantly with age.

To demonstrate that the effect of age on valence was distinct from the effect of age on risk, a forced entry multiple regression was performed with age and *PropRisk$_{all}$* as predictors and *ImpValence* as the dependent variable. Age, as a single independent variable, significantly predicted *ImpValence* ($\beta$ = -0.30; $r^2$ = 0.089; p = 0.020). When *PropRisk$_{all}$* was added as a second independent variable to the model, the effect of age on *ImpValence* remained significant ($\beta$ = -0.30; p = 0.02). *PropRisk$_{all}$* was not a significant predictor of *ImpValence* ($\beta$ = -0.03; $\Delta r^2$ = 0.001; p > 0.8). The change in the impact of valence during adolescence was not driven by a change in responses to either Gains or Losses alone, with neither $PropRisk_{gain}$ ($\beta$ = -0.20; $r^2$ = 0.04; p = 0.13) nor $PropRisk_{loss}$ ($\beta$ = 0.13; $r^2$ = 0.02; p > 0.3) significantly predicted by age.

## 2.4 Discussion

First, this study demonstrated that risk and valence influence decision-making in female adolescents aged 11 to 16 years. Second, the data revealed that the degree to which risk and valence impact on individuals' decisions are not related, consistent with previous data in adults (Wright et al., 2012). Third, the influences of risk and valence on decisions showed different developmental patterns across the age range studied: while the impact of risk did not change with age, there was a significant reduction with age in the degree to which valence influenced decisions.

### 2.4.1 Risk-taking in adolescence is stable in this non-affective task

Previous work has suggested that the development of risky decision-making in affective ('hot') and non-affective ('cold') tasks varies during adolescence. Several studies have reported a peak in risk-taking in mid-adolescence when employing affective tasks, for example tasks that involve emotions (Burnett et al., 2010; Cauffman et al., 2010; Figner et al., 2009a, 2009b), whereas non-affective tasks demonstrate either no change or a decrease in risk-taking with age (Crone et al., 2008; Figner et al., 2009a, 2009b; Paulsen et al., 2011; Rakow & Rahim, 2010). The current study adapted a non-affective task used by Wright et al. (2012) to dissociate the influences of risk and valence on decision-making in adults. Adolescents were risk-averse in this gambling task, meaning that overall they made fewer riskier than safe decisions. The present study also demonstrated distinct development patterns in the impacts of risk and valence during young to mid-adolescence.

Developmental stability in risk-taking during adolescence has been reported in previous studies examining risky decision-making in a non-affective task (Figner et al., 2009a). In contrast, tasks employing an affective context often find evidence for a peak in risk-taking around mid-adolescence (Burnett et al., 2010; Figner et al., 2009a, 2009b). The results of the current study support those of previous studies (Figner et al., 2009a), suggesting that, in the absence of affective task components, the propensity to take risks does not change during adolescence.

### 2.4.2 The impact of valence declines across young to mid-adolescence

Adolescent decisions were influenced by valence, such that fewer riskier decisions were made for losses than for gains. The effect of valence on risky decision-making decreased across adolescence: compared with mid-adolescents, younger adolescents were more biased away from the riskier option by losses relative to gains. This effect was not driven by a change in responses to gains or losses alone; thus, the decrease in the effect of valence could be explained by a symmetrical reduction of the difference between risky decisions in the gain and loss domains. This would suggest that the effect does not derive from younger adolescents more frequently choosing the computationally simpler option in each trial, as does the consistent risk-aversion seen here across development.

In a previous study that used a gambling paradigm requiring adolescents to learn to play from advantageous decks of cards and to avoid playing from disadvantageous decks, there was an age-dependent increase in the propensity to avoid the disadvantageous decks over the course of the experiment (Cauffman et al., 2010). In other words, older participants learned more quickly to avoid playing the disadvantageous decks; this was interpreted as an increase in loss-aversion during adolescence. In contrast, the reduction in the impact of valence during adolescence seen here is consistent with a recent study examining changes during adolescence in the effect of valence during a probabilistic reversal learning decision task (van der Schaaf et al., 2011). In that study there was a reduction in the effect of valence on decisions with increasing age (from 10 to 17 years), such that younger adolescents displayed a greater sensitivity to unexpected financial losses compared to unexpected gains than did older adolescents. Thus, the developmental change in the effect of valence seen in the gambling task here might reflect more general developmental changes in the influence of such approach-avoidance processes on decisions (van der Schaaf et al., 2011).

Since the conception of this study, two studies investigating the development of loss aversion and its neural correlates between adolescence and adulthood have been published (for details see 1.3.3). In a study employing a mixed gamble with monetary gains and losses, both adolescents (aged 13 - 17 years) and adults demonstrated a similar degree of loss aversion in their choice behaviour, however activation when rejecting a mixed gamble (compared to a baseline) in the left caudate and bilateral frontal pole was greater in adolescents relative to adults (Barkley-Levenson et al., 2013). In another study investigating neural correlates to primary reinforcers (squirts of sugar water and squirts of salt water), adolescent pleasantness ratings were more affected by valence than were adult ratings and striatal activation during the delivery of appetitive stimuli (bilateral VS) and the delivery of aversive stimuli (left caudate) relative to water were increased in adolescents relative to adults (Galván & McGlennen, 2013). In the current study, adolescents demonstrated a similar impact of valence on risky decisions, i.e. fewer riskier decisions for losses than for gains, as adult participants in a previous study (although a comparison of the magnitude of this effect is not possible, Wright et al., 2012). Consequently, while the developmental pattern of behavioural loss aversion between adolescence and adulthood is currently not clear, fMRI findings indicate that the neural substrates processing punishment (in the form of monetary loss or aversive liquids) change between adolescence and adulthood.

### 2.4.3 Distinct developmental patterns of the impacts of risk and valence

The finding that the impacts of risk and valence on decisions have different developmental patterns provides a new source of evidence in a debate between models of risky economic decision-making. The prevailing view in psychology and economics is that risk and valence are related to each other in a specific fashion (risk-aversion for gains and risk-seeking for losses for the probabilities used in the current task), and that these preferences arise as the product of a utility function that is concave for gains and convex for losses (Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). An alternative neurobiology-based hypothesis is that valence and risk exert independent influences on decisions (Wright et al., 2012). This hypothesis has been supported in adults by behavioural evidence for a dissociation between the influences of risk and valence on decisions, and also by neural evidence for dissociable neural substrates related to the manipulations of valence and risk, in orbitofrontal and parietal cortices respectively (Wright et al., 2012). The finding in the current study that the effects of risk and valence on decisions show different developmental patterns during adolescence is readily accommodated by such neurobiological models where multiple interacting neural decision-systems contribute to decisions (Dayan, 2008). For example, decision-systems themselves (or those regulating the balance between them) might develop differently across adolescence.

The current study found that adolescent participants were more risk-averse in the loss domain than in the gain domain, which parallels the findings by Wright et al. (2012). This contrasts with other studies, which often report that participants are risk-seeking in the loss domain and risk-averse in the gain domain, for the probabilities used in this study (Kahneman & Tversky, 1979). This difference could be due to the different format of the tasks employed. Here, on each trial, participants considered whether to accept a lottery or reject it in favour of a sure option; when the lottery contained losses this may induce participants to avoid it. When instead individuals were asked to evaluate two options and select between them, they could not express avoidance by withdrawal but could potentially avoid losses by selecting the riskier option. Such a variant of the task used in adults showed precisely this reversal in the direction of the valence effect (i.e. more gambling for gains than for losses) (Wright et al., 2012). With respect to the Prospect Theory (Kahneman & Tversky, 1979), while the data in the current study do not support the ‘reflection effect’ (i.e. risk-seeking with losses and risk-aversion with gains), an approach-avoidance account is consistent with ‘loss aversion’ where losses have greater weight (‘loom larger’) than gains.

### 2.4.4 Limitations and implications

As noted earlier, changes to the task format can change the direction of the effect of valence. Future developmental studies could examine the effects of valence and risk on decisions in other paradigms and other domains of risky decision-making, for example, in mixed gain-loss gambles. This study intentionally avoided including an affective component in the task, in order to study the effects of risk and valence on decisions without the influence of emotion. Future studies could examine how such a manipulation of affective context (for example, the presence of peers) might interact with the influence of risk and valence on decisions. Despite the developmental change in the influence of valence on decisions during adolescence, collapsing across age, adolescents showed similar impacts of risk and valence on decisions as found in adults (Wright et al., 2012). Therefore, adolescents and adults might generally use similar strategies when making risky decisions in a non-affective context. This study tested female adolescents only. While this maximised the homogeneity of the sample, it limits the generalizability of the data (see 7.2.1 for a general discussion). The developmental stability of risk-taking in a non-affective task has been previously demonstrated in a study including both males and females (Figner et al., 2009a), thus suggesting that this effect is not limited to females. However, on the basis of the current study, it is not clear whether adolescents in general show a reduction in the impact of valence on risky choices with age or whether this effect is restricted to females. Consequently, future studies should assess whether the developmental effects can be replicated in males, or whether the effects differ between female and male adolescents.

In sum, the current study showed that the influences of risk and valence on decision-making in a non-affective context followed different developmental patterns: while the influence of risk did not change with age, the impact of valence decreased across the period of adolescence. Speculatively, the results may have wider implications for public health policy. Types of public health information provided, and the way they are presented, should be tailored to specific age groups to maximise their impact. Parsing the influences on risky decisions, and understanding how they develop will help determine which to stress for a given age group. Framing something as a loss, for example, may be more effective with younger than older adolescents.

While this study investigated the developmental trajectory of risk-taking in a non-affective task, the next chapter investigates another aspect of the development of risky and reward-related decision-making. **Chapter 3** examines developmental changes in the effect of social influence on the valuation of an object and the modulation of value-related signals by social influence in adolescence and adulthood.

# CHAPTER 3: DEVELOPMENT OF THE MODULATION OF THE REWARD VALUE SIGNAL BY SOCIAL INFLUENCE

*Recently, fMRI studies have attempted to elucidate the neural basis of social influence in adults. Agreeing with others has been found to activate reward-related regions, such as the VS and social influence has been shown to modulate value-related signals in the VS. Developmental studies have suggested that reward sensitivity during adolescence is elevated and this might rely on the social context - such as the presence of peers. This chapter examines the modulation of the reward value signal by social influence in 19 female adolescents (14 - 16 years) and 16 female adults (23 - 28 years). This was investigated in a music choice task, for which participants provided a list of songs they like prior to scanning. In the scanner, participants were asked to select their preferred song out of two songs; they then learned about the preferences of three music experts (Review outcome) and finally they received a token for their preferred or the alternative song (Object outcome). Adolescents and adults activated the VS both when receiving a token for the preferred song relative to the alternative (bilateral VS, non-social reward contrast) and when agreeing with music experts relative to disagreeing (right VS, social reward contrast). Agreeing versus disagreeing with the music experts also activated social brain regions (bilateral ATC, extended right STS activation into the pSTS). Activation in the pSTS during music expert feedback correlated with the behavioural sensitivity to social influence. These main effects were not further modulated by Age group. There was a four-way interaction between Object outcome, Review outcome, Age group and the behavioural sensitivity to social influence.*

## 3.1 Introduction

The powerful influence of others' attitudes and opinions on individual preferences and choices has been demonstrated in a large body of research on social influence in adults (Asch, 1956; R. Bond & Smith, 1996; Cialdini & Goldstein, 2004). For example, Asch's pioneering line judgement paradigm found that participants conformed to a wrong majority opinion of a group of confederates: despite almost perfect performance when no social influence was exerted (> 99% accuracy), participants made on average 37% erroneous responses when faced with the wrong opinion of a group (Asch, 1956). With regard to the motivations underlying conforming behaviour, researchers have contrasted normative to informational influence (Cialdini & Goldstein, 2004; Deutsch & Gerard, 1955). The first theory proposes that individuals conform to gain social approval and/or avoid social rejection by others (*normative influence*). The second theory proposes that conforming behaviour is driven by the aim to be accurate, when others' opinions and behaviours are used as source of information (*informational influence*).

In recent years, fMRI studies in adults (see 1.7.4) have provided insight into the neural mechanisms of conformity. Matching preferences with others - although only when agreeing with a liked group - activates typical reward-related regions (VS/NAcc and OFC), which are also associated with the processing of non-social rewards (Campbell-Meiklejohn et al., 2010; Izuma & Adolphs, 2013; Klucharev et al., 2009). In contrast, disagreeing with others' opinions was found to activate the right TPJ – which is part of the social brain network - as well as the dACC and the anterior insula (Campbell-Meiklejohn et al., 2010). Finally, social influence was found to modulate the neural value signal in the VS and OFC (Campbell-Meiklejohn et al., 2010; Zaki et al., 2011). For example, activation in the VS when receiving a token for a valued music song was modulated by the opinion of music experts and was associated with individuals' tendencies to adjust their preferences in line with the music experts' opinions (Campbell-Meiklejohn et al., 2010).

Adolescence is characterised as a period of life during which the attitudes and opinions of peers are particularly important, and adolescents' attitudes and behaviours are strongly influenced by their peers (Brechwald & Prinstein, 2011; Brown, 2004). While there are some behavioural and questionnaire-based studies investigating the development of conformity during adolescence, developmental imaging studies on the neural correlates of conformity are scarce. With regard to behavioural studies on conformity in adolescence, experimental studies (see 1.7.2) showed that adolescents do not only publicly comply to their peers' norms, but also privately accept these norms (G. L. Cohen & Prinstein, 2006; Teunissen et al., 2012). Developmental trajectories of conformity during adolescence have been examined in studies employing Asch's line paradigm and in questionnaire-based approaches with some findings supporting an inverted U-shape during adolescence (Berndt, 1979; Costanzo & Shaw, 1966; Steinberg & Silverberg, 1986) and some describing a linear decrease of conformity during adolescence (Steinberg & Monahan, 2007; M. B. Walker & Andrade, 1996).

Research on social influence in adolescence has mostly focused on the influence of peers on behaviours with potential negative outcomes, such as smoking, alcohol and drug abuse, risky driving or engagement in criminal or anti-social acts (Brown, 2004; Dishion & Tipsord, 2011). In experimental settings, risk-taking in a car-driving simulation was elevated in adolescents when they were with two peers relative to when alone, while adult risk-taking was not influenced by peers (Gardner & Steinberg, 2005). This increase in risk-taking in the presence of peers has been linked to a modulation of reward sensitivity by peers (L. O'Brien et al., 2011; A. R. Smith, Chein, et al., 2014; Weigard et al., 2014). In line with this, the presence of peers was found to affect the activation in reward-related regions, such as the VS, in adolescence (Chein et al., 2011; A. R. Smith, Steinberg, et al., 2014). More generally (Blakemore & Robbins, 2012), evidence from several studies has suggested that reward-related activation in the VS during adolescence relative to adulthood is heightened (although see 1.3.2 for studies showing the opposite pattern or no developmental change) (Ernst et al., 2005; Galván et al., 2006; Geier et al., 2010; Padmanabhan et al., 2011; Van Leijenhorst, Moor, et al., 2010; Van Leijenhorst, Zanolie, et al., 2010).

In light of findings from adult social influence studies, heightened reward sensitivity might be linked to developmental differences in the sensitivity to social influence. Studies investigating the development of the neural correlates of conformity are very limited. One study examined the neural correlates of the influence of online popularity ratings (from 'Myspace') on music preferences in adolescents aged 12 - 17 years (Berns et al., 2010). Similar to the activation pattern found in disagreement contrasts in adults (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009), when adolescents had viewed popularity ratings between the first and second time rating a song, activation in the dACC and anterior insula at the second time of listening to the song correlated positively with individual sensitivity to social influence. Previous studies have, however, not investigated the development of the neural correlates of social influence between adolescence and adulthood. Consequently, this study aimed to examine developmental differences in a social influence task that independently manipulated whether participants received a token for a song (non-social reward) and whether an alleged group of three music experts agreed (or disagreed) with the participant regarding the value of the song (social reward) (Campbell-Meiklejohn et al., 2010) in a group of female adolescents (aged 14 - 16 years) and adults (aged 23 - 28 years). In the task, participants first chose between two songs, then viewed feedback informing them whether the music experts agreed or disagreed with their song choice and finally received a token for one of the two songs. This paradigm enabled the investigation of developmental differences in the neural correlates of agreeing with others and disagreeing with others, as well as in the modulation of value-related activation by social influence.

In terms of **behaviour**, on the basis of a large literature of social influence studies, it was predicted that participants would adjust their subjective song value in line with the music experts' opinions. With developmental studies suggesting that adolescents are particularly sensitive to social influence, adolescents might also be more influenced than adults by the music experts' opinions. In terms of **neuroimaging results**, collapsing across age groups, it was predicted that receiving a token for the preferred song relative to the alternative (object reward), as well as agreeing with the music experts relative to disagreeing (social reward), would activate the VS. Based on previous developmental studies demonstrating heightened reward sensitivity during adolescence, adolescents might show elevated VS activation relative to adults when receiving a valued object as well as when matching opinions with others. Receiving reviewer feedback might activate social brain regions (mPFC, TPJ, pSTS and ATC) and there might be developmental differences in the activation of these regions. Finally, it was predicted that the object value signal in the VS would be modulated by the opinion of the music experts in dependence on individual tendencies to adjust their preferences in line with the music experts and, further, that this modulation might be greater in adolescents than in adults.

## 3.2 Methods

### 3.2.1 Participants

Twenty-three female mid-adolescents and 18 female adults participated in the study. Data from 19 mid-adolescents (aged 14.2 - 16.7 years, mean ± SD = 15.2 ± 0.9) and 16 adults (aged 23.1 - 28.8 years, 24.7 ± 1.3) were included in the final analysis. Three participants were excluded since they doubted that the music experts were real (see 3.2.5), one participant was excluded due to excessive head movement in two scanning sessions (see 3.2.4.2) and two participants were excluded on the basis of their performance (see 3.2.4.1 and 3.2.4.2*).* Adolescent participants were mostly recruited from selective schools in the Greater London area. Adult participants were students or graduates, recruited via advertisement at university. In order to maximise susceptibility to the social influence manipulation and to match adolescent and adult participants, adults were not invited to participate if they had taken part in five or more psychology or neuroscience experiments, or if they were students or graduates of Psychology, Neuroscience or related subjects. The local Research Ethics Committee approved study procedures. Legal guardians and adult participants gave their informed consent for the study. Participants were reimbursed £10 per hour for their participation and received 10 music songs.

Verbal IQ of participants was assessed with the vocabulary subtest of the Wechsler Abbreviated Scale of Intelligence (WASI, Wechsler, 1999), to check age groups were matched in terms of cognitive ability. Adolescent (119.2 ± 8.2) and adult (120.3 ± 6.4) participants did not significantly differ in verbal IQ ($p > 0.65$).

### 3.2.2 Experimental design

This study followed an event-related design with two within-subjects factors: Review outcome (Agree; Disagree) and Object outcome (Preferred; Alternative) and one between-subjects factor: Age group (adolescent; adult).

The study employed an adapted version of a social influence task previously used in adult participants by Campbell-Meiklejohn et al. (2010). In the week prior to scanning, participants were asked to submit a list of 20 songs they liked but did not own (participant-submitted songs), along with a rating of each song on a scale of 1 - 10, (1: 'I do not want this song' to 10: 'I really want this song'). Participants were told that they would receive tokens in the study for their 20 songs and 20 alternative songs, which were provided by the lab. In order to match familiarity of the alternative songs between participants, the songs were real but selected so that they would be unknown to the participants. Unfamiliarity of the alternative songs was tested prior to scanning. Out of these 40 songs (the participants' songs plus the 20 alternatives), the 10 songs that received the most tokens during the experiment were sent to them on a CD after the study. Participants were informed that these 40 songs would be sent to a group of three music experts, who would listen to the songs and submit their opinion about them.

In reality, there were no music experts, but instead their alleged music preferences were experimentally manipulated (Campbell-Meiklejohn et al., 2010). Prior to scanning, participants read a description of the alleged music experts (see Appendix 3.1), which was designed to convey a degree of music expertise across a broad range of music tastes. Photos and descriptions of the experts did not include ages, but they were selected to appear to be in their late teens to mid-twenties, to allow both adolescent and adult participants to view them as similar-aged. Participants rated on a scale of 1 (not at all) to 7 (very much) how much the music experts could be trusted to pick music the participant would like (this will from now on be referred to as 'trust ratings') prior to and after the experiment (Pre-scan; Post-scan). Participants were instructed on the task by the experimenter and carried out a practice session to familiarise themselves with the task. The practice session included five books the participant liked and five 'classics', which were provided by the lab.

### *3.2.2.1 Decision period*

In each trial (see Figure 3.1 for timings), participants were presented with a choice between one of the participant-submitted songs and one of the alternative songs, presented on the upper left and upper right of the task screen (positions counterbalanced across trials). A picture of the three music experts was displayed below the songs and a symbol for the participant (a square with the word 'ME') was shown at the bottom of the screen, both centred to the middle of the screen. Participants were asked to move their symbol underneath the song they preferred, using the index finger of their right hand to move it left and the middle finger of their right hand to move it right. The words 'I prefer' appeared under the participant's symbol and a scrambled version of their symbol was placed under the song they did not choose. If participants failed to make a choice in time, a large cross was shown on the screen for the remainder of the trial. Only trials in which participants chose the participant-submitted song were included as regressors of interest in the fMRI analysis. Trials in which participants chose the alternative song were modelled in a regressor of no-interest (see 3.2.4).

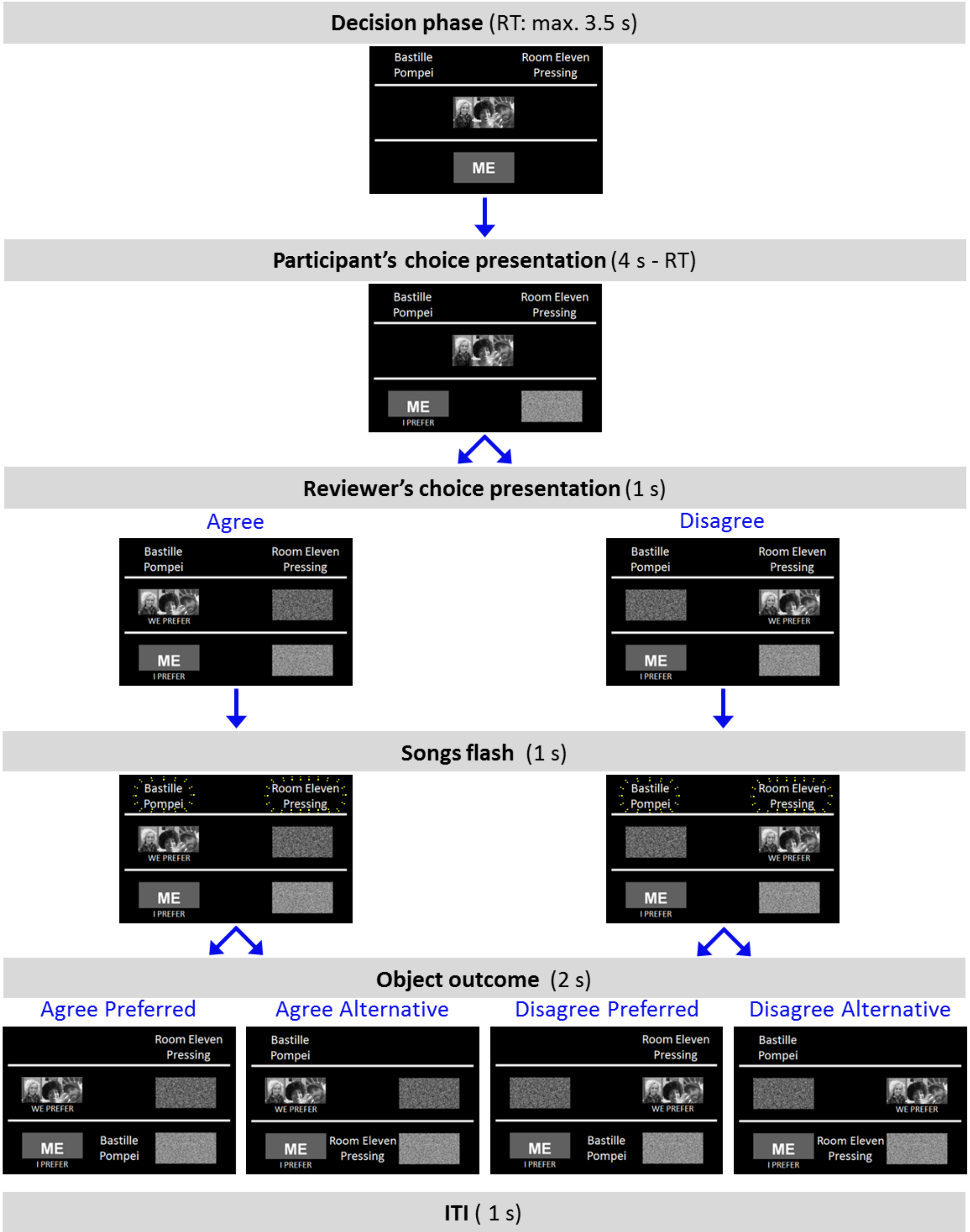


**Figure 3.1**: Social influence task. The task followed a 2 (Review outcome: Agree; Disagree) x 2 (Object outcome: Preferred; Alternative) factorial design. In the week prior to the experiment, participants submitted a list of 20 songs (participant-submitted songs) they liked but did not own. At the beginning of each trial, participants were asked to make a choice between one of their (participant-submitted) songs and an unfamiliar, alternative song (max. 3.5 s compared to 2 s in Campbell-Meiklejohn et al., 2010) by moving their symbol ('ME') underneath the song they preferred. The participant's choice was then displayed for 4 s minus the response time (RT). Next, participants learned whether the music experts preferred the same song ('**Agree**') or the other song ('**Disagree**'; Review outcome was displayed for 1 s) as the participant, when the reviewers' picture moved underneath the song they preferred. The songs then flashed in grey and white for 1 s and participants were told that the computer chose

a song. Finally, participants received a token for either the participant-submitted song ('**Preferred**') or the alternative song ('**Alternative**'; Object outcome was displayed for 2 s). A fixation cross was displayed for 1 s in the inter-trial interval (ITI).

### *3.2.2.2 Review outcome*

In the next trial phase - the '*Review outcome*' - participants learned about the experts' opinion. The photo of the music experts was moved underneath the song they allegedly preferred along with the words 'we prefer', while a scrambled picture of them was shown under the song they did not choose. In 50% of the trials, the music experts preferred the same song as the participant (Agree) and in 50% they preferred the other song (Disagree). Each participant-submitted song was paired with six alternative songs, and for each pair the music experts could either pick the participant-submitted song (agreeing with the participant) or pick the alternative song (disagreeing with the participant). In total, the music experts could agree with the participant between 1 and 5 times for each of the participant-submitted song. This resulted in five levels of net music expert opinion (number of 'Agrees' – number of 'Disagrees': -4, -2, 0, 2, 4). The 20 participant-submitted songs were equally distributed across the five levels of net music expert opinion.

### *3.2.2.3 Object outcome*

In the next phase, the songs flashed in grey and white (alternating every 100 ms). Participants were told that the computer would then select one of the two songs, while the songs were flashing. In order to motivate participants to choose their actual preference, they were informed that the song they chose had a 55% chance of being selected for the token (although both songs were actually equally likely to be chosen). In the final phase – the so called '*Object outcome*', the participant won a token for one of the two songs, which appeared at the bottom of the screen, next to the participant's symbol. In 50% of trials participants won a token for the participant-submitted song ('Preferred') and in the other 50% a token for the alternative song

(‘Alternative’). Participants were told that the ten songs with the most tokens at the end of study would be purchased and given to them.

### 3.2.3 Data acquisition

Brain imaging data were acquired on a Siemens Avanto 1.5 Tesla MRI scanner (Erlangen, Germany). Structural data were acquired with a T1-weighted fast-field echo structural image sequence lasting 5 min 30 s. Functional data were acquired in three sessions each lasting 6 min 15 s with a multi-slice T2*-weighted echo-planar sequence with blood-oxygen level dependent (BOLD) contrast (repetition time (TR) = 2.975 s, echo time (TE) = 0.05 s). In each session, 126 volumes were sampled and each volume comprised 35 axial slices (in-plane resolution: 3 x 3 x 3 mm) covering most of the cerebrum. Participants also performed another independent task in the scanner with two runs (see **Chapter 6**), each of which lasted 8 min 6 s (prior to the collection of the structural data and the functional data for this task).

Each of the three sessions contained 40 trials each lasting 9 s. For each session, ten trials of each condition (Agree Preferred, Agree Alternative, Disagree Preferred, and Disagree Alternative) were randomly selected from a total set of 120 trials (4 x 30 trials). Order of trials within a session was pseudo-randomized, so that each condition did not appear more than twice in a row.

The task was presented and responses were acquired with Cogent 2000 (www.vislab.ucl.ac.uk/Cogent/index.html) using Matlab R2010b (Mathwork Inc. Sherborn, MA). Stimuli were front-projected onto a screen, which participants viewed via a mirror mounted on their head coil.

### 3.2.4 Data analysis

#### *3.2.4.1 Behavioural data analysis*

Behavioural data were analysed with SPSS 21 (Armonk, NY: IBM Corp.). The difference between pre-scan and post-scan ratings of song desirability was used a measure of change in song value. One participant was an extreme outlier with regard to the difference in song desirability rating (i.e. lower than three interquartile ranges from the lower quartile) and therefore her data were excluded from the analysis (her song ratings decreased on average by 4.5 points, while the mean difference of included participants was $-0.01 \pm 0.45$). For each participant, the metric $B_{inf}$ was determined, which indicated the degree to which participants' song values changed in relation to the music experts' opinion. $B_{inf}$ was calculated as the standardised beta coefficient obtained when running a linear regression with the net music expert opinion (number of times they preferred the participant-submitted song – number of times they preferred the alternative song; range: -4, -2, 0, 2, 4) as a predictor of the change in song value (reported by the participants). In order to assess whether participants changed their song value in line with the music experts' opinion, a one-sample t-test was performed to assess whether $B_{inf}$ was significantly different than 0. Developmental differences between adolescents and adults in $B_{inf}$ were assessed using a two-sample t-test. A 2 (Time: Pre-scan; Post-scan) x 2 (Age group: adolescents; adults) mixed-design analysis of variance (ANOVA) was employed to investigate changes in trust ratings during the experiment and between Age groups. Additionally, a correlation analysis was performed to investigate whether $B_{inf}$ was related to pre-scan trust ratings or the difference between pre-scan and post-scan trust ratings. Marginally significant results ($p < 0.1$) are reported in the results, but only significant results ($p < 0.05$) are discussed further. Reported p-values are two-tailed.

### *3.2.4.2 fMRI data analysis*

Functional imaging data were preprocessed and analysed using SPM8 (Statistical Parametric Mapping, Wellcome Trust Centre for Neuroimaging, http://www.fil.ion.ucl.ac.uk/spm/). To allow for T1 equilibration effects, the first four volumes of each session were discarded. Images were realigned to the first analysed volume with a second-degree B-spline interpolation to correct for movement during the session. The bias-field corrected structural image was coregistered to the mean realigned functional image and segmented on the basis of Montreal Neurological Institute (MNI)-registered International Consortium for Brain Mapping (ICBM)-tissue probability maps. Resulting spatial normalisation parameters were applied to the realigned images to obtain normalised functional images with a voxel size of 3 x 3 x 3 mm, which were smoothed with an 8 mm full width at half maximum (FWHM) Gaussian kernel.

Realignment estimates were used to calculated framewise displacement (FD) for each volume, which is a composite, scalar measure of head motion across the six realignment estimates (Siegel et al., 2014). Volumes with an FD $> 0.9$ mm were censored and excluded from general linear model (GLM) estimation by including regressors of no interest for each censored volume. Scanning sessions with more than 10% of volumes censored (one session in one participant) or a root mean square (RMS) movement greater than 1.5 mm (a different session in the same participant, thus this participant was excluded from the analysis) were excluded from the analysis. Adolescent and adult participants did not significantly differ in the number of censored volumes (adolescents = $1.74 \pm 3.23$, adults = $0.50 \pm 1.21$; $p > 0.15$), mean RMS movement (adolescents = 0.20 mm $\pm$ 0.06, adults = 0.20 mm $\pm$ 0.08; $p > 0.9$) or mean FD (adolescents = 0.11 mm $\pm$ 0.04, adults = 0.10 mm $\pm$ 0.03; $p > 0.4$).

Only trials in which participants chose the song they had originally submitted were included in the fMRI analysis as regressors of interest (mean: 96.7%). One participant, who chose her submitted songs in only 36.7% of trials, was excluded from the analysis, since there were not enough trials per condition to perform the 1st level analysis.

Scanning sessions were treated as separate time series and each series was modelled by a set of regressors in the GLM. Censored volumes (FD > 0.9) were modelled as separate regressors of no interest in the GLMs. To investigate the main effect of Review outcome ('Review outcome analysis'), onsets were modelled in the middle of the Review outcome period. The GLM included two event-related regressors of interest (two Review outcome conditions: Agree; Disagree) and one regressor of no-interest (alternative song chosen), which were convolved with the haemodynamic response function.

To investigate the main effect of Object outcome and a modulation of Object outcome by Review outcome ('Object outcome analysis'), onsets were modelled in the middle of the Object outcome period (Campbell-Meiklejohn et al., 2010). The GLM included four event-related regressors of interest (four task conditions: Agree Preferred; Agree Alternative; Disagree Preferred; Disagree Alternative) and one regressor of no-interest (alternative song chosen), which were convolved with the haemodynamic response function.

Data were high-pass filtered (128 s). First-level single-subject contrasts were entered into random-effects analyses. Subject x Age group x Condition flexible factorial designs were employed. For the Review outcome analysis, Condition included two levels corresponding to the Review outcome (Agree; Disagree). For the Object outcome analysis, Condition included four levels corresponding to the two possible Review outcomes and two possible Object outcomes. Condition, Age group and Subject were modelled as main effects (the Subject factor was included to account for the repeated-measure nature of the data), and the model also included the interaction between Age group and Condition. In addition, to investigate whether individual differences in activation in the Review outcome contrast were associated with the behavioural sensitivity to social influence ($B_{inf}$), this contrast was entered in a two-sample t-test modelling Age group as a between-subject factor and $B_{inf}$ as a covariate of interest. A similar two-sample t-test was performed to investigate whether individual differences in activation in the Review outcome x Object outcome interaction contrast were associated with $B_{inf}$.

The results are reported whole-brain if significant at voxel-level $p < 0.001$ uncorrected and at cluster-level corrected $p_{FWE} < 0.05$ or if significant at voxel-level $p_{FWE} < 0.05$. Anatomical labelling of activity clusters was performed using Automated Anatomical Labeling (AAL) (Tzourio-Mazoyer et al., 2002). Coordinates are listed in MNI space. In addition, given the a priori hypotheses and previous findings with this task in adult participants in the VS, a small volume correction (SVC) within the striatum using a cluster-level correction of $p_{FWE} < 0.05$ was performed to adjust the results for false-positive findings. An anatomical bilateral striatal mask was generated using the NAcc from FMRIB Software Library (FSL) and Caudate as well as Putamen from the Wake Forest University (WFU) PickAtlas toolbox for SPM (Maldjian, Laurienti, Kraft, & Burdette, 2003). Significant interactions were followed up by extracting the mean signal across all voxels of significant clusters with Marseille Boîte À Région d'Intérêt (MarsBaR; Brett, Anton, Valabregue, & Poline, 2002).

### 3.2.5 Debriefing

After the study, participants were called on the phone and asked what they thought about the music experts. Participants were then informed that, in fact, the music experts were not real and that their choices had been generated by a computer. Participants who reported that they doubted during the experiment that the music experts and their choices were real were not included in the analysis (included participants: n = 21/23 adolescents, n = 17/18 adults).

## 3.3 Results

### 3.3.1 Behavioural results

Collapsing across both Age groups, participants' $B_{inf}$ was significantly greater than 0 ($0.09 \pm 0.21$; $t(34) = 2.43$; $p = 0.021$, see Figure 3.2). In other words, on average participants adjusted their subjective song value between the pre-scan and post-scan rating in line with the net music expert opinion of a song. Thus, participants tended to increase their song value when the net music expert opinion was positive and decrease their song value when the net music expert opinion was negative. Participants with high initial pre-scan ratings might have had a limited range of scores to increase their song desirability rating in line with the music experts' opinion. To address the question whether participants with higher initial pre-scan ratings might have lower $B_{inf}$ scores, a correlation analysis between $B_{inf}$ and pre-scan ratings was performed. This analysis demonstrated that the two variables were not correlated ($p > 0.9$), suggesting that there was no systematic bias of lower $B_{inf}$ scores in participants with high initial pre-scan ratings due to a limited range of higher song desirability scores. Adolescents ($0.10 \pm 0.18$) and adults ($0.07 \pm 0.25$) did not significantly differ in $B_{inf}$ ($p > 0.6$, see Figure 3.2).

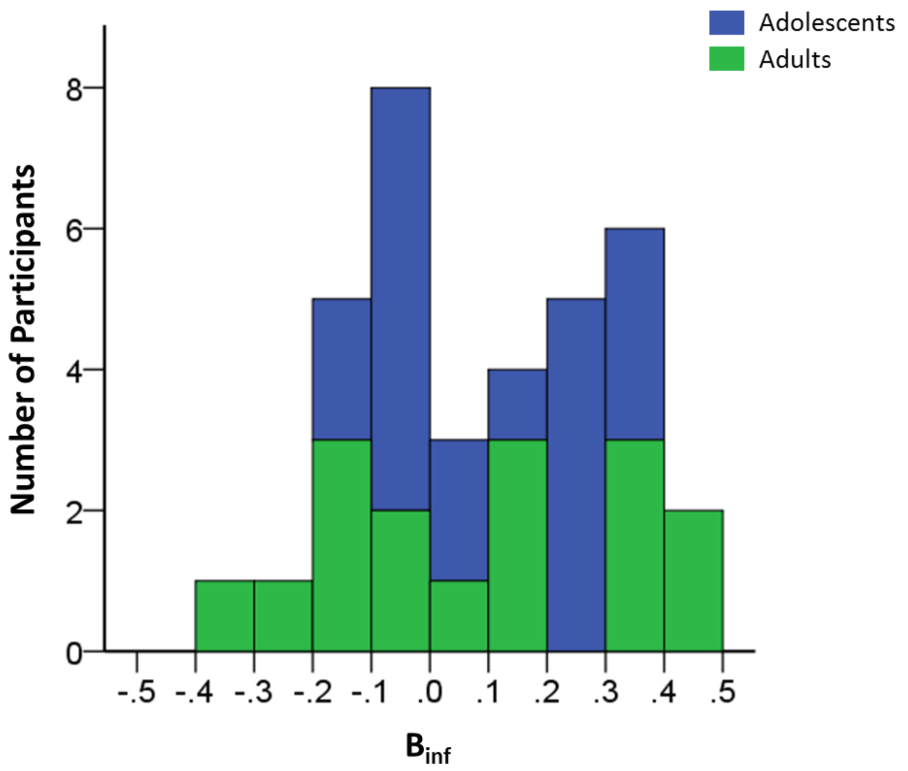


**Figure 3.2**: Frequency histogram of $B_{inf}$ for adolescent and adult participants: $B_{inf}$ indicates participants' sensitivities to change their song ratings in line with the music experts' opinion. $B_{inf}$ is the standardized beta coefficient of the linear regression testing whether the change in song value (post-scan rating – pre-scan rating) is predicted by the music experts' opinion, for each participant. Collapsing across age groups (0.09 ± 0.21), $B_{inf}$ was significantly greater than 0. Adolescents (0.10 ± 0.18) and adults (0.07 ± 0.25) did not significantly differ in $B_{inf}$.

Mean trust ratings, collapsing across Age group and Time, were high (4.89 ± 0.92; with 1 (not at all) to 7 (very much) being the range of possible trust ratings), indicating that participants generally trusted that the music experts would choose music the participant liked. Analysis of trust ratings showed no main effect of Age group or Time ($ps > 0.4$). There was a marginally significant interaction between Age group and Time ($F(1,33) = 3.56$; $p = 0.068$). Neither pre-scan trust ratings ($p > 0.1$) nor the difference between pre- and post-scan trust ratings ($p > 0.8$) correlated with $B_{inf}$ within Age groups.

### 3.3.2 fMRI results

#### *3.3.2.1 Agreement and disagreement with music experts*

Analysis of the main effect of Review outcome was performed during the Review outcome period (see methods 3.2.4.2). There was a main effect of Review outcome (Agree>Disagree) across Age groups: the condition in which the music experts selected participants' preferred song relative to selecting the other song was associated with activations in the temporal cortex bilaterally, predominantly in the ATC in the left hemisphere, extending along the STS into the posterior temporal cortex and occipital cortex in the right hemisphere, as well as in the precuneus, extending into the calcarine sulcus and PCC (Table 3.1, Figure 3.3a). Within the striatum agreeing relative to disagreeing with the music experts also activated the right VS (Figure 3.4a; $k = 21$, $Z = 3.57$). The reverse contrast revealed no significant clusters. There were no regions showing an Age group x Review outcome interaction.

To test whether individuals' activations in the main effect of Review outcome were associated with the behavioural sensitivity to social influence, $B_{inf}$ was included as a covariate of interest in the GLM. This analysis revealed that the activation in the right pSTS in the Agree>Disagree contrast was further modulated by $B_{inf}$ : there was a negative correlation between $B_{inf}$ and activation in the Agree>Disagree contrast (see Table 3.1, Figure 3.3b and 3.3c), i.e. participants with lower $B_{inf}$ showed greater activation in the Agree (relative to Disagree) condition, while participants with higher $B_{inf}$ showed greater activation in the Disagree (relative to Agree) condition. The reverse contrast revealed no significant clusters. $B_{inf}$ did not differentially modulate activation during the Review outcome in adolescents and adults, i.e. no region showed a significant Age group x Review outcome x $B_{inf}$ interaction.

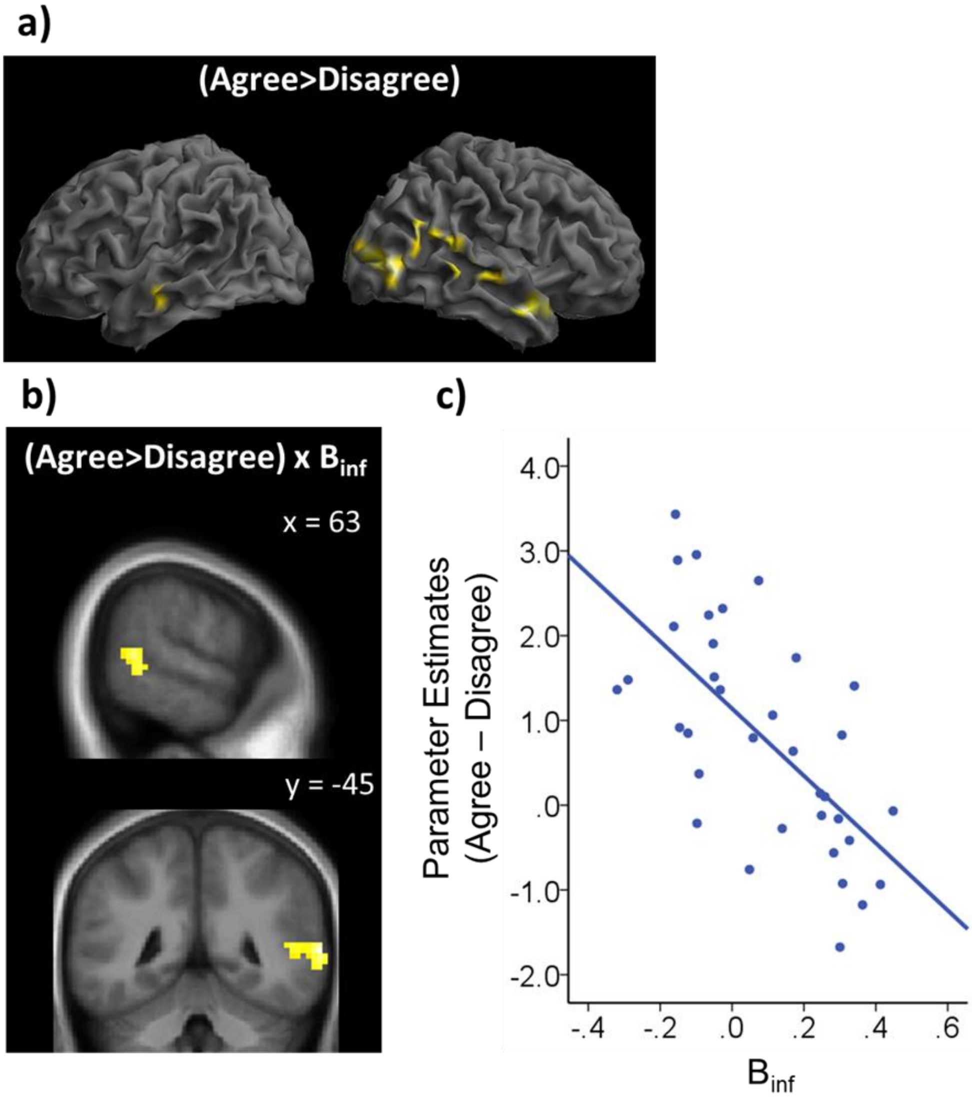


**Figure 3.3**: a) Brain activation in the contrast (Agree>Disagree) during the Review outcome period, collapsing across adolescent and adult participants (voxel-level uncorrected $p < 0.001$, cluster-level corrected $p_{FWE} < 0.05$). These regions (see Table 3.1) showed greater activation when the music experts' opinion matched the participant's choice relative to when it differed. The statistical map is rendered on the left and right brain surfaces (left and right panels respectively). b) Brain activation in the contrast (Agree>Disagree) correlated negatively with individuals' behavioural sensitivity to social influence ($B_{inf}$) during the Review outcome period, collapsing across adolescent and adult participants (voxel-level uncorrected $p < 0.001$, cluster-level corrected $p_{FWE} < 0.05$). The cluster is plotted on the average structural brain of the 35 participants. c) Correlation between $B_{inf}$ and the mean parameter estimates of the (Agree>Disagree) x $B_{inf}$ cluster for the difference in the Agree versus Disagree condition, plotted for illustrative purposes.

**Table 3.1**: Activations at Review outcome: Results are reported at $p < 0.001$ uncorrected at the voxel-level, and $p_{FWE} < 0.05$ at the cluster-level ($^{SVC}$: small volume correction for a priori volume of interest in the striatum) listed in MNI coordinate space. R: Right, L: Left

| Cluster | Brain region | Size (Voxel) | Z | Peak voxel (in mm) x | y | z |
|---|---|---|---|---|---|---|
| | | **Agree > Disagree** | | | | |
| **R Anterior Temporal** | **R Middle Temporal Gyrus** | **104** | **4.69** | **51** | **2** | **-23** |
| | R Middle Temporal Gyrus | | 4.17 | 60 | -4 | -17 |
| | R Middle Temporal Gyrus | | 3.67 | 48 | -10 | -23 |
| **R Occipital** | **R Cuneus** | **185** | **4.55** | **12** | **-100** | **7** |
| | R Middle Occipital Gyrus | | 4.29 | 48 | -76 | 1 |
| | R Middle Occipital Gyrus | | 4.06 | 33 | -91 | 10 |
| **R Precuneus-Calcarine** | **R Precuneus** | **112** | **4.17** | **9** | **-55** | **19** |
| | R Calcarine | | 4.03 | 3 | -61 | 10 |
| | R Precuneus | | 3.26 | 24 | -61 | 28 |
| **R Posterior Temporal** | **R Middle Temporal Gyrus** | **72** | **4.04** | **51** | **-58** | **19** |
| | R Middle Temporal Gyrus | | 3.18 | 45 | -67 | 13 |
| **R Temporal** | **R Middle Temporal Gyrus** | **139** | **3.97** | **66** | **-40** | **10** |
| | R Superior Temporal Gyrus | | 3.69 | 57 | -40 | 13 |
| | R Middle Temporal Gyrus | | 3.55 | 60 | -16 | -11 |
| **L Anterior Temporal** | **L Middle Temporal Gyrus** | **86** | **3.95** | **-57** | **-13** | **-17** |
| | L Superior Temporal Gyrus | | 3.92 | -42 | -19 | -11 |
| | L Middle Temporal Gyrus | | 3.59 | -45 | -28 | -11 |
| **Bilateral Precuneus-Cingulate** | **R Precuneus** | **83** | **3.74** | **9** | **-52** | **37** |
| | R Posterior Cingulate Cortex | | 3.68 | 12 | -40 | 34 |
| | L Precuneus | | 3.59 | -3 | -46 | 40 |
| **R Ventral Striatum (SVC)** | **R Ventral Striatum** | **21** | **3.57** | **9** | **14** | **-5** |
| | R Ventral Striatum | | 3.48 | 6 | 17 | -8 |
| | R Ventral Striatum | | 3.37 | 12 | 5 | -2 |
| | | **(Agree > Disagree) x $B_{inf}$** | | | | |
| **R Posterior Temporal** | **R Middle Temporal Gyrus** | **71** | **4.49** | **66** | **-46** | **7** |
| | R Middle Temporal Gyrus | | 3.61 | 51 | -46 | 10 |

### *3.3.2.2 Object reward*

Analysis of the main effect of Object outcome and a modulation of this main effect by Review outcome was performed during the Object outcome period (see methods 3.2.4.2). Within the striatum, the main effect of Object outcome (Preferred>Alternative) across Age groups - i.e. receiving a token for the preferred song relative to the alternative - revealed activations in the bilateral VS (left VS: k = 46, Z = 4.67; right VS: k = 43, Z = 3.65; Table 3.2, Figure 3.4b). There was no other significant activation at the whole-brain level. No regions showed an Age group x Object outcome interaction. Employing the contrast Preferred>Alternative as a mask to test for overlapping activation with the Agree>Disagree contrast revealed a partial overlap of 10 voxels (out of k = 21 in the Agree>Disagree contrast; Figure 3.4c).

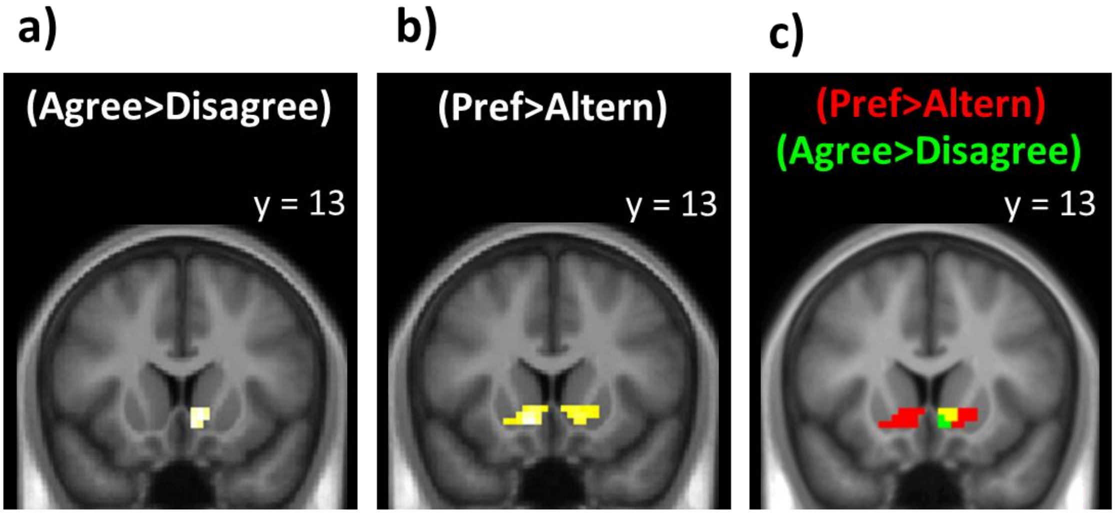


**Figure 3.4:** Striatal activations collapsing across adolescent and adult participants (voxel-level uncorrected $p < 0.001$, cluster-level corrected $p_{FWE} < 0.05$ within the striatum). The clusters are plotted on the average structural brain of all 35 participants. a) Social reward activation (Agree>Disagree) during the Review outcome period: regions activated when the music experts' opinion matched with the participant's choice relative to when it differed. b) Non-social reward activation (Preferred>Alternative) during the Object outcome period: regions activated when participants received a token for the song they originally preferred relative to the alternative song. c) Overlay of non-social reward activation (Preferred>Alternative; red) and social reward activation (Agree>Disagree; green); voxels activated by both contrasts are plotted in yellow. Pref: Preferred; Altern: Alternative.

**Table 3.2**: Activations at Object outcome: Results are reported at $p < 0.001$ uncorrected at the voxel-level, and $p_{FWE} < 0.05$ at the cluster-level ($^{SVC}$: small volume correction for a priori volume of interest in the striatum) listed in MNI coordinate space. R: Right, L: Left, Pref: Preferred, Altern: Alternative

| **Cluster** | **Brain region** | **Size (Voxel)** | **Z** | **Peak voxel (in mm)** | | |
|---|---|---|---|---|---|---|
| | | | | **x** | **y** | **z** |
| **Preferred>Alternative** | | | | | | |
| **L Ventral Striatum $^{(SVC)}$** | **L Ventral Striatum** | **46** | **4.67** | **-9** | **14** | **-8** |
| **R Ventral Striatum $^{(SVC)}$** | **R Ventral Striatum** | **43** | **3.65** | **12** | **14** | **-5** |
| | R Ventral Striatum | | 3.60 | 15 | 5 | -14 |
| | R Ventral Striatum | | 3.46 | 6 | 14 | -2 |
| **[(Agree Pref>Agree Altern) - (Disagree Pref>Disagree Altern)] x $B_{inf}$ x Age Group** | | | | | | |
| **L Ventral Striatum $^{(SVC)}$** | **L Ventral Striatum** | **16** | **4.24** | **-21** | **14** | **-8** |
| | L Ventral Striatum | | 3.52 | -12 | 20 | -8 |

### *3.3.2.3 Modulation of object reward signal by music experts' opinion*

In order to test whether the value-related activation when receiving a token for the preferred song relative to the alternative would be modulated by the music experts' opinion, the following contrast [(Agree Preferred > Agree Alternative) – (Disagree Preferred > Disagree Alternative)] and its association with $B_{inf}$ were tested. Collapsing across Age groups, there was no significant activation for the contrast or for an association of the contrast with $B_{inf}$. However, there was a four-way interaction between Object outcome, Review outcome, $B_{inf}$ and Age group in a left VS cluster (Figure 3.5). In adolescents there was a positive correlation between $B_{inf}$ and the mean parameter estimates of the [(Agree Preferred > Agree Alternative) – (Disagree Preferred > Disagree Alternative)] contrast, while there was a negative correlation in adults.

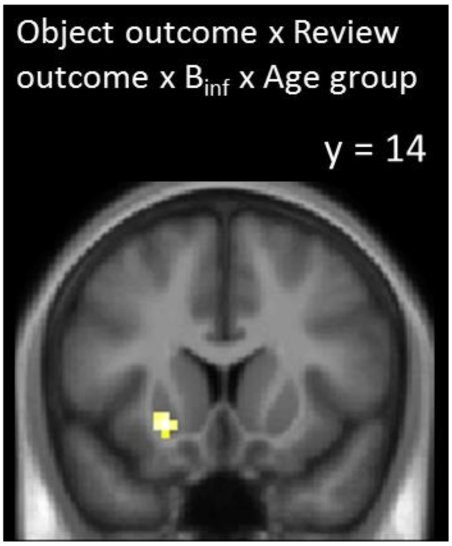


**Figure 3.5**: Striatal activation in the four-way interaction between the Object outcome, Review outcome, Age group and $B_{inf}$ during the Object outcome period (voxel-level uncorrected $p < 0.001$, cluster-level corrected $p_{FWE} < 0.05$ within the striatum).

## 3.4 Discussion

This study investigated the effect of social influence on subjective song value and the modulation of value-related activity in the VS in a group of female adolescents and female young adults. The behavioural findings revealed that both adolescent and adult participants' subjective song values changed in line with music experts' opinion. The fMRI analysis demonstrated that both adolescents and adults showed heightened bilateral VS activation when receiving a token for their preferred song relative to the alternative. Participants also showed greater activation in the right VS as well as activation in bilateral temporal lobes when the music experts agreed with participants' song choices relative to when they disagreed. The more participants' subjective song values were influenced by the music experts' preference (i.e. the greater the value of $B_{inf}$), the greater the activation was in a right posterior temporal cluster when disagreeing relative to agreeing with the music experts. There was no evidence that Object outcome or Review outcome was further modulated by age. However, there was a four-way interaction between Object outcome, Review outcome, Age group and $B_{inf}$.

### 3.4.1 Behavioural conformity in music preferences to music experts

A large literature of social influence studies in adults has demonstrated that individuals adjust their opinions, choices and behaviours to conform to those of others (Cialdini & Goldstein, 2004). A previous study (Campbell-Meiklejohn et al., 2010) using a similar paradigm to assess social influence on song valuation described a range of $B_{inf}$ in adults: some participants were strongly influenced by the music experts (positive $B_{inf}$), some showed little or no sensitivity to social influence ($B_{inf}$ close /equal to 0) and some participants showed anti-conformity (negative $B_{inf}$), i.e. their valuation of music songs changed in the opposite direction to the music experts' opinion. In the current study, collapsing across both Age groups, there was a similar range of $B_{inf}$ values to that in Campbell-Meiklejohn et al. (2010). Overall, mean $B_{inf}$ was significantly greater than 0, indicating that participants tended to adjust their valuation of music songs in line with the music experts' opinion.

While there is a large literature on social influence effects in adults, the development of conformity during adolescence is less well studied. Studies investigating conformity **within adolescence** have found evidence for both a linear decrease of conformity (Steinberg & Monahan, 2007; M. B. Walker & Andrade, 1996) and an inverted U-shape of conformity across age (Steinberg & Monahan, 2007; M. B. Walker & Andrade, 1996). Regarding developmental changes in **conformity between adolescents and adults**, one study demonstrated greater conformity to peers in a version of Asch's line paradigm in young adolescence (aged 11 - 13 years) compared to early adulthood (aged 19 - 21 years), with intermediate levels of conformity in 15 - 17-year-olds (Costanzo & Shaw, 1966). Another study assessed the influence of risk-adverse advice by an adult financial expert on risky choices, and showed that adolescents (aged 12 - 17 years) were more influenced by the financial expert than were adults in terms of their choices (aged 18 - 45 years) (Engelmann et al., 2012). In the current study, adolescents and adults did not differ in $B_{inf}$, in other words, they were similarly influenced in their valuation of music songs by the opinion of a group of music experts. In addition to differences in the tasks assessing the sensitivity to social influence, differences between the findings in the current study and the two previous studies might be attributable to who is exerting social influence and how it is exerted. In the study of Engelmann et al. (2012), an adult financial expert advised participants on their choices and particularly younger participants might have followed the expert's advice to maximise their earnings in the task. In contrast, following the music experts' advice in the current study entailed no obvious benefits. In addition, it is not clear whether adolescents were more influenced than were adults by the adult financial expert because he was an expert or because he was an adult. The current study attempted to avoid this confound by giving no explicit age references for the music experts; instead, the descriptions and photos of the music experts were chosen so that both adolescents and adults would view them as approximately similar-aged.

Costanzo & Shaw (1966) measured social influence to three physically present school peers. Four participants sat in four adjacent half-open testing cubicles. Participants believed they could see their peers' responses on a lamp panel inside their cubicle; however these responses were experimentally manipulated. On social influence trials, the lamp panel indicated to the participants that their three peers had all chosen the incorrect response, and the participants thought they were responding last. Participants frequently conformed to the incorrect response in this social pressure condition, even though in the absence of social influence participants showed almost perfect performance, suggesting the behaviour is likely to reflect normative social influence (i.e. *conforming to be 'liked'*). In other words, when facing social pressure by their peers, participants conformed to their judgements, possibly to avoid social exclusion or gain social approval. In contrast, in the current study, participants rated song desirability in private after having learned about the music experts' opinion. Consequently, there was no social pressure by the music experts to adjust song values in line with them, and participants may have instead used the music experts' preferences as a source of information to adjust their own preference (i.e. informational social influence: *conforming to be 'right'*). It would be interesting to investigate whether adolescents show greater $B_{inf}$ than adults when physically present peers evaluate the songs, and to assess developmental differences in the change in ratings depending on whether participants rate songs publicly or privately.

### 3.4.2 Social brain activation during reviewer feedback

Agreeing with music experts on music choices relative to disagreeing activated a network of temporal regions in the right hemisphere (ATC and an extended activation along the STS into the pSTS) and the left ATC in both adolescents and adults. Consequently, when others' opinions agreed with participants, there were activations in regions within the social brain network (Blakemore, 2008; Frith & Frith, 2006; Saxe, 2006; Van Overwalle, 2009). A similar pattern of activation as was found in the current study for the right temporal cortex was found in a recent study that examined the processing of social versus symbolic information (Dumontheil, Hillebrandt, Apperly, & Blakemore, 2012). Adolescents (aged 11 - 16 years) and adults showed this pattern of activation when the instruction to move an object to a different slot in a set of shelves required the consideration of a director's viewpoint relative to when the instructions required to follow a symbolic cue. This pattern of activation in the right temporal cortex was also found when both adolescents (aged 12 - 14 years) and adults inferred affective mental states from short video clips (Vetter, Weigelt, Döhnel, Smolka, & Kliegel, 2014)

When participants received feedback that the music experts agreed with them relative to when they disagreed, participants also activated cortical midline structures including the PCC, precuneus and calcarine sulcus. Previous social influence studies have also found PCC and precuneus activation when participants agreed with others relative to when they disagreed (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009). PCC and precuneus activation has also been associated with receiving positive social feedback (i.e. being liked on the basis of a photograph; Davey et al., 2010; Moor et al., 2010). Receiving feedback from others might also trigger self-referential processing, for example, thinking how one's music taste is perceived by others. Cortical midline structures – including the PCC and precuneus - have been consistently implicated in self-referential processing (Northoff et al., 2006).

Activation in the main effect of Review outcome (Agree>Disagree) in a right pSTS cluster was further modulated by $B_{inf}$, in other words, there was a negative correlation between $B_{inf}$ and activation in the Agree>Disagree contrast. Thus, participants who did not conform or who changed their ratings in the opposite direction to the music experts' opinion (lower $B_{inf}$ values) showed greater right pSTS activation in the Agree (relative to Disagree) condition, while participants who adjusted their ratings in line with the music experts (higher $B_{inf}$ values) showed greater activation in the Disagree relative to Agree condition (this could be considered a conflict signal). Participants who showed a conflict signal in the right pSTS subsequently conformed more strongly than participants who showed greater activation during Agreement. Thus, pSTS activation in the conflict contrast, found in strongly influenced participants, might signal the need to update the value of the song in line with the music experts' opinion. Activation in the pSTS has also been found when predictions about the intentions of an actor or avatar's actions have been violated, requiring an update of the actor's intentions that the participant had inferred (Frith & Frith, 2007). Consequently, the pSTS might play a more general role in social learning.

### 3.4.3 Non-social and social reward activation

In both adolescents and adults, receiving a token for the preferred song relative to the alternative (non-social reward outcome) activated the bilateral VS. There is an extensive literature implicating the VS in primary and secondary reward processing (for reviews Delgado, 2007; Haber & Knutson, 2010). Likewise, in the previous study employing a similar paradigm, adult participants also showed elevated activity in the bilateral VS when receiving a token for their preferred song relative to the alternative (Campbell-Meiklejohn et al., 2010).

Several developmental studies have demonstrated that VS activation in adolescents in response to reward is increased relative to children and adults and have suggested that adolescents are hyper-responsive to rewards (Barkley-Levenson & Galván, 2014; Ernst et al., 2005; Galván et al., 2006; Galván & McGlennen, 2013; Geier et al., 2010; Padmanabhan et al., 2011; Van Leijenhorst, Moor, et al., 2010; Van Leijenhorst, Zanolie, et al., 2010). In contrast, a few studies have shown decreased VS activation in adolescents relative to adults during reward assessment (Geier et al., 2010) and reward anticipation (Bjork et al., 2004, 2010). Finally, some studies have found no difference between VS activation in adolescents and adults during reward anticipation (Galván & McGlennen, 2013; Van Leijenhorst, Zanolie, et al., 2010) and reward outcome (Bjork et al., 2004, 2010), suggesting that the theory of adolescent hyper-responsiveness to rewards might be too simplistic. In the current study, there was no evidence for an age effect in VS activation (or in any other brain region) during non-social reward outcome. These differences in observed patterns of VS activation in adolescents and adults might be due to the different trial phases analysed (reward assessment, reward anticipation, reward outcome) and the type of paradigm that was employed (for a discussion Crone & Dahl, 2012; Galván, 2010). In addition, all but one (Galván & McGlennen, 2013, which used primary liquid rewards) of the studies listed above have employed monetary rewards, while the current study used tokens for music songs. With the increasing use of free music-streaming services like Spotify or Grooveshark, the subjective value of owning music songs might have decreased in the recent years. Speculatively, the use of music songs as secondary rewards might thus be less powerful than primary or monetary rewards to detect age differences in reward processing between adolescents and adults.

A number of fMRI studies has demonstrated that the VS is also involved in the processing of social rewards (for reviews Bhanji & Delgado, 2014; Fareri & Delgado, 2014). Activation in the VS has been shown for instance for anticipating and receiving positive social feedback (Izuma et al., 2008; Rademacher et al., 2010; Spreckelmeyer et al., 2009) and also for simply engaging in social interactions (Pfeiffer et al., 2014). Within the striatum, agreeing with the music experts relative to disagreeing elicited activation in the right VS in the current study. This activation partly overlapped with the activation in response to the non-social reward. These findings are in line with the previous study in adult participants employing a similar social influence task (Campbell-Meiklejohn et al., 2010). Consequently, the findings in the current study and from previous studies reviewed above suggest that the VS might be a common substrate in the processing of both non-social and social rewards.

While there is a relatively large number of developmental studies examining the neural correlates of non-social reward processing during adolescence, studies investigating developmental changes in social reward processing are limited. In one study, employing happy (versus calm) faces as appetitive social stimuli, relative to children and adults, adolescents showed increased VS activation in response to social rewards in a social go/no-go task (Somerville et al., 2011). In the current study, there were no developmental differences in VS activation during the social reward outcome, i.e. when agreeing with music experts relative to when disagreeing. This again suggests that the theory of adolescent hyper-responsiveness to rewards might be too simplistic and might be dependent on the type of task and reward used. Although the current study and previous studies (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009) have demonstrated that matching opinion with virtual others (i.e. the opinion of music-experts or a group of participants) is suffice to elicit VS activation, the use of real and/or familiar peers might evoke stronger VS activation in adolescents than in adults. The developmental pattern of VS activation in response to agreement with peers versus non-peers or in response to opinions of physically present versus virtual peers should be investigated in future studies.

### 3.4.4 Modulation of the value signal by social influence

FMRI studies in adults have demonstrated that the magnitude of VS activation is positively correlated with the value of a choice (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; Galván et al., 2005; Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Knutson, Adams, Fong, & Hommer, 2001; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Tom et al., 2007) (for reviews Delgado, 2007; Knutson, Delgado, & Phillips, 2008). This positive association between VS activation and reward value has also been demonstrated in adolescents (Barkley-Levenson & Galván, 2014; Bjork et al., 2004; Galván et al., 2006; Van Leijenhorst, Moor, et al., 2010). The previous study in adults demonstrated that the value signal when receiving a token for the preferred song relative to alternative was modulated by the reviewers' opinion in dependence on the behavioural sensitivity to social influence ($B_{inf}$; Campbell-Meiklejohn et al., 2010). The current study did not replicate this three-way interaction, collapsing across Age group. However, there was a four-way interaction between Object outcome x Review outcome x Age group x $B_{inf}$ in a left VS cluster. In adolescents, activation in this cluster showed a positive relationship between $B_{inf}$ and neural modulation of reward value activation by music experts' opinion. This was also found in the previous study in adults, although the activation cluster here is more lateral than in the previous similar study ([-21, 14, -8] versus [-6, 14, -8], (Campbell-Meiklejohn et al., 2010)) and than the reward-related activation in the current Preferred>Alternative main contrast ([-21, 14, -8] versus [-9, 14, -8]). The relationship between $B_{inf}$ and neural modulation in adults showed the reverse pattern as in adolescents. Thus, adult participants in the current study did not show the same relationship between behavioural sensitivity to social influence and the modulation of the reward-related activation by music experts' opinion as has been found in the previous study in adults (Campbell-Meiklejohn et al., 2010). This is somewhat surprising and might be due to the smaller sample size (16 adults in current study versus 28 adults in Campbell-Meiklejohn et al., 2010), including only female participants or a potential decrease in the subjective value of a song token in the last few years (discussed above).

### 3.4.5 Conclusion

In the current study, adolescents and adults showed similar tendencies to adjust their music song preferences in line with a group of music experts. Activation in the bilateral VS in response to receiving a token for the preferred music song relative to receiving a token for the alternative song did not differ between adolescents and adults. This suggests that the theory of adolescent hyper-responsiveness to rewards might be too simplistic and requires future work to disseminate what factors contribute to heightened reward-related activation during adolescence. Adolescents and adults also showed similar activation in the right VS when music experts agreed with their choices relative to when they disagreed as well as in bilateral temporal regions which are part of the social brain network. Consequently, adolescents' and adults' sensitivity to social influence as well as activation patterns when matching choices with others were overall very similar in the current task. This indicates that differences in adolescent and adult sensitivity to social influence might be relatively subtle and possibly rely on the motivational salience of either the object of social influence or the individuals exerting social influence.

While the current study investigated the development of individual tendencies to adjust preferences in line with others' preferences and its neural correlates, the following chapter examines the development of a very different aspect of social influence during adolescence. **Chapter 4** investigates how the presence of a peer audience affects performance in a high-level cognitive task and its development between adolescence and adulthood.

# CHAPTER 4: DEVELOPMENT OF THE AUDIENCE EFFECT ON RELATIONAL REASONING PERFORMANCE

*Adolescents have been shown to be particularly sensitive to peer influence. However, the data supporting these findings have been mostly limited to the impacts of peers on risky and reward-related decision-making. This chapter describes a behavioural study that investigated the influence of peers on performance in a high-level cognitive task (relational reasoning) during adolescence. Previous studies have compared a peer to an alone condition; here it was additionally assessed whether this audience effect on performance would be dependent on the identity of the audience, either a friend (peer) or the experimenter (non-peer). Peer audience effects were compared in young adolescent (10.6 - 14.2 years, n = 24), mid-adolescent (14.9 - 17.8 years, n = 20) and adult (21.8 - 34.9 years, n = 18) female participants. The presence of an audience affected adolescent, but not adult, relational reasoning performance. This audience effect on adolescent performance was influenced by the participants' age and the identity of the audience. This chapter shows that adolescents demonstrate a similar heightened sensitivity to peer influence on performance in a high-level cognitive task as has been found previously for risky- and reward-related decision-making.*

## 4.1 Introduction

During the transition from childhood to adolescence, relationships with peers become increasingly elaborate, more personal and emotional (Brown, 2004). Interactions with peers also dominate adolescents' social environment, with American adolescents spending more than half of their awake-time with peers (Csikszentmihalyi & Larson, 1984). Adolescent decision-making is particularly influenced by their peers. For example, when performing a driving video game, adolescents (13 - 16 years) took more risks when being observed by peers relative to when alone, while adults' risk-taking was not affected by the presence of peers (Gardner & Steinberg, 2005). Questionnaire-based studies have also found that adolescents are particularly sensitive to peer influence, especially in the context of risk-taking (Berndt, 1979; Brechwald & Prinstein, 2011; Steinberg & Monahan, 2007; Steinberg & Silverberg, 1986). Previous experimental studies of peer influence in adolescence have predominantly focused on the influence of peers on risky choices and the link between increased levels of adolescent risk-taking and the modulation of reward-sensitivity by peers (Chein et al., 2011; L. O'Brien et al., 2011; A. R. Smith, Steinberg, et al., 2014). For instance, in an fMRI version of the driving video game adolescents – but not adults - showed increased activation in reward-related regions (VS and OFC) in the peer relative to the alone condition when making decisions whether to drive or to stop (Chein et al., 2011). The current study investigated the hypothesis that heightened sensitivity to the influence of peers during adolescence would extend beyond risky and reward-related decision-making to the performance of a high-level cognitive task, known to rely on a network of fronto-parietal brain regions (Krawczyk, 2012). This was examined by comparing the effect of peer audience observation on high-level task performance in adolescent and adult participants.

One explanation as to why adolescents are especially sensitive to peer influence is that social information has particularly high salience for this age group (Blakemore & Mills, 2014, for details see 1.5). For example, adolescents appear to be hypersensitive to social exclusion (Sebastian et al., 2010). In a recent neuroimaging study, participants aged 8 - 22 years were told that sometimes they were being watched by a peer via a camera (Somerville et al., 2013). When adolescents thought they were being observed by a peer, they showed higher autonomic arousal as measured by skin conductance, relative to both children and adults. Self-reported embarrassment and activation in the mPFC - a key region of the social brain (Frith & Frith, 2007) - were also elevated in adolescence relative to late childhood (Somerville et al., 2013). Previous peer influence studies have compared peer observation with no observation (Gardner & Steinberg, 2005; L. O'Brien et al., 2011; A. R. Smith, Chein, et al., 2014; Weigard et al., 2014), making it impossible to attribute effects to the specific presence of a peer rather than to general effects of the presence of another person. The present study manipulated audience observation across three levels: peer audience (participant's friend), non-peer audience (experimenter) and no audience. By comparing peer versus non-peer observation conditions, the current study attempted to control for any general (e.g. distracting) effects of having someone present while performing a task.

There is a long history of social psychology studies on the effects of the presence of another person on performance – predominantly in adults (see Aiello & Douthitt, 2001; Zajonc, 1965 and 1.8). These audience effects describe the influence of an audience on performance measures, such as accuracy and RT. The pattern revealed by these studies is a performance improvement associated with being observed in simple and well-learned tasks and an impairment in complex or learning tasks (see C. F. Bond & Titus, 1983 for a meta-analysis). However, there does not seem to be a general agreement on what classifies a task or task-level as 'simple' or 'complex', particularly as a wide variety of tasks have been used to study social facilitation (C. F. Bond & Titus, 1983). In their meta-analysis, Bond & Titus (1983) classified tasks according to their label in the original papers, rather than using a systematic rule to classify tasks as simple or complex across studies.

Few developmental studies have investigated the audience effect (Meddock et al., 1971; Newman et al., 1978; Quarter & Marcus, 1971). In an EEG study, Kim et al. (2005) investigated whether the presence of a friend influenced error-related negativity (ERN) in a go/no-go task in 7 - 11-year-olds. There was no effect on behaviour, however participants showed increased ERN-amplitudes in the presence of a friend, relative to being alone, indicating that 7 - 11-year-old children are already sensitive to the presence of peers when performing a go/no-go task.

To investigate developmental changes in peer influence on high-level cognitive task performance the study employed a relational reasoning paradigm, which involves evaluating and integrating the relationships between multiple mental representations (Krawczyk, 2012).

Examples of such relationships are analogies (Holyoak, 2012), in which a new piece of information is understood by comparing it to existing knowledge, which facilitates problem solving in novel situations and knowledge transfer across different contexts (Krawczyk, 2012). Relational reasoning has been found to be associated with mathematics performance, reading and academic knowledge (Ferrer, O'Hare, & Bunge, 2009; Träff, 2013). The difficulty of relational reasoning problems can be quantified by the number of relations that need to be considered to solve it (Raven, 1941). To solve a 1-relational problem, variation along one dimension must be considered, while solving 2-relational (and higher) problems requires integrating two or more dimensions of variation. While children under 5 years can solve 0- and 1-relational problems, they fail to solve 2-relational (or higher) problems (Halford, 1984). Relational reasoning continues to improve in late childhood and throughout adolescence (Crone et al., 2009; Dumontheil, 2014; Dumontheil, Houlton, et al., 2010; Rosso, Young, Femia, & Yurgelun-Todd, 2004; Wendelken et al., 2011). In light of the adult audience effect literature (C. F. Bond & Titus, 1983), two task-levels were included to assess the potential specificity of audience effects to different levels of task difficulty. However, as relational reasoning is usually considered a high-level, complex task, even at relatively low levels, it was not clear whether there would be differential audience effects for the two difficulty levels.

Previous studies suggest that the effects of peer influence may differ with age during adolescence. On the one hand, questionnaire-based studies demonstrated that the increase in resistance to peer influence (RPI) is most pronounced between age 14 and 18 years (Steinberg & Monahan, 2007), suggesting young adolescents might show greater performance changes in the presence of a peer. As mentioned above, experimental work showed that female adolescents (aged 11.9 - 15.8 years), and in particular younger adolescents (aged 11.9 - 13.9 years), are hypersensitive to social exclusion (Sebastian et al., 2010), suggesting young adolescents may be more concerned about failing in front of their friend. On the other hand, results from a questionnaire-based study demonstrated that 15 - 18-year-olds reported increased levels of fear of social evaluation relative to 12 - 14-year-olds and 8 - 11-year-olds (Westenberg et al., 2004). The present study included participants aged 10 to 17 years, to allow investigation of potential developmental differences within adolescence, although, based on mixed evidence from previous research; it was unclear whether young or mid-adolescents would show greater audience effects on task performance.

The *first* aim of the current study was to investigate how relational reasoning performance is influenced by the presence of an observer. *Second*, the study examined whether young adolescents, mid-adolescents and adults would show differential audience effects on relational reasoning. *Third*, on the basis of evidence that social relationships with peers play a predominant role during adolescence, the study investigated whether the audience effect was affected by the identity of the observer (same-aged friend versus experimenter). *Lastly*, it was examined whether audience effects on relational reasoning performance would be related to individual differences in self-reported resistance to peer influence or friendship quality scores. To study these questions, female *participants* solved relational reasoning problems in three different social conditions: *Alone*, observed by a friend (*Friend-present*) or observed by the experimenter (*Experimenter-present*).

## 4.2 Methods

### 4.2.1 Participants

Pairs of volunteers were recruited for this study and randomly assigned at the beginning of the study (using a coin-flip) to either the role of the *participant*, who would perform the task, or the *observer*, who would watch the *participant* in one session and subsequently evaluate the *participant's* performance. The term 'volunteers' refers to both the *participants* and the *observers*.

Forty-four pairs of adolescent and 20 pairs of adult friends took part. Grouping of the adolescent *participants* was performed by a median split, resulting in a group of 24 young adolescents (aged 10.6 - 14.2) and 20 mid-adolescents (aged 14.9 - 17.8) (median age of all adolescent *participants* = 14.2 years, see Table 4.1 for ages). Volunteers were recruited from the Greater London area. Adolescents were recruited from local schools and sports clubs and adults were recruited from local universities and the Science Museum. Most adolescents attended academically selective secondary schools and the majority of adults were university graduates. Volunteers were paid £8/hour for their time. Procedures were approved by the local Research Ethics Committee and all volunteers (or their parents/guardians) gave informed consent.

Two adult *participants* were excluded from the analysis (one performed below chance and one verbalised her strategies during the task); thus the analysis included 24 young adolescents, 20 mid-adolescents and 18 adults. Verbal IQ of *participants* was assessed with the vocabulary subtest of the Wechsler Abbreviated Scale of Intelligence (WASI, Wechsler, 1999), to check groups were matched in terms of cognitive ability.

### 4.2.2 Questionnaire measures

Cronbach's alpha reliability-coefficients for the sample were calculated for all questionnaire measures and are provided. *Participants* completed the resistance to peer influence questionnaire (RPI, Steinberg and Monahan, 2007), consisting of ten statement-pairs pertaining to peer influence. *Participants* chose which statement described them best and rated it as 'really true' or 'sort of true'. Responses were coded on a four-point scale - high scores indicating greater resistance ($\alpha = 0.65$). All volunteers (except one young adolescent *observer*) completed the McGill friendship questionnaire–Friend's Function (MFQ-FF, Mendelson & Aboud, 1999): 30 questions assessed how much the friend fulfils friendship functions and were rated on a nine-point scale (from 0 - 8) – with high scores indicating greater friendship quality. For each volunteer-pair a combined score of *participant* and *observer* reported friendship quality was generated (α = 0.95).

### 4.2.3 Experimental design

The study employed a 2 x 3 x 3 mixed factorial design in which there were two within-subjects factors: Task level (Low-relational; High-relational), and Social condition (Friend-present; Experimenter-present; Alone); and one between-subjects factor: Age group (young adolescents; mid-adolescents; adults).

#### *4.2.3.1 Relational reasoning task*

Participants solved problems that had the general form of the Raven's Progressive Matrices test (RPM, Raven, 1941). Similar to Crone et al. (2009), some of the reasoning problems were derived from the actual RPM test and additional equivalent problems were developed to obtain a sufficient number of simple and complex stimuli. As in the RPM, the problems contained a pattern or a 3 x 3 grid of stimuli in which the lower right stimulus was missing. Task level was manipulated by changing the number of dimensions that needed to be considered to reach the correct solution. Low-relational trials included 36 1-relational or simple 2-relational matrices (see Figure 4.1a). High-relational trials included 36 complex 2-relational (i.e. with permutation of the features within a row and/or a column) and 3- or more relational matrices (see Figure 4.1b).

In each trial, *participants* were presented with four possible response options, and used a mouse to indicate their response (Figure 4.1c). Stimulus presentation was self-paced (within a maximum period of 40 s per trial). *Participants* were instructed to respond as quickly and accurately as possible. The *participant's* choice was subsequently highlighted in blue for 0.8 s and followed by feedback about accuracy and RT for 0.8 s.

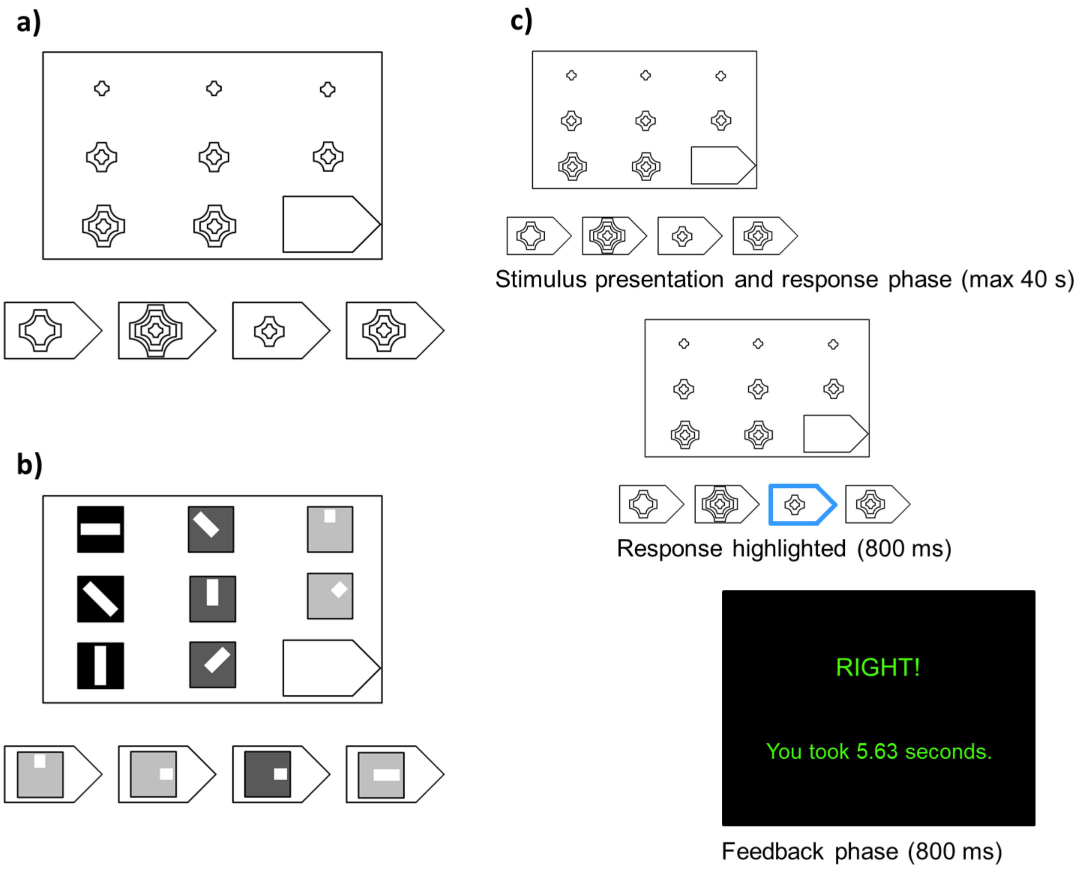


**Figure 4.1** Relational Reasoning Task. a) Example of a Low-relational problem: 1-relational reasoning matrix, with a vertical increase in the number of items (the correct response is the first from the right). b) Example of a High-relational problem: 3-relational reasoning matrix, with a horizontal change in colour, a horizontal change in the length of the bar and a change in rotation of the bar (the correct response is the second from the left). c) The stimuli were presented until the *participants* responded. Next, *participants'* responses were highlighted in blue. Finally, *participants* received feedback about their performance.

At the start of the testing session instructions were displayed on the screen and read out to the volunteer pairs. *Participants* then performed a practice session, consisting of two Low-relational and four High-relational trials. Stimuli were presented with Cogent 2000 (www.vislab.ucl.ac.uk/Cogent/index.html) implemented in Matlab R2010b (Mathworks Inc., Sherborn, MA).

#### *4.2.3.2 Social conditions*

The three Social conditions (Alone, Friend-present and Experimenter-present) were manipulated in three different sessions, and order of sessions was counterbalanced between *participants*. In each session the *participants* performed two tasks. Only the relational reasoning task is described here (the other – a perceptual discrimination task – will be analysed separately and described in **Chapter 5**). Sessions lasted on average 6.6 min and the whole study lasted 60 to 75 min.

In the Friend- and Experimenter-present conditions, the observer sat quietly behind the *participant* and watched and evaluated the *participant's* performance on the relational reasoning task. These two conditions thus differed only in terms of the relationship between the observer and *participant*. *Participants* were aware that their performance would be evaluated by the observer in both social observation conditions. In the *Friend-present* condition, the *observer* was instructed (in the presence of the *participant*) to follow the *participant's* performance closely by paying attention to both the accuracy and RT feedback and silently count the number of wrong responses (59/62 of the *observers* reported these correctly). Volunteers were instructed not to interact during the session. Similarly, in the *Experimenter-present* condition, a female experimenter explained that she would be watching the *participant's* performance closely by paying attention to both the accuracy and RT feedback, and silently counting the number of wrong responses. In the *Alone* condition, *participants* performed the task without being observed by someone else.

Volunteers were tested in a quiet, spacious room. In all three Social conditions, a student was working in a distant corner of the room facing away from the *participant*, to ascertain that volunteers were not communicating during the Friend-present condition. In each session, *participants* completed a set of 12 Low-relational and a set of 12 High-relational matrices, randomly selected from a total set of 72 (3 sessions x 24 matrices = 72 matrices). These two sets were presented in a counterbalanced order between *participants*.

### 4.2.4 Data analysis

The current study employed age groups to study the effect of age on peer audience effects on relational reasoning due to the relatively complex experimental design and the need to counterbalance the experimental factors. Furthermore, previous experimental studies investigating the effects of peer influence (Chein et al., 2011; Gardner & Steinberg, 2005; A. R. Smith, Steinberg, et al., 2014) compared age effects between an adolescent and adult group of participants. Thus the use of age groups allowed a better comparison between the results from the current study and previous studies (see also 1.9 for a discussion of age analyses).

Mean accuracy, and mean RT from correct trials, were analysed using 2 x 3 x 3 mixed-design ANOVAs with Task level (Low-relational; High-relational) and Social condition (Alone; Experimenter-present; Friend-present) as within-subjects factors and Age group (young adolescents; mid-adolescents; adults) as between-subjects factor, using SPSS 19.0 (Armonk, NY: IBM Corp.). Trials with RTs over 3 interquartile ranges above or below the upper or lower quartile of all trials were excluded from the analysis (15 out of 2232 trials). Significant interactions with age were followed up with separate repeated-measures ANOVAs for each Age group, and post-hoc pairwise comparisons. One-way ANOVAs were employed to test for age-effects on verbal IQ, RPI and friendship quality. To investigate whether audience effects were related to individual differences in self-reported RPI or friendship quality, correlation analyses between significant audience effects and RPI or friendship quality scores were performed. Marginally significant results ($p < 0.1$) are reported in the results, but only significant results ($p < 0.05$) are further discussed. Reported p-values are two-tailed.

## 4.3 Results

### 4.3.1 Accuracy

There was a main effect of Task level ($F(1,59) = 308.97$; $p < 0.001$, Figure 4.2) with higher accuracy for Low-relational (93.2% ± 5.7) than High-relational trials (60.1% ± 17.5). There was no main effect of Age group, nor an Age group by Task level interaction ($ps > 0.9$). The accuracy data revealed a main effect of Social condition ($F(2,118) = 3.49$; $p = 0.034$) with *participants* responding less accurately in the Friend-present condition than the Experimenter-present condition overall ($t(61) = 2.78$; $p = 0.006$). The other post-hoc comparisons were not significant ($ps > 0.1$). There was no Age group by Social condition interaction, nor a Social condition by Task level interaction ($ps > 0.25$).

There was a significant three-way interaction between Social condition, Task level and Age group ($F(4,118) = 2.91$; $p = 0.024$), which was followed up by separate Social condition by Task level repeated-measures ANOVAs for each Age group. The adult group showed neither a main effect of Social condition nor an interaction between Social condition and Task level ($ps > 0.4$; Figure 4.2). In the young adolescent group there was a Social condition by Task level interaction ($F(2,46) = 3.85$; $p = 0.028$), which was further explored by separate one-way ANOVAs investigating the effect of Social condition on accuracy in Low-relational and High-relational trials. The effect of Social condition in High-relational trials in young adolescents was not significant ($p = 0.106$), however there was a significant effect of Social condition on Low-relational trials ($F(2,46) = 4.66$; $p = 0.014$). This was due to a lower accuracy in the Friend-present condition relative to the Experimenter-present condition ($t(23) = 3.89$; $p = 0.001$) and a marginally lower accuracy in the Friend-present condition relative to Alone condition ($t(23) = 1.97$; $p = 0.061$) (Figure 4.2). The Alone condition and the Experimenter-present condition did not significantly differ ($p > 0.6$). In the mid-adolescent group there was a main effect of Social condition ($F(2,38) = 4.86$; $p = 0.013$) with lower accuracy in the Friend-present condition relative to the Experimenter-present condition across Task levels (t(19) = 3.53; p = 0.002) (Figure 4.2). The other post-hoc comparisons were not significant (ps > 0.1).

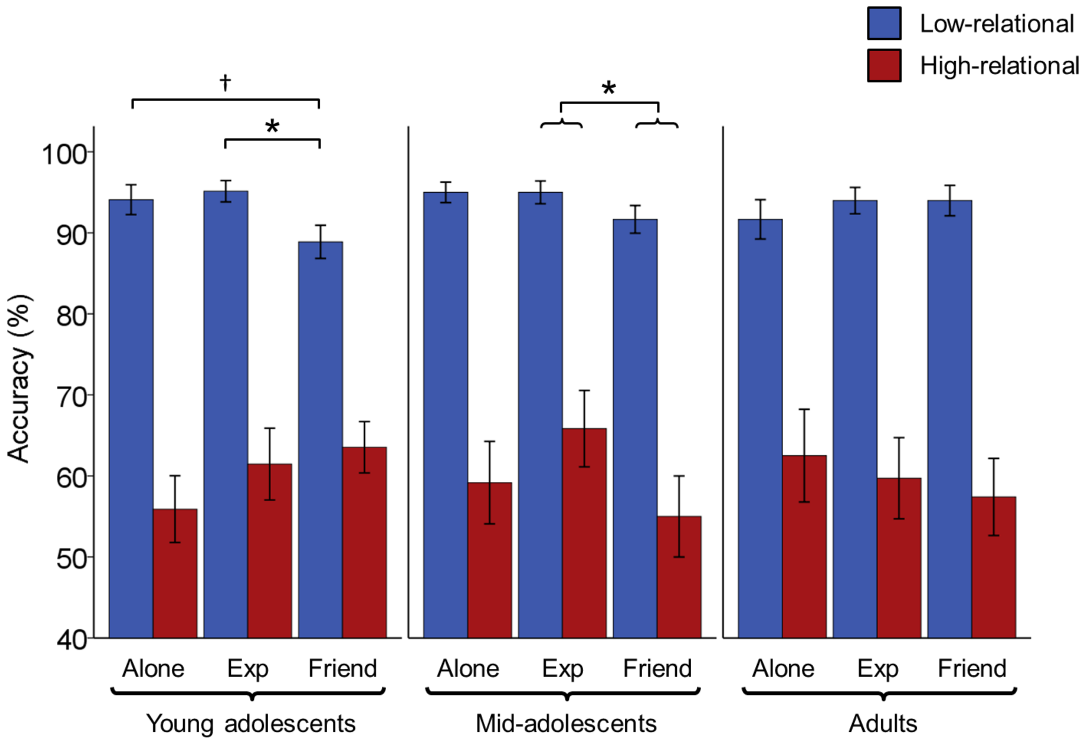


**Figure 4.2** Audience Effects on Relational Reasoning Accuracy. Accuracy data (mean ± SE): there was a three-way interaction between Social condition, Task level and Age group. Adults' accuracy was not affected by Social condition, while mid-adolescents (14.9 - 17.8 years) showed a main effect of Social condition driven by lower accuracy in the Friend-present relative to the Experimenter-present condition, across Task levels. Young adolescents (10.6 - 14.2 years) showed a Social condition x Task level interaction, driven by lower accuracy in the Friend-present relative to the Experimenter-present condition, and marginally lower accuracy in the Friend-present relative to the Alone condition, in the Low-relational condition only. Significant differences are represented by * (p < 0.05) and trends are represented by † (p < 0.1).

To summarise, no audience effect on relational reasoning accuracy was observed in adults; in contrast, mid-adolescents showed poorer performance when being observed by their friend relative to the experimenter, independent of Task level, while young adolescents only showed this difference in Low-relational trials.

### 4.3.2 Response times

There was a main effect of Task level on RT ($F(1,59) = 412.88$; $p < 0.001$, Figure 4.3) with faster responses for Low-relational (3.62 s ± 0.74) than High-relational trials (11.95 s ± 3.62). There was no main effect of Age group, nor an interaction between Age group and Task level (ps > 0.3).

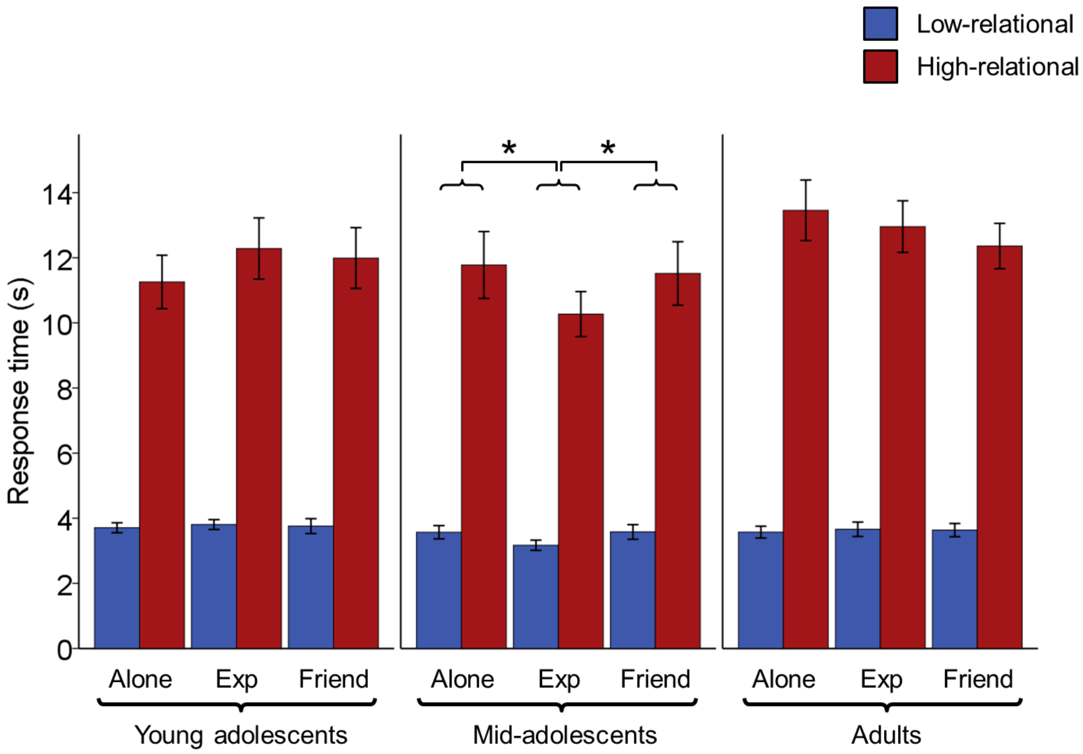


**Figure 4.3** Audience Effects on Relational Reasoning RT. RT data for correct trials (mean ± SE): there was a two-way interaction between Social condition and Age group. Following up this two-way interaction, only mid-adolescents (14.9 - 17.8 years) showed an effect of Social condition: RTs were significantly faster in the Experimenter-present relative to the Friend-present and Alone conditions. Significant differences are represented by * ($p < 0.05$).

Regarding Social condition, there was no main effect nor a Social condition by Task level interaction (ps > 0.6). The analysis revealed a two-way interaction between Social condition and Age group ($F(4,118) = 2.84$; $p = 0.027$) (Figure 4.3), while the three-way interaction was not significant ($p > 0.1$). Separate one-way repeated-measures ANOVAs within each Age group were used to further explore the interaction between Social condition and age. Social condition did not have a significant effect on RT in the young adolescents or adults (ps > 0.25).

However in the mid-adolescent group, Social condition significantly affected RT ($F(2,38) = 3.59$; $p = 0.037$) with faster responses in the Experimenter-present condition than in both the Friend-present ($t(19) = 2.25$; $p = 0.037$) and Alone ($t(19) = 2.12$; $p = 0.047$) conditions. The Alone and Friend-present conditions did not significantly differ ($p > 0.7$).

To summarise, across Task levels, mid-adolescents demonstrated faster RTs in the presence of the experimenter relative to the other Social conditions.

### 4.3.3 Questionnaire measures

The three Age groups did not differ significantly (Table 4.1) in their verbal IQ scores ($p > 0.25$) or their RPI scores ($p > 0.1$). Young adolescents (combined friendship quality score: mean ± SD: 6.7 ± 0.7), mid-adolescents (6.9 ± 0.5) and adults (6.5 ± 0.9) did not differ in friendship quality ($p > 0.25$).

**Table 4.1.** Age, Verbal IQ and Resistance to Peer Influence Scores. Verbal IQ of the *participant* groups were estimated with the vocabulary subtest of the WASI (Wechsler, 1999). *Participants* completed the resistance to peer influence questionnaire (RPI, Steinberg & Monahan, 2007).

| | | Age | | | | Verbal IQ[a] | | | RPI scores[c] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Age Group** | **n** | **Range** | **Mean** | **SD** | **n** | **Mean** | **SD** | **n** | **Mean** | **SD** |
| **Participants** | **Young adolescents** | 24 | 10.6 - 14.2 | 12.8 | 1.0 | 24 | 121.3 | 8.4 | 24 | 2.9 | 0.4 |
| | **Mid-adolescents** | 20 | 14.9 - 17.8 | 16.4 | 1.0 | 20 | 116.7 | 10.0 | 20 | 2.9 | 0.5 |
| | **Adults** | 18 | 21.8 - 34.9 | 27.3 | 3.7 | 16[b] | 117.6 | 10.7 | 18 | 3.1 | 0.3 |
| **Observers** | **Young adolescents** | 24 | 10.9 - 14.6 | 13.1 | 1.1 | | | | | | |
| | **Mid-adolescents** | 20 | 14.8 - 17.6 | 16.3 | 0.9 | | | | | | |
| | **Adults** | 18 | 22.4 - 31.4 | 26.5 | 2.7 | | | | | | |

[a] $p > 0.25$
[b] Verbal IQ was not collected for two adult *participants*.
[c] $p > 0.1$

To investigate whether audience effects within Age groups were related to differences in RPI or friendship quality, correlation analyses between these measures with the significant differences in audience effects were performed. However, none of the significant effects from the main analysis was correlated with RPI ($ps > 0.3$) or friendship quality scores ($ps > 0.1$).

## 4.4 Discussion

The current study investigated the effect of being observed by an audience, either a friend or an experimenter, on relational reasoning performance in adolescents and adults. The study revealed three main findings. *First*, being observed by a friend or an experimenter affected relational reasoning in adolescents, but not in adults. *Second*, performance in the mid-adolescent group (aged 14.9 - 17.8 years) was affected by the identity of the audience: independent of relational reasoning Task level, accuracy was lower and responses were slower when in the presence of a friend relative to the experimenter. *Third*, similar to mid-adolescents, young adolescents (aged 10.6 - 14.2 years) were also less accurate when being observed by a friend relative to the experimenter, however only in the Low-relational trials. Thus, the data in the current study suggest that there is an audience effect on relational reasoning, and this is critically dependent on the age of the *participants* and identity of the audience.

Numerous studies in social psychology have investigated audience effects on task performance in adults (for a review see Aiello & Douthitt, 2001; Zajonc, 1965). The general pattern found in these studies is a performance improvement in simple tasks and an impairment in complex tasks (C. F. Bond & Titus, 1983; Zajonc, 1965). However, as reviewed in the introduction (4.1) and 1.8.1, this classification of task difficulty is not straightforward since there are inconsistencies within the literature, likely due to the many different tasks, audiences and methods employed (C. F. Bond & Titus, 1983). In the current study, even though there was a significant interaction between the Social condition, Task level and Age group for the accuracy data; simple effects analysis revealed no improvement with an audience in the Low-relational condition. Mid-adolescents showed consistent accuracy and RT impairments in the Friend-present relative to the Experimenter-present condition both for the Low-relational and High-relational conditions and young adolescents' accuracy performance in this comparison was impaired for Low-relational trials only. Few studies have manipulated task difficulty within a single experiment; thus it is difficult to conclude that task level determines the direction of the audience effect (C. F. Bond & Titus, 1983; Guerin, 1993). In addition, the fact that relational reasoning is generally considered a high-level, complex task, might also explain why no performance improvements with an audience were found. The current study found no evidence that adults' relational reasoning performance was influenced by the presence of an audience. This lack of an audience effect in adults might be specific to this kind of reasoning task.

There is little experimental research on developmental changes in how peer influence affects cognitive performance, particularly in typically developing adolescents. In a sample of 9 - 14-year-olds with behavioural problems, performance in a relational reasoning task decreased in the presence of a classmate (Bevington & Wishart, 1999). However, in this sample it is difficult to disentangle the effects of the presence of the peer on performance from the effects of disruptive behaviour. In contrast, the current study design ensured that the *participant* and *observer* did not interact. Consequently, the decrease in performance with the friend relative to the experimenter in adolescents cannot be attributed to distracting behaviour of the friend.

Previous studies of relational reasoning showed performance improvements throughout late childhood and adolescence (Dumontheil, Houlton, et al., 2010; Rosso et al., 2004; Sternberg & Rifkin, 1979; Wendelken et al., 2011). Although not a primary aim of the study, the study examined developmental differences in relational reasoning abilities. The data showed no evidence of age-effects on this measure. The lack of developmental effects might be a consequence of the constant feedback provided to the *participant*, which has not been given in previous studies (Crone et al., 2009; Dumontheil, Houlton, et al., 2010), and/or the more lenient time limit of 40 s per trial (compared to 12 s in Crone et al., 2009; and 6 s in Wendelken et al., 2011).

Existing experimental studies examining the effects of social influence in adolescence are limited in number, and have predominantly focused on the influence of peers on risky and reward-related decision-making (Chein et al., 2011; Gardner & Steinberg, 2005; L. O'Brien et al., 2011; Reynolds et al., 2013). These studies have supported findings from questionnaire-based research, showing that adolescents are especially sensitive to peer influence. For example, adolescents but not adults took more risks when they were observed by peers compared to when alone (Gardner & Steinberg, 2005). The age-dependent pattern of performance in the current study is consistent with findings from studies on risky decision-making: the presence of an audience did not affect adult performance. In contrast, and also consistent with previous risk-taking studies, adolescents' relational reasoning performance was sensitive to the presence of an evaluative audience. Consequently, the current study has demonstrated that adolescents show a similar heightened sensitivity to peer influence on performance in a high-level cognitive task as they do when making risky or reward-related choices. A strength of the current study design was that in addition to comparing the effect of being observed by a peer to an alone condition, the effect of peer observation was also compared to a non-peer observation condition. This controlled for general (e.g. distracting) effects of having someone present when performing a task. Furthermore the current study demonstrates that, in addition to the age of *participants*, the relationship between the *participant* and the observer, i.e. whether the observer is a peer or a non-peer, appears to be a critical factor in the audience effect in adolescence.

A recent study demonstrated that, when adolescents believed they were being observed by a peer, they showed heightened autonomic arousal relative to both children and adults (Somerville et al., 2013). Relative to other Age groups, the current study found that mid-adolescents' performance was most strongly and consistently influenced by an audience. When observed by a friend relative to an experimenter they showed impairments in both accuracy and RT, across task difficulty levels. Young adolescents' accuracy was impaired by the observation of a friend relative to an experimenter in Low-relational trials only. Thus, there is stronger evidence for peer-related audience effects in the mid-adolescent group than the young adolescent group. Data from a questionnaire-based study showed that resistance to peer influence (RPI) increases most strongly between 14 - 18 years (Steinberg & Monahan, 2007), which might have predicted greater peer audience effects in young adolescents. However, here, the extent to which an individual *participant*'s performance was influenced by a peer audience was not correlated with *participant*'s RPI scores. Consequently, this questionnaire measure might be a better predictor of an individual's sensitivity to peer influence in the context of risky choices than of sensitivity to the presence of a peer audience when performing high-level cognitive tasks. Instead, the peer influence effects observed in the current study might be more related to fears of being judged by a peer. In the current study, fear of social evaluation was not measured, however, data from another study demonstrated that 15 - 18-year-olds were more afraid of social evaluation than 8 - 11-year-olds and 12 - 14-year-olds (Westenberg et al., 2004). Thus, stronger peer audience effects in the mid-adolescents compared to the young adolescents are consistent with heightened fear of social evaluation in mid-adolescents from this questionnaire-based study.

While it is unclear what mechanisms underlie performance differences under evaluative observation, three potential mechanisms are discussed in the following. *Firstly*, performance changes might occur as a result of changes in arousal in the presence of others (Zajonc, 1965). Autonomic arousal is increased in adolescents relative to both children and adults when being observed by a peer (Somerville et al., 2013) and increased arousal in adolescents in the presence of a peer might lead to developmental differences in audience effects. *Second*, 15 - 18-year-olds report elevated levels of fear of social evaluation relative to 12 - 14-year-olds and 8 - 11-year-olds (Westenberg et al., 2004). In the presence of peers, increased fear of social evaluation might lead to adolescents spending more time mentalising about how peers judge their intellectual abilities on the basis of their task performance. This might distract *participants* from the experimental task, resulting in an impairment of performance. Such distraction is arguably greater with a peer audience, as the current study controlled for general distraction caused by the presence of an observer by comparing a peer to a non-peer audience. *Third*, the presence of others could increase participants' self-awareness of potential discrepancies between their current and the ideal performance (Duval & Wicklund, 1972). This perceived discrepancy is thought to motivate performance improvement successfully in simple tasks; however in complex tasks excessive monitoring might impair performance. A recent study showed that, with increasing age, adolescents become increasingly aware of their own performance in a perceptual judgement task (Weil et al., 2013). In the reasoning task used in the current study, and in the presence of peers, increased self-awareness - particularly in mid-adolescents - may have led to a greater cognitive load due to excessive monitoring, and thus poorer performance. These three putative mechanisms should be investigated in future studies.

There were several limitations in this study. Both the adolescent and adult volunteers were from high-achieving academic backgrounds, resulting in a relatively high IQ sample. Although this benefitted the homogeneity of the sample, it limits the generalizability of the current study (see 7.1.1 and 7.2.1 for a general discussion). Future studies should test whether similar audience effects can be found in more academically diverse samples. Sample homogeneity also benefitted from the exclusively female sample. Questionnaire-based studies suggest that adolescent girls display higher levels of public self-consciousness (Rankin et al., 2004), place greater importance on peer approval for self-esteem (S. F. O'Brien & Bierman, 1988) and are more afraid of negative evaluation by peers (La Greca & Lopez, 1998; La Greca & Stone, 1993; Rudolph & Conley, 2005), than boys. This suggests that the developmental differences in peer audience effects reported in this study may be greater in females than in males. With more time and resources, a larger sample could have been tested, which would have allowed including sex as a between-subjects factor to analyse whether this is the case or whether adolescents in general show greater peer audience effects than adults. This could be assessed in future studies. The current study extends previous research on peer influence by including a second social observation condition, allowing to control for general effects of being observed. However, while the familiarity of the peer and non-peer was matched in adolescents and adults, the age difference between the peer and non-peer was not. Consequently, the current experimental design does not allow concluding whether the difference in age or the difference in familiarity between the peer or non-peer observer underlies the observed pattern of audience effects. This could also be addressed in future studies that fully balance these two factors of age and familiarity. Finally, the study draws on a relatively small sample size and further replications are needed.

Lessons, exams and homework are often carried out in the presence of other people – students, teachers, siblings and/or parents. In these situations, adolescents' performance is often either implicitly or explicitly evaluated by others. Although the current study did not test for audience effects in an educational setting, it demonstrated audience effects on relational reasoning, a cognitive capacity which is critical for children's learning and related to academic knowledge, reading and mathematics performance (Ferrer et al., 2009; Träff, 2013). The current study suggests that performance on a relational reasoning task in adolescence is sensitive to the identity of the person observing and evaluating their performance. This study extends findings from peer influence studies on risky- and reward-related decision-making by demonstrating that adolescents, compared to adults, also show heightened sensitivity to peer audience effects on a high-level cognitive task. The next chapter investigates whether this developmental pattern of sensitivity to peer influence effects is also generalizable to peer audience effects in a low-level perceptual task.

# CHAPTER 5: DEVELOPMENT OF THE AUDIENCE EFFECT ON VISUAL PERCEPTION TASK PERFORMANCE

*The previous chapter examined whether heightened levels of sensitivity to peer influence during adolescence, which have been shown for risky or reward-related decision-making, are also found for peer audience effects on a high-level cognitive task. This study demonstrated that adolescents' but not adults' relational reasoning performance was affected by a peer audience. The current chapter aims to examine how generalizable this developmental effect is by investigating whether a similar developmental pattern can be found for a low-level perceptual task. The same Age group and Audience factors were employed as in* ***Chapter 4****. Participants completed an object oddity task (Buckley, Booth, Rolls, & Gaffan, 2001), in which participants were asked to detect the 'odd one out' in an array of six displayed objects with varying Noise levels (High-noise versus Low-noise). There was limited evidence for an audience effect in this low-level perceptual task: the only audience effect found was an increase in RT in the Experimenter-present relative to the Alone condition. In contrast to the findings in* ***Chapter 4****, there were no developmental differences in peer audience effects on performance in this object oddity task between adolescents and adults.*

## 5.1 Introduction

The behavioural data presented in **Chapter 4** demonstrated that relational reasoning performance in adolescents but not adults was affected when being observed by an audience and that these effects were further dependent on the age of the adolescents, the identity of the audience (friend versus experimenter) and the task level. Mid-adolescents' performance was impaired in both accuracy and RT – across task difficulty levels - when being observed and evaluated by a friend relative to an experimenter. Young adolescents showed impairments in accuracy when under observation of a friend relative to an experimenter in low-relational trials only. These results extend findings from previous peer influence studies on risky and reward-related decision-making, which have suggested that adolescent relative to adult decision-making is particularly affected by the presence of peers (Chein et al., 2011; Gardner & Steinberg, 2005). The current study aimed to investigate whether this heightened adolescent sensitivity to the presence of peers is generalizable to performance in a low-level perceptual task.

This question was investigated in the object oddity task (Buckley et al., 2001), a perceptual discrimination task requiring *participants* to identify the 'odd one out' in an array of six object displays, of which five show the same object in different orientations and the sixth one shows a different object. As in **Chapter 4**, a group of young adolescents (aged 10.6 - 14.2 years), mid-adolescents (aged 14.9 - 17.8 years) and adults (aged 21.8 - 34.9 years) performed the task either without observation (Alone), under evaluative observation by their friend (Friend-present) or under evaluative observation by the experimenter (Experimenter-present). Task difficulty in the current study was manipulated by adding either a low level (Low-noise) or a high level (High-noise) of noise to the stimuli display.

It has been suggested that the general pattern for audience effects are improvements for simple or well-learned tasks and impairments for complex or learning tasks (C. F. Bond & Titus, 1983; Zajonc, 1965). However, as discussed in the **Chapter 4** and 1.8.1, there is a lack of a consistent classification system and only a small number of studies have manipulated task difficulty within the same paradigm. Consequently, it is not clear what property of task difficulty modulates the direction of the audience effect. The object oddity task, requiring low-level perceptual discriminations, could be considered a 'simple' task relative to the high-level relational reasoning task employed in **Chapter 4**. In this case, performance improvements might be found across Low- and High-noise trials with an audience. Alternatively, the intrinsic difficulty of a task, i.e. the average performance level of *participants* (in terms of accuracy and RT) for different task levels, might be critical for the direction of the effect and consequently audience effects might differ for the Low-noise and High-noise condition in the task.

Thus, the current study investigated how performance in a perceptual discrimination task is influenced by the presence of an observer. Further, the study examined whether increased levels of sensitivity to peer presence on risky and reward-related decision-making as well as on performance in a high-level cognitive task during adolescence, can be extended to the performance in a low-level perceptual task. Consequently, the study investigated whether young adolescents, mid-adolescents and adults would show differential audience effects on performance in the object oddity task and whether audience effects would be dependent on the identity of the observer.

## 5.2 Methods

### 5.2.1 Participants

The same group of *volunteer pairs* that completed the relational reasoning task in **Chapter 4** took part in the current study (see 4.2.1 and 4.2.2 for details about recruitment as well as verbal IQ, RPI ($\alpha = 0.67$) and friendship quality assessment ($\alpha = 0.95$)). From the object oddity task analysis, two young adolescent *participants* were excluded (due to mean RT or mean accuracy measures deviating more than 3 interquartile ranges from the lower or upper quartile of the *participants'* mean); thus the analysis included data from 22 young adolescents, 20 mid-adolescents and 20 adults (see Table 5.1 and 5.3.3 for ages, verbal IQ, RPI and friendship quality).

### 5.2.2 Experimental design

The study employed a 2 x 3 x 3 mixed factorial design in which there were two within-subjects factors: Noise level (Low-noise; High-noise), and Social condition (Friend-present; Experimenter-present; Alone); and one between-subjects factor: Age group (young adolescents; mid-adolescents; adults).

### *5.2.2.1 Object oddity task*

*Participants* were presented with six pictures of differently oriented objects, of which five views showed the same object and one showed a different object (i.e. the odd one out). The *participants* were instructed to identify the odd one out. Task stimuli were designed similar to the object oddity task used in Buckley et al. (2001). The stimuli comprised grey scale pictures of familiar objects (e.g. peppermill, scissors or fork). Three different sets of 20 object pairs (one set for each social condition session) were created by pairing 40 object pictures used by Buckley et al. (2001) and Lee et al. (2005) in terms of their brightness and size. Each pair of objects (e.g. object 1 and object 18) appeared twice within the session, once with object 1 as the odd one out, and once with object 18 as the odd one out, and once with Low-noise and once with High-noise. Noise level was manipulated by overlaying varying proportions of grey tone pixels on each individual stimulus. In the Low-noise condition, 30% of pixels from the original image were randomly selected and overlaid on the image to create the experimental stimulus (see Figure 5.1a). In the High-noise condition, 75% of pixels were overlaid (see Figure 5.1b).

In each trial *participants* were presented with an object oddity problem, in which they were asked to select the odd object out with a mouse response (see Figure 5.1c). Stimulus presentation was self-paced (although *participants* had a maximum of 20 s to respond). *Participants* were instructed to respond as quickly and accurately as possible. *Participants'* choices were subsequently highlighted in blue for 0.8 s and followed by feedback about accuracy and RT for 0.8 s.

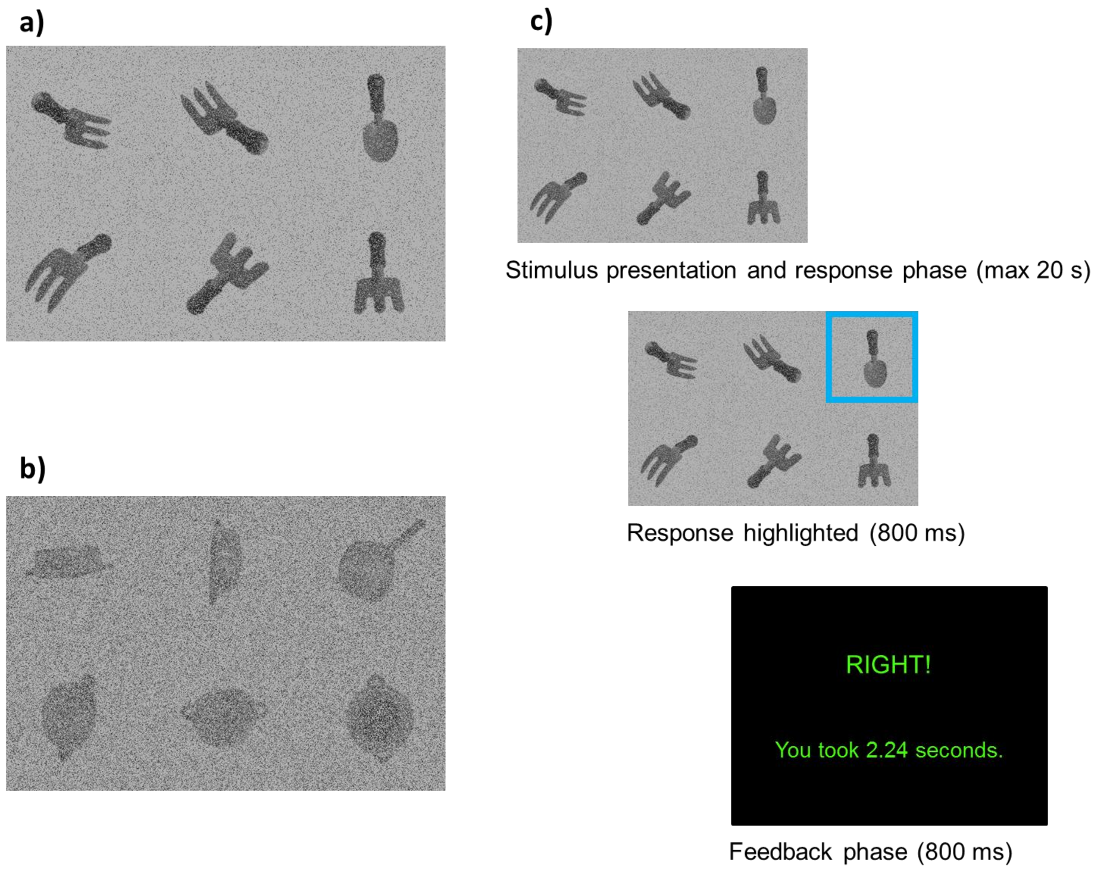


**Figure 5.1** Object Oddity Task a) Example of a Low-noise trial in which 30% noise was added to the stimulus set (the correct response is the upper right object). b) Example of a High-noise problem in which 75% noise was added to the stimulus set (the correct response is the upper right object). c) The stimuli were presented until the *participant* responded. Next, *participants'* responses were highlighted in blue. Finally, *participants* received feedback about their performance.

At the start of the testing session instructions were displayed on the screen and read out to the volunteer pairs. *Participants* then performed a practice session, consisting of five Low-noise and five High-noise trials. Stimuli were presented and responses recorded in Cogent 2000 (www.vislab.ucl.ac.uk/Cogent/index.html) implemented in Matlab R2010b (Mathworks Inc., Sherborn, MA).

### *5.2.2.2 Social conditions*

The three Social conditions (Friend-present; Experimenter-present; Alone) were manipulated in three different sessions, as described in **Chapter 4.** As in **Chapter 4**, the *observer* silently counted the number of wrong responses in the Friend-present condition (58/62 of the *observers* reported these correctly).

In each session, *participants* completed 2 sets of 10 Low-noise and 10 High-noise object oddity trials (ABAB or BABA, 40 trials per session). Presentation order (ABAB or BABA) was counterbalanced between *participants*. All *participants* saw the same three stimulus sets, each containing 40 unique stimuli in the first, second and third session (3 sessions x 40 stimuli = 120 unique stimuli). The order of the 20 Low-noise and 20 High-noise stimuli was randomised within each session, and the order of the social condition was counterbalanced between *participants*.

### 5.2.3 Data analysis

The current study investigated the effect of age on peer audience effects on a perceptual discrimination task by comparing a group of young adolescent, mid-adolescent and adult female participants. Reasons for the approach to employ age groups are discussed in 4.2.4.

Mean accuracy, and mean RT from correct trials, were analysed using 2 x 3 x 3 mixed-design ANOVAs with Noise level (Low-noise; High-noise) and Social condition (Alone; Experimenter-present; Friend-present) as within-subjects factors and Age group (young adolescents; mid-adolescents; adults) as between-subjects factor. Trials with RTs lying more than 3 interquartile ranges above or below the upper or lower quartile of all trials were excluded from the analysis (69 out of 7680 trials). Significant interactions with Noise level were followed up with repeated-measures ANOVAs for each Noise level separately, and post-hoc pairwise comparisons. One-way ANOVAs were employed to test for age-effects on verbal IQ, RPI and friendship quality. Marginally significant results ($p < 0.1$) are reported in the results, but only significant results ($p < 0.05$) are discussed further. Reported p-values are two-tailed.

## 5.3 Results

### 5.3.1 Accuracy

There was a main effect of Noise level ($F(1,59) = 268.84$; $p < 0.001$) with higher accuracy for Low-noise (96.6% ± 3.1) than for High-noise trials (83.1% ± 7.7). There was no main effect of Age group, nor an Age group by Noise level interaction (ps > 0.6). With regard to the influence of Social condition, there was no main effect of Social condition or significant interaction with Age group and, or Noise level (ps > 0.3).

To summarise, no audience effects on accuracy were observed in this perceptual object discrimination task.

### 5.3.2 Response times

There was a main effect of Noise level on RT ($F(1,59) = 428.84$; $p < 0.001$, Figure 5.2) with faster responses for Low-noise (1.88 s ± 0.39) than for High-noise trials (2.70 s ± 0.60). There was no main effect of Age group, nor an Age group by Noise level interaction (ps > 0.2). With regard to the influence of Social condition, there was no main effect of Social condition ($p > 0.1$) or Social condition by Age group interaction ($p > 0.4$). The analysis showed a Social condition x Noise level interaction ($F(2,118) = 3.82$; $p = 0.025$), which was further explored by separate one-way repeated-measures ANOVAs on the effect of Social condition within each Noise level. There was no significant effect of Social condition in the Low-noise condition ($p > 0.7$). In the High-noise condition, RT was significantly affected by Social condition ($F(2,122) = 3.69$; $p = 0.028$), with slower responses in the Experimenter-present condition than in the Alone condition ($t(61) = 2.79$; $p = 0.007$) and marginally slower responses in the Experimenter-present condition than in the Friend-present condition ($t(61) = 1.90$; $p = 0.062$). There was no significant difference between the Alone and the Friend-present condition ($p > 0.5$). The three-way interaction was not significant ($p > 0.8$).

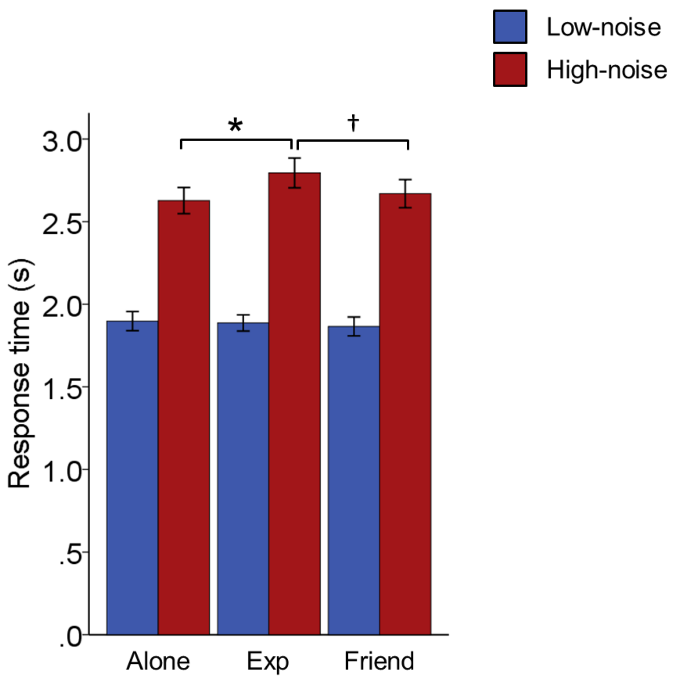


**Figure 5.2** Audience Effects on Object Oddity RT. RT data for correct trials (mean ± SE): there was a two-way interaction between Social condition and Noise level. Following up this two-way interaction, Social condition influenced RT only in the High-noise condition, with slower RTs in the Experimenter-present relative to the Alone condition and marginally slower RTs in the Experimenter-present relative to the Friend-present condition. Significant differences are represented by * ($p < 0.05$) and trends are represented by † ($p < 0.1$).

To summarise, across Age groups, participants showed slower response times in presence of the experimenter relative to being alone in the High-noise trials of this perceptual object discrimination task.

### 5.3.3 Questionnaire measures

The three Age groups did not differ significantly (Table 5.1) in their verbal IQ scores ($p > 0.15$). There was a marginally significant effect of Age group on RPI scores ($F(2,59) = 2.61$; $p = 0.08$). Young adolescents (combined friendship quality score: mean ± SD: 6.7 ± 0.7), mid-adolescents (6.9 ± 0.5) and adults (6.6 ± 0.9) did not differ in friendship quality ($p > 0.3$).

**Table 5.1:** Age, Verbal IQ and Resistance to Peer Influence Scores. Verbal IQ of the *participant* groups were estimated with the vocabulary subtest of the WASI (Wechsler, 1999). *Participants* completed the resistance to peer influence questionnaire (RPI, Steinberg & Monahan, 2007).

| | | Age | | | | Verbal IQ[a] | | | RPI scores[c] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Age Group** | **n** | **Range** | **Mean** | **SD** | **n** | **Mean** | **SD** | **n** | **Mean** | **SD** |
| **Participants** | Young adolescents | 22 | 10.6 - 14.2 | 12.8 | 1.0 | 22 | 121.9 | 8.5 | 22 | 2.8 | 0.4 |
| | Mid-adolescents | 20 | 14.9 - 17.8 | 16.4 | 1.0 | 20 | 116.7 | 10.0 | 20 | 2.9 | 0.5 |
| | Adults | 20 | 21.8 - 34.9 | 27.1 | 3.6 | 18[b] | 117.2 | 10.6 | 20 | 3.1 | 0.3 |
| **Observers** | Young adolescents | 22 | 10.9 - 14.6 | 13.0 | 1.1 | | | | | | |
| | Mid-adolescents | 20 | 14.8 - 17.6 | 16.3 | 0.9 | | | | | | |
| | Adults | 20 | 22.4 - 31.4 | 26.4 | 2.6 | | | | | | |

[a] $p > 0.15$

[b] Verbal IQ was not collected for two adult *participants*.

[c] $F(2,59) = 2.61$; $p = 0.08$

## 5.4 Discussion

This study investigated whether the developmental differences in peer audience effects observed in the relational reasoning task in **Chapter 4** are also found for a low-level perceptual task. Accuracy in the object oddity task was not affected by the presence of an audience. *Participants* were slower when being observed by the experimenter relative to being alone (and marginally so relative to being observed by a friend) in High-noise trials only, however this audience effect was not modulated by the age of *participants*. Thus, these findings suggest that, in contrast to the high-level relational reasoning task, there is less evidence for audience effects in a low-level perceptual task and, critically, there were no significant developmental differences.

The audience effect pattern that was found for the object discrimination task is quite different to the pattern in the relational reasoning task. A key difference between the two tasks is the cognitive load requirement. Both tasks require the processing of visual stimuli presented in an array. While the object oddity task simply requires the identification of an object as different from other objects, the relational reasoning task requires *participants* to analyse the relationships between the different stimuli, hold them in working memory, and integrate them to correctly solve the relational problem (Heekeren, Marrett, & Ungerleider, 2008; Krawczyk, 2012). In the object oddity task, RT impairments were only observed in the High-noise condition. In contrast, in the more cognitively demanding relational reasoning task, performance impairments in mid-adolescents were found for both accuracy and RT across task difficulty levels. These findings also support the theory that the difficulty level of a task matters for the direction of the audience effect (C. F. Bond & Titus, 1983; Zajonc, 1965). With the Low-noise condition of the object oddity task being a relatively simple task, performance improvements might have been expected. However, it is possible that a ceiling effect might have masked a potential improvement in accuracy in the Low-noise task. In addition, it is not clear whether audience effects are generally found for both RT (or response rate) and accuracy as often only one measure is reported (C. F. Bond & Titus, 1983; Guerin, 1993). Furthermore, when they are both reported, they do not necessarily both show an audience effect (e.g. Ito et al., 2011).

In the current study, across Age groups *participants* were slower in the High-noise condition when observed by the experimenter relative to being alone. In contrast, in the relational reasoning task in **Chapter 4**, mid-adolescents were slower with the friend relative to the experimenter (as well as when alone relative to the experimenter). RT impairments in the relational reasoning task in the Friend-present relative to the Experimenter-present condition were in the same direction as the accuracy impairments and thus suggest that the presence of a friend relative to the experimenter generally impaired performance. However, there were no audience effects on accuracy in the object oddity task; consequently it is difficult to interpret the finding of longer RTs in the current study, which might either reflect a distraction by the audience or *participants* simply trying harder in the presence of the experimenter.

One explanation for the presence of developmental differences in peer audience effects in the relational reasoning task found in **Chapter 4** and the absence of these in the object oddity task might be the different levels of cognitive load required to complete these tasks. As discussed in

4.4, poorer performance in the presence of peers during adolescence might be due to increased self-awareness (Duval & Wicklund, 1972; Weil et al., 2013), resulting in excessive performance monitoring and thus increased cognitive load. Cognitive load demands are higher in the relational reasoning task than the perceptual discrimination task; consequently additional cognitive load due the presence of peers might only affect performance in the relational reasoning task. This might explain the performance impairments found in the relational reasoning task in adolescence and the absence of peer audience effects in the object oddity task. In line with this interpretation are the findings from Ito et al. (2011): under evaluative observation by two experimenters relative to performing alone, accuracy in an n-back working memory task was only impaired in the highest working memory load condition (3-back), while performance in the 1-back and 2-back conditions was not affected. These findings suggest that in tasks with a high cognitive load – i.e. tasks with a high working memory requirements and/or requiring relational integration - the additional cognitive load resulting from the audience leads to performance impairments. In contrast, in tasks with lower cognitive load such as perceptual discrimination tasks or tasks with low working memory requirements, performance seems to be less affected by an audience.

Another explanation for the developmental difference in peer audience effects in the relational reasoning task and the object oddity task could be the heightened levels of fear of social evaluation during mid- to late adolescence (see 4.4, Westenberg et al., 2004). Adolescents might worry more about an evaluation of their logic abilities in the relational reasoning task compared to an evaluation of their visual discrimination abilities. As a result, adolescents might be more occupied mentalising about whether their friend thinks they are 'stupid' when making errors in the relational reasoning task than in a visual discrimination task. A larger number of off-task thoughts in the relational reasoning task relative to the object oddity task might lead to greater distraction and thus higher performance impairments in the presence of an evaluative peer audience.

To conclude, while increased levels of sensitivity to peer influence on risky and reward-related decision-making in adolescence relative to adulthood extend to an increased sensitivity to a peer audience on relational reasoning performance, this developmental pattern was not found for a low-level perceptual discrimination task. As discussed above, different cognitive load requirements or varying motivational salience to perform well in the tasks, might have contributed to the different developmental patterns in audience effects in the relational reasoning task from **Chapter 4** and the object oddity task in the current chapter.

While **Chapter 4** and the current chapter investigated behavioural differences in peer audience effects between adolescence and adulthood, **Chapter 6** investigates the development of the modulation of activation in a task-related network by a peer audience. With the absence of developmental changes in peer audience effects in the object oddity task and the presence of them in the relational reasoning task, **Chapter 6** examines the audience effects on the neural correlates of relational reasoning and their development between adolescence and adulthood.

# CHAPTER 6: AUDIENCE EFFECTS ON THE NEURAL CORRELATES OF RELATIONAL REASONING IN ADOLESCENCE

*Evidence from the behavioural study described in* ***Chapter 4*** *indicates that adolescents' relational reasoning performance is sensitive to being observed by peer audience, while adults' performance was not affected. This chapter investigates the peer audience effect on the neural correlates of relational reasoning. Relational reasoning tasks engage a fronto-parietal network including the inferior parietal cortex, pre-supplementary motor area, dorsolateral and rostrolateral prefrontal cortices. Using fMRI, peer audience effects on activation in this fronto-parietal network were compared in a group of 19 female mid-adolescents (aged 14 - 16 years) and 14 female adults (aged 23 - 28 years) employing a minimal, virtual peer audience manipulation (Somerville et al., 2013). Adolescent and adult relational reasoning accuracy was influenced by a peer audience as a function of task difficulty: the presence of a peer audience led to decreased accuracy in the complex, relational integration condition in both groups of participants. The fMRI results demonstrated that a peer audience differentially modulated activation in regions of the fronto-parietal network in adolescents and adults. Activation was increased in adolescents in the presence of a peer audience, while this was not the case in adults.*

## 6.1 Introduction

While previous studies investigating peer influence in adolescence have focussed on risky- or reward-related decision-making, **Chapter 4** examined peer audience effects on relational reasoning performance. Similar to the pattern observed for risky- and reward-related decision-making, adolescents also demonstrated greater sensitivity to peer audience effects in this high-level cognitive task than did adults. The current study aimed to investigate developmental changes in the effect of a peer audience on the neural correlates of relational reasoning. Previous peer influence studies have linked increased levels of risk-taking during adolescence to a modulation of reward-related activation by the presence of peers. When choosing whether to go or to stop in a driving game, adolescents (aged 14 - 18 years) activated reward-related regions (the VS and OFC) more in the presence of peers than when alone (Chein et al., 2011, see 1.6.2.1.2 for details). In contrast, activation patterns in young adults (aged 19 - 22 years) in these regions were not significantly affected by peer presence. A recent study also provided preliminary evidence that adolescents (aged 14 - 19 years) showed greater NAcc responses relative to adults when receiving a monetary reward under peer observation, while there was no developmental difference when participants were alone (A. R. Smith, Steinberg, et al., 2014). These studies suggest that the presence of peers modulates the activation of reward-related regions during adolescence. The current fMRI study examined whether there would also be developmental differences in the modulation of the recruitment of a high-level cognitive task network, such as relational reasoning, in the presence of an evaluative peer audience between adolescence and adulthood.

A recent fMRI study demonstrated that simply being told that a peer was watching via a camera while participants were lying in the scanner resulted in higher levels of reported embarrassment and greater activation in the mPFC – a key region of the social brain - in adolescents compared to children (Somerville et al., 2013, see 1.5.1). In addition, autonomic arousal levels, measured by skin conductance, were heightened in adolescents relative to both children and adults, suggesting that the presence of peers is particularly salient and arousing during adolescence. A similar minimal, virtual peer audience manipulation was employed in the current fMRI task to investigate the effect of an evaluative peer audience on performance and brain activity during a relational reasoning task.

Solving relational reasoning problems requires the generation of abstract mental relationships of features in a puzzle (e.g. a change in size, number or shape), and the integration of those relationships. Relational reasoning involves a fronto-parietal network including the inferior parietal lobule (IPL), the pre-supplementary motor area (preSMA), the dorsolateral prefrontal cortex (DLPFC) and the rostrolateral prefrontal cortex (RLPFC), the latter region being specifically associated with relational integration (Christoff et al., 2001; Crone et al., 2009; Dumontheil, Houlton, et al., 2010; Krawczyk, 2012). As relational reasoning abilities develop throughout childhood and adolescence, there is a concomitant developmental change in the activation pattern of this fronto-parietal network (Crone et al., 2009; Dumontheil, Houlton, et al., 2010; Eslinger et al., 2009; Wendelken et al., 2011 for a review see Dumontheil, 2014).

The current study examined the effect of being observed and evaluated by an unfamiliar peer on activation within a functionally defined relational-integration neural network, in a group of female mid-adolescents (14 - 16 years) and adults (23 - 28 years). A relational reasoning paradigm that has been employed in previous neuroimaging studies with adults and adolescents (Christoff, Ream, Geddes, & Gabrieli, 2003; Dumontheil, Houlton, et al., 2010; R. Smith, Keramatian, & Christoff, 2007; Wendelken et al., 2011) was adapted for the current study. The paradigm includes both a simple Control task, in which problems are solved by considering a single relation (one-relational) and a complex Relational task, in which two relations need to be jointly considered and integrated (two-relational). This allows a comparison between peer audience effects in simple and in complex versions of the task.

With regard to **behaviour**, the study *first* asked whether relational reasoning performance is affected when participants think they are being observed by a peer via a camera. Previous audience effect studies have shown differential audience effects for simple and complex tasks (C. F. Bond & Titus, 1983); consequently the study examined whether peer audience effects might differ between the relational integration task and the control task. *Second*, the study investigated whether the peer audience effect is different for adolescents and adults. Heightened peer audience effects on relational reasoning performance in adolescents relative to adults, which were described in **Chapter 4,** suggest that there might be greater audience effects in adolescents.

With regard to the **neuroimaging analysis**, it was *first* anticipated that a fronto-parietal network would be activated in the relational integration task relative to the control task, as has been previously shown, and that there might be developmental changes in this network (for a review Dumontheil, 2014). *Second*, the study investigated whether a peer audience modulates the activation within this relational-integration network. A voxel-wise analysis was conducted within the relational-integration network to identify task-related regions that are modulated by peer audience observation. At the time of designing the study, no published fMRI studies had investigated the effect of a peer audience on the neural correlates on a comparably high-level cognitive task. A NIRS study investigated the effect of an evaluative audience of two experimenters in a competitive scenario on an n-back working memory task in adults (Ito et al., 2011, see also 1.8.4). In the most difficult n-back condition (3-back), participants made more errors when in the social context (competitive audience condition) than when they were alone, and this behavioural difference was correlated with heightened activation in the prefrontal cortex in the 3-back condition compared to a baseline task. However, the audience condition of the study included a competitive component and a non-peer audience. Thus, it is not clear whether the current study would find similar effects and whether the peer audience would lead to increased or decreased activation in the relational reasoning network. *Third*, the study examined whether a peer audience modulates the activation of the relational-integration network differently for the manipulation of single relations (Control) or the integration of relations (Relational) and crucially whether this differs between adolescents and adults.

## 6.2 Methods

The paradigm used in this fMRI study was adapted from the behavioural study in Chapter 4. *First*, to simplify the design, the fMRI study only compared one adolescent group (instead of two groups) to an adult group. With mid-adolescents showing greater and more consistent audience effects on relational reasoning performance (see **Chapter 4**) than young adolescents, the adolescent sample was recruited to be approximately in the age range of the mid-adolescents from **Chapter 4**. Age effects were analysed in age groups rather than a continuous analysis of age in order to be able to compare the results better with those of **Chapter 4** and due to the restricted sample size in this fMRI study (see also 1.9 for a discussion of age analyses). *Second*, to further simplify the design, the Audience factor was reduced from three to two levels, i.e. comparing a Peer versus an Alone condition. This approach has also been adopted by previous fMRI studies investigating peer influence effects in a scanner environment (Chein et al., 2011; A. R. Smith, Steinberg, et al., 2014; Somerville et al., 2013). *Third*, the High-relational problems in the behavioural study in **Chapter 4** were designed to be substantially more difficult (higher RT and lower accuracy) than the Low-relational problems, in order to maximise an effect of Task level. However, this relatively large difference in RT between Low-relational and High-relational problems in the behavioural paradigm would result in highly variable block durations, which is not optimal for an fMRI task. Additionally, high error rates are also problematic in fMRI paradigms, as incorrect responses are usually excluded from the analysis. Consequently, the fMRI study employed a well-established relational reasoning paradigm, which has been used in previous studies in both adolescents and adults (Christoff et al., 2003; Dumontheil, Houlton, et al., 2010; R. Smith et al., 2007; Wendelken et al., 2011). Accuracy in this paradigm is relatively high (96% for the simple Control and 88% for the complex Relational task, in a sample of 11 - 30-year-olds (Dumontheil, Houlton, et al., 2010)) and the response window was fixed to 4 s. *Fourth*, in a recent study Somerville et al. (2013) employed a minimal, virtual, peer audience manipulation (see introduction), in which participants were simply told that they were being observed by an unfamiliar peer (which the participant never met) via a camera in the scanner. A similar approach was adopted in the current fMRI study.

### 6.2.1 Participants

Twenty-three female mid-adolescents and 18 female adults participated in the study. Data from 19 mid-adolescent participants (aged 14.2 - 16.7 years, mean ± SD = 15.5 ± 0.9) and

14 adult participants (aged 23.1 - 28.8 years, 24.8 ± 1.4) were included in the final analysis (see Debriefing section, 6.2.5). For details about participant recruitment see 3.2.1. Study procedures were approved by the local Research Ethics Committee. Adult participants and parents or legal guardians of adolescent participants gave their informed consent for the study. Participants were reimbursed £10 per hour for taking part in the study.

Age groups were assessed on the verbal IQ measure as described in 3.2.1. Adolescent (118.5 ± 8.4) and adult (121.4 ± 5.2) participants did not significantly differ in verbal IQ ($p > 0.25$). Participants also completed the resistance to peer influence questionnaire (RPI, see 4.2.2 for details about the questionnaire measure, Steinberg & Monahan, 2007). Adolescents (2.97 ± 0.22) and adults (3.08 ± 0.22) did not significantly differ in their RPI scores ($p > 0.15$).

### 6.2.2 Experimental design

The fMRI study employed a block design with two within-subjects factors: Task (Relational; Control) and Audience (Peer; Alone) and one between-subjects factor: Age group (adolescent; adult).

#### *6.2.2.1 Task factor*

The study employed a non-verbal relational reasoning task previously used by Dumontheil et al. (2010; adapted from Christoff et al., 2003; Smith et al., 2007). Methodological details can be seen in Figure 6.1 and Dumontheil et al. (2010). Briefly, relational reasoning puzzles comprised two pairs of geometrical items aligned in a two-by-two grid. These items varied in shape (six different shapes) and pattern (six different patterns). In the Control condition, participants were asked whether the bottom two items (identical in this condition) *matched* either of the top two items along a specified dimension (shape or pattern) (Figure 6.1a). In the Relational condition, participants were asked whether the top pair of items *varied* along the same dimension as the bottom pair of items (Figure 6.1b). Task instructions were given at the beginning of a Task block (Control: 'Match Shape' or 'Match Pattern'; Relational: 'Match Change') and in each trial a word cue in the middle of the screen reminded participants of the Task type. Participants entered 'yes' or 'no' responses with the index or middle finger of their right hand. Prior to scanning, participants were instructed on the task and trained to a criterion of 75% accuracy (all participants met this criterion after a few minutes of training (range: 1 min 46 s - 4 min 21 s)).

#### *6.2.2.2 Audience factor*

Before the experiment began, participants were told that an unfamiliar, similar-aged, same-sex peer would observe them and evaluate their performance at several points during the experiment via a camera mounted near the participant's face in the scanner. The peer was described as a work-experience student from a secondary school to the adolescent participants and as a junior post-graduate student to adult participants; the intention of this manipulation was to convince each participant that they and their performance would sometimes be observed by an unknown peer of around their own age. Prior to each Audience block, a screen indicated whether the camera was turning on (Peer condition, flashing green light, Figure 6.1c) or the camera was off (Alone condition, constant red light, Figure 6.1d). During each Audience block a constant green or red light reminded participants whether the camera was on or off. A similar camera manipulation has been previously used by Somerville et al. (2013).

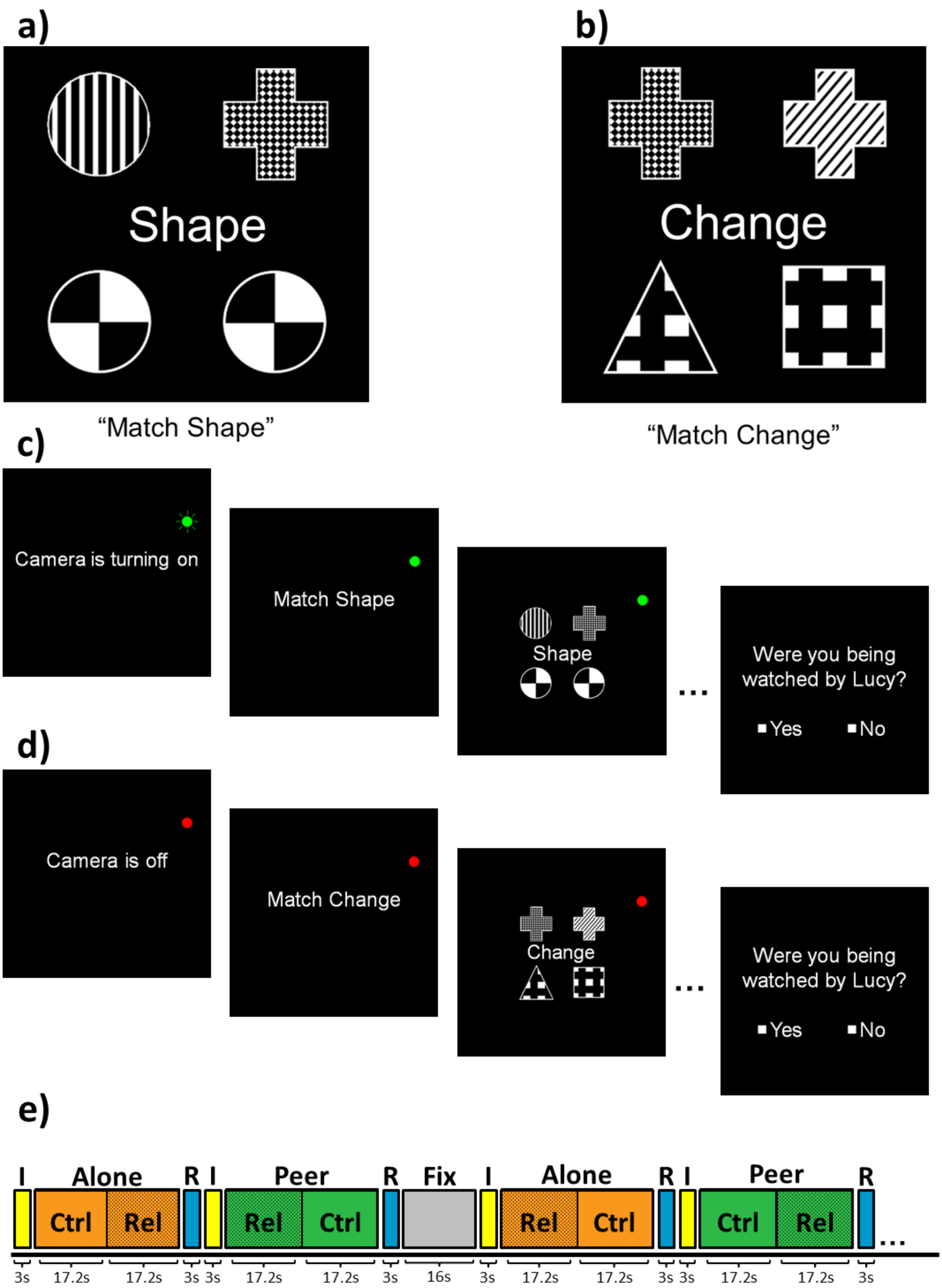


**Figure 6.1**: Relational reasoning task and peer audience manipulation. The instructions: 'Shape', 'Pattern' or 'Change' appeared in the middle of the screen in each trial to remind participants of the task they were performing. **a)** Example of a **Control** condition trial: participants were asked if either of the top two items are the same shape (or pattern) as the bottom two items. In this 'Match Shape' example, the top left item is the same shape (circle) as the bottom two items, thus the answer is 'yes'. **b)** Example of a **Relational** condition trial: participants were asked if the top two items change in the same way as the bottom two items. Here, the top pair differs in the 'pattern'

dimension, while the bottom pair differs in the 'shape' dimension, thus the answer is 'no'. **c)** Example of a **Peer** block: Prior to the Peer block, a screen along with a green, flashing light informed participants that the camera was turning on. Throughout the rest of the Peer block a green, constant light reminded participants that the camera was on. **d)** Example of an **Alone** block: Prior to the Alone block, a screen informed participants that the camera was off, along with a constant red light that was present throughout the Alone block. **e)** In each session, participants performed ten alternating Audience blocks (five **Peer** and five **Alone**). Prior to each Audience block, participants viewed an instruction screen (**I** in Figure) indicating whether the camera was turning on (Peer) or was off (Alone). Following an Audience block, participants were asked whether or not they had been observed (Camera rating, **R** in Figure). After every second Audience block there was a Fixation baseline block (**Fix**). Each Audience block contained one Control block (**Ctrl**, 4 trials) and one Relational block (**Rel**, 4 trials). Five Audience blocks started with a Control block and five with a Relational block; this was randomized within a session.

Participants were told that the peer would be observing them and evaluating their performance when the camera was on, but not when the camera was off. The camera, which was directed towards the participant's face in the scanner, was pointed out to participants while they were being prepared for the scanning session. To enhance the credibility of the audience manipulation, participants performed a practice session inside the scanner. The alleged goal of this practice session was to test whether the camera connection with the peer was working, which was always positively confirmed after this brief practice. In order to make sure participants were paying attention to the Audience manipulation, participants were asked to indicate by a button press ('yes' or 'no') after each Audience block whether or not they had been observed ('Camera rating'). They were told their responses to this question were required for the peer to know which sessions' data to evaluate afterwards.

#### *6.2.2.3 Block design*

Participants performed two sessions of the relational reasoning task, each comprising ten alternating Audience blocks (five Peer and five Alone, Figure 6.1e). Whether a session started with a Peer or an Alone block was counterbalanced across the two sessions within and between subjects. After every two Audience blocks, there was a fixation baseline block (16 s, 4 per session). Each Audience block lasted 34.4 s and was preceded by a 3 s information screen about the status of the camera, and followed by 3 s window for participants to input whether the camera had been on or off ('Camera rating'). Within each Audience block, there was one Control block and one Relational block each lasting 16 s, consisting of 4 trials preceded by a 1.2 s Task block instruction screen. Participants equally often started an Audience block with a Relational or a Control block, and this was randomized within a session. Participants had a maximum of 4 s to input their response on each trial, during which time the stimulus was displayed for 3.5 s and followed by a blank screen for 0.5 s.

### 6.2.3 Data acquisition

Brain imaging data were acquired on a Siemens Avanto 1.5 Tesla MRI scanner (Erlangen, Germany). For details about the acquisition parameters and testing set-up see 3.2.3. Functional data were acquired in two sessions each lasting 8 min 6 s. In each session, 162 volumes were collected and each volume comprised 35 axial slices (in-plane resolution: 3 x 3 x 3 mm) covering most of the cerebrum. The task was presented and responses were acquired with Cogent 2000 (www.vislab.ucl.ac.uk/Cogent/index.html) using Matlab R2010b (Mathwork Inc. Sherborn, MA).

### 6.2.4 Data analysis

#### *6.2.4.1 Behavioural analysis*

Behavioural data were analysed with SPSS 21 (Armonk, NY: IBM Corp.). Mean accuracy, mean RT (correct trials only) and RT variability (SD) (all trials) were calculated for each participant in each condition. Separate 2 x 2 x 2 mixed-design ANOVAs with Audience (Alone; Peer) and Task (Control; Relational) as within-subjects factors and Age group (adolescents; adults) as between-subjects factor were employed to analyse each of these three measures. Reported p-values are two-tailed.

*6.2.4.2 fMRI data analysis*

Functional imaging data were preprocessed and analysed using SPM8 (Statistical Parametric Mapping, Wellcome Trust Centre for Neuroimaging, http://www.fil.ion.ucl.ac.uk/spm/). For details about the preprocessing steps and movement correction see 3.2.4.2.

Scanning sessions with more than 10% of volumes censored or a RMS movement over the whole session greater than 1.5 mm (one session for two adolescent participants) were excluded from the analysis. Adolescent and adult participants did not significantly differ in the number of censored volumes (adolescents = 2.32 ± 3.99, adults = 1.64 ± 3.39; $p > 0.6$), mean RMS movement (adolescents = 0.25 mm ± 0.09, adults = 0.26 mm ± 0.09; $p > 0.8$) or mean FD (adolescents = 0.12 mm ± 0.03, adults = 0.11 mm ± 0.05; $p > 0.6$).

Scanning sessions were treated as separate time series and each series was modelled by a set of regressors in the GLM. The GLM included seven box-car regressors (four task conditions, Instructions, Camera-rating, and Fixation) and one event-related regressor for errors per session, which were convolved with a canonical haemodynamic response function. Censored volumes (FD > 0.9) were modelled as separate regressors in the GLM. Data were high-pass filtered (128 s). Resulting parameter estimates were used to create four contrasts comparing each of the four task conditions to the fixation baseline. These contrasts were then entered into a random-effects analysis using a Subject x Age Group x Condition flexible factorial design, modelling all three factors as main effects (the Subject factor was included to account for the repeated-measure nature of the data) and an Age Group x Condition interaction. *First*, the relational-integration network was functionally defined as voxels which were significantly activated in the Relational>Control contrast (voxel-level $p < 0.001$ uncorrected, cluster-level $p_{FWE} < 0.05$ corrected). *Second*, a voxel-wise ANOVA was conducted to test for a modulation within this relational-integration network by Age group, Audience and/or Task. Voxel-wise analysis was performed to test for regions within the relational-integration network that showed age-related differences in activation during relational integration (Age group x Task interaction). The main research question was investigated by testing for regions in the relational-integration network in which activation was modulated by Audience differently in the two Age groups (Audience x Age group interaction), and whether this was additionally modulated by the Task factor (Audience x Age group x Task interaction). This is an unbiased method as all interaction analyses performed in the relational-integration network are orthogonal to the Task main effect (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). In addition, a voxel-wise two-sample t-test including the behavioural audience effect as covariate of interest was performed to test whether the magnitude of the behavioural audience effect was correlated with individual differences in activation in the audience main effect. *Finally*, a correlation analysis between RPI scores and individual differences in activation in the audience main effect was performed.

The results are reported if significant at voxel level $p < 0.001$ uncorrected and cluster-level corrected at $p_{FWE} < 0.05$ or voxel-level corrected at $p_{FWE} < 0.05$. Anatomic labelling of activity clusters was performed using AAL (Tzourio-Mazoyer et al., 2002). Coordinates are listed in MNI space. Significant interactions were followed up by extracting the mean signal across all voxels of significant clusters with MarsBaR (Brett et al., 2002) and analysing simple effects in SPSS using t-tests (with Bonferroni correction for multiple comparisons).

### 6.2.5 Debriefing

After the study, participants were called on the phone and asked what they thought about being watched by the unfamiliar peer in the experiment. Participants were then informed that, in fact, no one had been observing their performance in the scanner. Participants who reported that they doubted during the experiment that they were being watched by the peer were not included in the analysis (included participants: n = 19/23 adolescents, n = 14/18 adults).

## 6.3 Results

### 6.3.1 Behavioural results

Accuracy and RT data were analysed with 2 (Audience) x 2 (Task) x 2 (Age group) mixed-design ANOVAs. For **accuracy** (see Table 6.1), there was a main effect of Task: participants were less accurate in the Relational (mean accuracy: 90.5% ± 7.6) relative to the Control condition (96.1% ± 3.0; $F(1,31) = 22.98$; $p < 0.001$, Figure 6.2). There was no main effect of either Audience ($p > 0.2$) or Age group ($p > 0.8$). There was a two-way interaction between Task and Audience ($F(1,31) = 5.98$; $p = 0.020$, Figure 6.2), which was driven by a significant decrease in accuracy in the Peer (89.1% ± 9.3) relative to the Alone condition for the Relational condition (92.0% ± 7.1; $t(32) = 2.52$; $p = 0.017$), but no significant difference between Peer versus Alone for the Control condition ($p > 0.15$). The Audience x Age group interaction ($p > 0.7$) and the

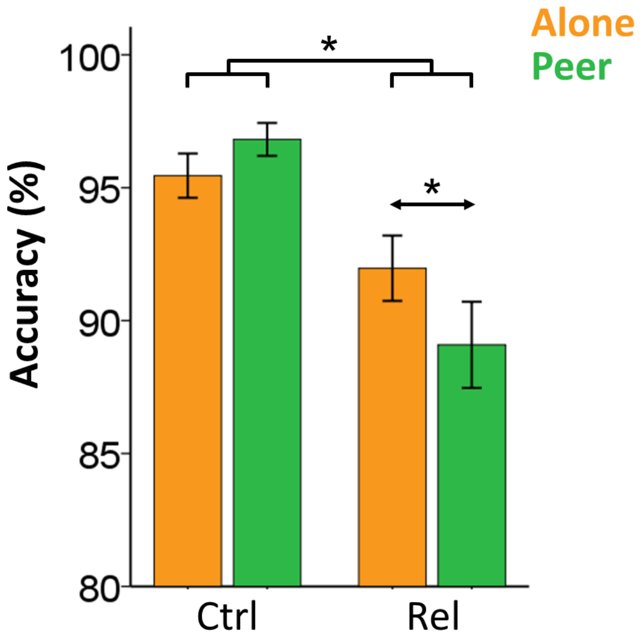


**Figure 6.2**: Behavioural audience effect. Accuracy data (mean ± between-subject SE): There was a significant Audience x Task interaction. Accuracy in the Relational condition in adolescents and adults was reduced in the presence of a peer audience relative to being alone. The increase in accuracy in the Control condition was not significant. Significant differences are represented by * ($p < 0.05$).

three-way interaction between Task, Audience and Age group ($p > 0.6$) were not significant. There was a marginally significant interaction between Task and Age group ($F(1,31) = 3.12$; $p = 0.087$).

For the **RT** data (see Table 6.1), there was a main effect of Task: participants were slower in the Relational (mean RT: 2008 ms ± 233) relative to the Control condition (1472 ms ± 190; $F(1,31) = 210.27$; $p < 0.001$). There were no other significant main effects or interactions for the RT data (all ps > 0.2). For the **RT variability** data (see Table 6.1), there was a main effect of Task: participants' RTs were less variable in the Control (SD RT: 453 ms ± 114) relative to the Relational condition (549 ms ± 113; $F(1,31) = 37.57$; $p < 0.001$). The main effects of Age group ($p > 0.9$) and Audience ($p > 0.3$) were not significant. The Task x Age group interaction ($p > 0.2$), the Audience x Age group interaction ($p > 0.6$) and the three-way interaction ($p > 0.3$) were not significant. There was a marginally significant interaction between Task and Audience ($F(1,31) = 3.11$; $p = 0.088$).

**Table 6.1**: Accuracy, RT and RT variability data in the relational reasoning task (mean and SD for the four conditions and the two Age groups).

| | | Control Alone | | Relational Alone | | Control Peer | | Relational Peer | |
|---|---|---|---|---|---|---|---|---|---|
| | | **Mean** | **SD** | **Mean** | **SD** | **Mean** | **SD** | **Mean** | **SD** |
| **Accuracy** | **Adolescents** | 94.74 | 5.71 | 92.76 | 6.34 | 95.92 | 3.56 | 90.39 | 7.87 |
| **(%)** | **Adults** | 96.43 | 3.06 | 90.89 | 8.06 | 98.04 | 3.28 | 87.32 | 11.03 |
| **RT** | **Adolescents** | 1453 | 247 | 1938 | 245 | 1481 | 208 | 1995 | 257 |
| **(ms)** | **Adults** | 1498 | 149 | 2055 | 195 | 1460 | 241 | 2075 | 248 |
| **RT variability** | **Adolescents** | 443 | 125 | 542 | 121 | 450 | 146 | 572 | 165 |
| **(ms)** | **Adults** | 479 | 99 | 515 | 88 | 446 | 127 | 561 | 110 |

### 6.3.2 fMRI results

#### *6.3.2.1 Definition of the relational-integration network*

In the first step of analysis, the relational-integration network was defined as the areas activated in the main effect of Task (Relational>Control), combined across Age groups. This contrast revealed activations in the preSMA, bilateral inferior and superior parietal lobules including the supramarginal gyrus, bilateral occipital cortex and two large bilateral frontal clusters extending from the middle frontal gyrus, inferior frontal sulcus and inferior frontal gyrus into the RLPFC (Table 6.2, Figure 6.3).

Voxel-wise ANOVAs were then performed to test for a modulation within this relational-integration network by Age group, Audience and/or Task.

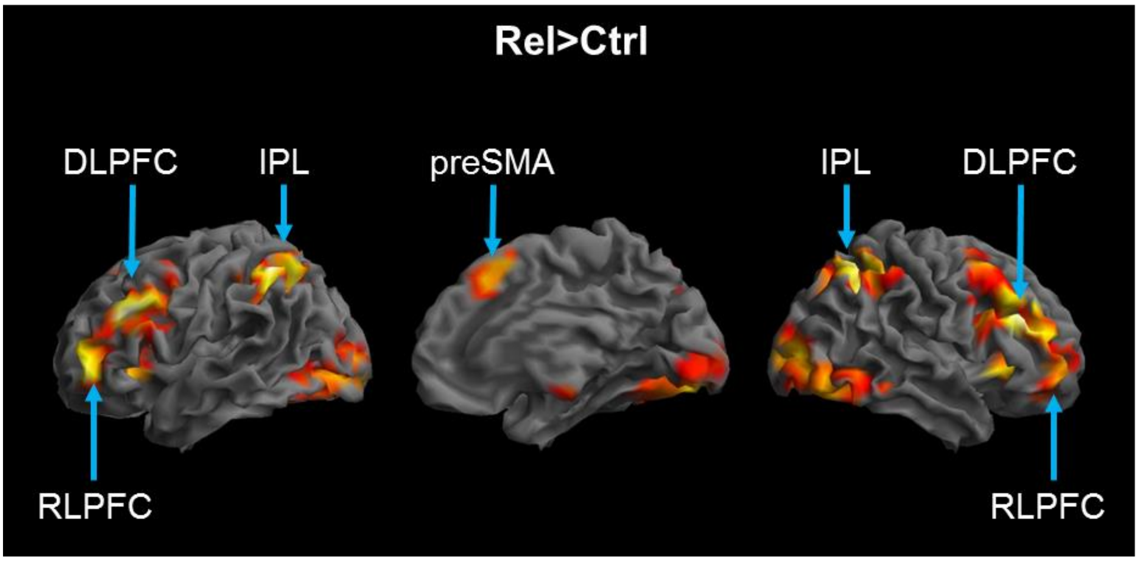


**Figure 6.3:** Relational-integration task network. The relational-integration network was defined as the main contrast: Relational>Control (voxel-level uncorrected $p < 0.001$, cluster-level corrected at $p_{FWE} < 0.05$) across the average of the two Age groups; the statistical map is rendered on the left, medial and right brain surfaces (left, middle and right panels respectively).

**Table 6.2:** Relational-integration network**.** Main effect of Task (Relational>Control; voxel-level uncorrected $p < 0.001$, cluster-level corrected at $p_{FWE} < 0.05$)

| Cluster | Brain region | Size (Voxel) | Z | Peak voxel (in mm) | | |
|---|---|---|---|---|---|---|
| | | | | x | y | z |
| **Left frontal** | **Inferior frontal gyrus (pars triangularis)** | **1344** | **>8** | **-48** | **26** | **28** |
| | Middle frontal gyrus (orbital part) | | 7.59 | -48 | 50 | -5 |
| | Middle frontal gyrus | | 6.53 | -39 | 53 | 7 |
| **Left parietal** | **Inferior parietal lobule** | **750** | **7.71** | **-45** | **-49** | **55** |
| | Inferior parietal lobule | | 7.30 | -42 | -43 | 40 |
| **Right frontal** | **Inferior frontal gyrus (pars triangularis)** | **1621** | **7.57** | **45** | **32** | **25** |
| | Insula | | 6.58 | 33 | 23 | -2 |
| | Superior frontal gyrus (orbital part) | | 6.14 | 21 | 44 | -11 |
| **Bilateral occipital** | **Lingual gyrus** | **2441** | **7.42** | **21** | **-85** | **-5** |
| | Middle occipital gyrus | | 7.02 | -18 | -91 | -2 |
| | Inferior occipital gyrus | | 6.54 | 45 | -70 | -17 |
| **Right parietal** | **Superior parietal lobule** | **963** | **7.18** | **39** | **-55** | **55** |
| | Angular gyrus | | 6.96 | 33 | -58 | 43 |
| | Inferior parietal lobule | | 6.86 | 42 | -43 | 43 |
| **Bilateral preSMA** | **preSMA** | **324** | **6.38** | **-3** | **17** | **52** |

### *6.3.2.2 Developmental changes in relational reasoning activation*

No regions within the relational-integration network showed an Age group x Task interaction at cluster-level correction ($p_{FWE} < 0.05$). At voxel-level correction ($p_{FWE} < 0.05$), the only difference between Age groups was a cluster in the lateral inferior frontal cortex ([-54, 17, 16], k = 43; Z = 4.24; $p_{FWE} = 0.032$, Figure 6.4), which showed increased activation in adults relative to adolescents in the Relational>Control contrast.

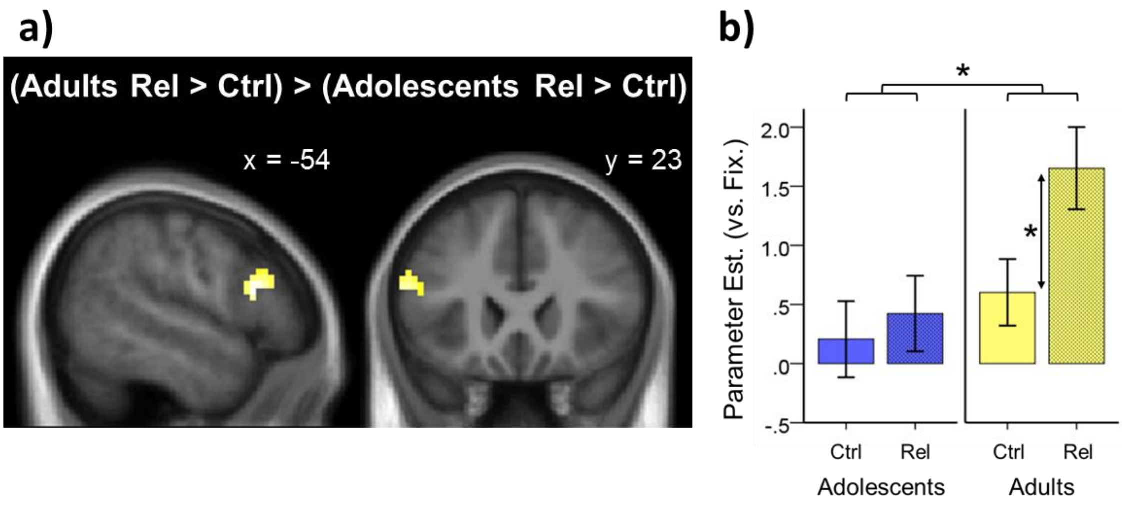


**Figure 6.4:** Interaction between Age group and Task in the inferior lateral frontal cortex. Age differences in Relational versus Control activation were tested within the relational-integration network. a) Brain activation in the Age group x Task interaction in the left inferior lateral frontal cortex (voxel-level $p_{FWE} < 0.05$; k = 43). The cluster is plotted on the average structural brain of the 33 participants. b) Activation in the left inferior lateral frontal cluster was greater in the Relational>Control contrast in adults compared to adolescents. The bar charts represent mean parameter estimates of the left inferior lateral frontal cortex cluster in the Control and Relational condition (averaging across the Alone and Peer condition) against Fixation (mean ± between-subject SE). Significant differences are represented by * (p < 0.05).

### *6.3.2.3 Developmental changes in the audience effect*

No regions in the relational-integration network showed a significant modulation of activation by Audience across Age group (no main effect of Audience or Task x Audience interaction). However, the analysis of the interaction between Audience and Age group revealed significant bilateral frontal clusters (inferior and middle frontal cortex), bilateral parietal clusters (inferior and superior parietal cortex), bilateral occipital clusters extending into the temporal cortex and a bilateral preSMA cluster (Table 6.3, Figure 6.5). The three-way interaction between Age group, Audience and Task showed no significant clusters, indicating that the Audience by Age group interaction was not further modulated by Task and that the peer audience affected activation both in the Control and the Relational task similarly. Paired t-tests ran on mean parameter estimates from the nine Audience x Age group clusters showed a consistent pattern in all clusters: adolescents activated these regions more when being observed by the Peer relative to when Alone, while adults showed the reverse effect (note that most of the adolescent effects survived Bonferroni correction for multiple comparisons, while adult effects did not; see Table 6.3 for pair-wise comparisons statistics). No regions were more activated in adults relative to adolescents in the Peer>Alone contrast.

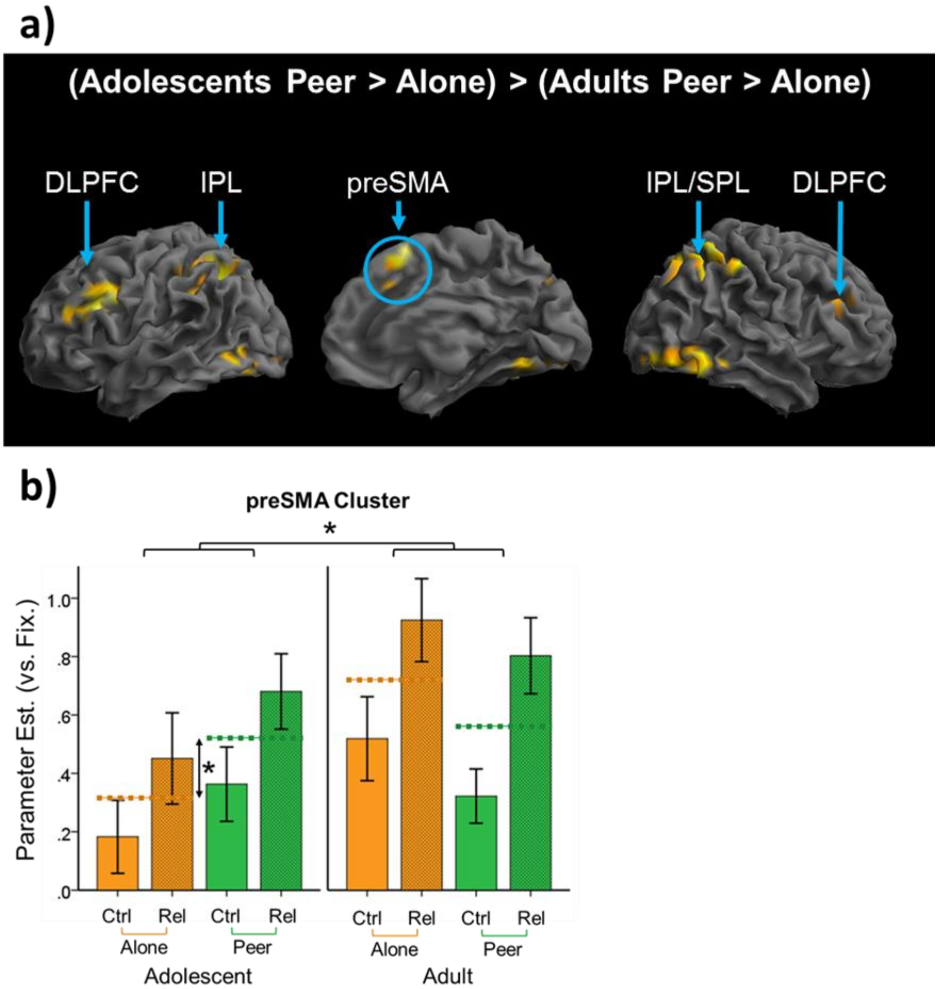


**Figure 6.5:** Peer audience effect on relational reasoning task activation. Differential modulation of the activation in the relational-integration network by a peer audience in adolescents and adults. a) The statistical map (voxel-level uncorrected $p < 0.001$, cluster-level corrected at $p_{FWE} < 0.05$) shows activation demonstrating an Audience x Age group interaction in several regions including: bilateral frontal clusters (inferior and middle frontal cortex), bilateral parietal clusters (inferior and superior parietal cortex), bilateral occipito-temporal clusters and a bilateral preSMA cluster. b) All Age group x Audience clusters showed a consistent activation pattern, exemplified here for the preSMA cluster. Adolescents showed increased recruitment when being observed relative to when alone (pairwise comparisons in the bilateral occipito-temporal, preSMA, right frontal and right parietal clusters survive Bonferroni correction). In contrast, adults showed decreased recruitment (although note this decrease did not survive Bonferroni correction for the multiple regions included in this analysis). The bar charts represent mean parameter estimates of the preSMA Age group x Audience cluster in each task condition plotted against Fixation (mean ± between-subject SE). The horizontal dotted lines represent the average parameter estimates of Control and Relational tasks combined against Fixation, illustrating the Age group x Audience interaction. Significant differences are represented by * ($p < 0.05$).

**Table 6.3:** Developmental changes in the effect of Audience in the relational-integration network**.** Regions within the relational-integration network showing an Audience x Age group interaction (contrast: [(Adolescent Peer > Adolescent Alone) > (Adult Peer > Adult Alone)]; voxel-level uncorrected $p < 0.001$, cluster-level corrected at $p_{FWE} < 0.05$ or [a] voxel-level corrected at $p_{FWE} < 0.05$). The columns on the far right provide the p-values for the pairwise comparisons of Peer versus Alone in each Age group using the mean parameter estimates of each cluster ([b] survive Bonferroni correction). Adol. : Adolescents.

| Cluster | Brain region | Size (Voxel) | Z | Peak voxel (in mm) | | | p-value of pairwise comparison (Peer versus Alone) | |
|---|---|---|---|---|---|---|---|---|
| | | | | x | y | z | Adol. | Adults |
| **Left parietal** | **Inferior parietal lobule** | **408** | **5.15** | **-33** | **-52** | **43** | 0.004 | 0.004 |
| | Superior occipital cortex | | 4.23 | -24 | -67 | 28 | | |
| | Superior parietal lobule | | 4.08 | -15 | -64 | 49 | | |
| **Left frontal** | **Inferior frontal gyrus (pars opercularis)** | **307** | **4.92** | **-39** | **11** | **28** | 0.003 | 0.003 |
| | Middle frontal gyrus | | 4.26 | -45 | 35 | 19 | | |
| **Right parietal** | **Superior parietal lobule** | **424** | **4.68** | **42** | **-49** | **61** | 0.002 [b] | 0.025 |
| | Inferior parietal lobule | | 4.10 | 36 | -52 | 46 | | |
| | Precuneus | | 3.96 | 12 | -67 | 49 | | |
| **Bilateral preSMA** | **preSMA** | **184** | **4.52** | **3** | **14** | **58** | 0.001 [b] | 0.012 |
| | Medial superior frontal gyrus | | 3.76 | -6 | 23 | 37 | | |
| | Medial superior frontal gyrus | | 3.61 | 3 | 26 | 37 | | |
| **Right occipito-temporal** | **Inferior temporal gyrus** | **262** | **4.49** | **51** | **-55** | **-20** | 0.002 [b] | 0.043 |
| | Inferior occipital gyrus | | 4.16 | 39 | -85 | -14 | | |
| | Fusiform gyrus | | 3.98 | 27 | -61 | -14 | | |
| **Left occipito-temporal** | **Fusiform gyrus** | **126** | **4.47** | **-27** | **-64** | **-17** | 0.002 [b] | 0.028 |
| | Inferior temporal gyrus | | 4.25 | -45 | -61 | -11 | | |
| | Inferior occipital gyrus | | 3.86 | -45 | -73 | -14 | | |
| **Left occipital** | **Lingual gyrus** | **50** | **3.96** | **-18** | **-82** | **1** | 0.008 | 0.023 |
| | Superior occipital gyrus | | 3.42 | -9 | -97 | 4 | | |
| | Lingual gyrus | | 3.16 | -12 | -91 | -11 | | |
| **Right frontal** | **Inferior frontal gyrus (pars triangularis)** | **54** | **3.78** | **42** | **29** | **28** | 0.001 [b] | 0.014 |
| **Left orbitofrontal [a]** | **Inferior frontal gyrus (orbital part)** | **23** | **4.39** | **-30** | **29** | **-5** | 0.003 | 0.008 |

### *6.3.2.4 Correlation between BOLD signal and behaviour*

A final series of voxel-wise analyses assessed whether individual differences in the neural correlates of the Audience effect were associated with the effect of Audience on accuracy, or individual RPI scores, across the whole sample or within the adolescent or adult group separately. Correlation analysis assessed whether the effect of Audience on performance – i.e. the decrease in accuracy in the Relational condition when the participant was observed versus alone – was related to the effect of peer audience on the activation in the Relational versus Fixation contrast. No significant clusters were found in this analysis. In a second analysis, there were no significant clusters in the Peer>Alone contrast that correlated with the RPI scores of participants.

## 6.4 Discussion

This study investigated how observation by a peer affects behavioural performance and neural activation during a high-level cognitive task in female mid-adolescents and young adults. The peer audience manipulation affected performance in the relational reasoning task, specifically in the condition requiring relational integration: both adolescents and adults showed a decrease in accuracy in the Relational task when being observed by a Peer relative to when Alone. Supporting previous studies (Christoff et al., 2003; Crone et al., 2009; Dumontheil, Houlton, et al., 2010), a fronto-parietal network of regions was activated during relational integration (Relational condition) in comparison to when participants had to consider only a single relation (Control condition). Only one region showed a developmental change in relational reasoning activation: adults activated the left inferior lateral PFC in the Relational relative to the Control condition more than did adolescents. Finally, the fMRI analysis revealed that several regions within the relational-integration network were modulated by the peer audience manipulation and that this effect was dependent on the Age group of the participants.

### 6.4.1 Relational-integration task network

In order to analyse the modulation of the relational-integration network by age and by peer audience, this network was first functionally defined as the regions activated in the Relational condition relative to the Control condition. This contrast revealed a fronto-parietal task network, extending anteriorly into the RLPFC, which is typically and robustly found in fMRI studies of relational integration (Christoff et al., 2003; Crone et al., 2009; Dumontheil, Houlton, et al., 2010; Krawczyk, 2012; R. Smith et al., 2007; Wendelken et al., 2011).

### 6.4.2 Developmental changes in the main effect of Task

The current study employed a relational reasoning paradigm (Christoff et al., 2003; R. Smith et al., 2007) that has previously been used to investigate the development of neural activation associated with relational reasoning (Dumontheil, Houlton, et al., 2010; Wendelken et al., 2011). These and other developmental studies have found improvement in relational integration abilities between late childhood (8 - 12 years) and adulthood (Crone et al., 2009) and within late childhood and adolescence (7 - 18 years, Wendelken et al., 2011). An analysis of longitudinal data demonstrated that improvements of fluid reasoning abilities are greatest in childhood and become smaller in adolescence (McArdle, Ferrer-Caja, Hamagami, & Woodcock, 2002). Improvements between mid-adolescence and adulthood are more difficult to detect, especially when the task only requires the integration of a maximum of two dimensions and smaller samples of participants are employed (Dumontheil, Houlton, et al., 2010, Experiment 2). Consistent with these previous results, the current study did not find significant developmental changes in performance between mid-adolescence and early adulthood.

Neuroimaging studies have reported developmental changes in the activation pattern of the fronto-parietal network involved in relational integration (for a review Dumontheil, 2014). Wendelken et al. (2011) found increasing specificity with age in left RLPFC and bilateral IPL activation for relational integration in 7 - 18-year-olds. In a group of young adolescents (11 - 14 years), mid-adolescents (14 - 18 years) and adults (22 - 30 years), Dumontheil et al. (2010) also described an increase in activation in the left RLPFC during the relational relative to the control task between young adolescence and mid-adolescence, followed by a decrease in activation between mid-adolescence and adulthood, with a similar decrease in activation in the left anterior insula. Activation in the preSMA decreased between young adolescence and adulthood. Here, as a first step in the analysis, general developmental differences in activation associated with relational integration were investigated. The only region that showed a developmental difference during relational reasoning was the left inferior lateral PFC, with greater activation in adults relative to adolescents during relational integration compared to the manipulation of single relations. The previously reported changes in RLPFC and parietal cortex activations with age (Dumontheil, Houlton, et al., 2010; Wendelken et al., 2011) were not observed in this study. This difference may be due to differences in the age distribution of participants, but also due to the more stringent statistical level of significance used for the voxel-wise analyses (cluster-wise or voxel-wise $p_{FWE} < 0.05$) compared to the ROI approaches used by Dumontheil et al. (2010) and Wendelken et al. (2011).

### 6.4.3 Peer audience effect on behaviour and neural activation

The behavioural results showed that relational reasoning accuracy was affected by the peer audience and this audience effect was dependent on Task: accuracy was decreased when being observed by a Peer relative to when Alone in the relational integration condition. Previous audience effect studies have found that the presence of an audience generally leads to improvements in performance in simple tasks and impairments in complex tasks (Zajonc, 1965; for a review C. F. Bond & Titus, 1983; Guerin, 1986). Consistent with this literature, accuracy in the more complex condition (the relational integration condition) was impaired when participants thought they were being observed by a peer. However, the increase in accuracy in the simple condition (Control condition) when participants thought they were being observed was not significant. As overall accuracy in this condition was high (> 96%), a potential improvement might have been masked by a ceiling effect. In a meta-analysis of the social facilitation literature, Bond and Titus (1983) found only a small effect size (Cohen's d = 0.11) for an improvement in accuracy in simple conditions in the presence of others. This small effect size might be due to possible ceiling effects as well as a publication bias towards results that fit with the predicted direction of the social facilitation effect. In addition, inconsistency in the literature in the classification of tasks as simple or complex might explain this small effect size (C. F. Bond & Titus, 1983).

The results in **Chapter 4** showed that, while adolescents' relational reasoning performance (in particular mid-adolescents' performance) was impaired in the presence of a friend relative to an experimenter, adults showed no peer audience effects on relational reasoning performance. In the current study, relational reasoning accuracy in adolescents and adults was similarly influenced by a peer audience. These differences in developmental changes in peer audience effects might be due to a number of reasons. *First*, different relational reasoning paradigms were employed in **Chapter 4** and the current study. For example, here, participants solved relational reasoning problems under time constraints (4 s), while in **Chapter 4**, in order to maximise the possibility to observe both audience effects on RT and accuracy, participants responded self-paced within a maximum response period of 40 s. *Second*, in the Peer condition in **Chapter 4**, participants were observed by a physically present friend, while the current study employed a minimal virtual peer manipulation (Somerville et al., 2013). *Third*, while each social session took on average 6.6 min in **Chapter 4**, audience blocks were 34.4 s in the current fMRI study. *Fourth*, the current study, but not the behavioural study in **Chapter 4,** explicitly asked participants to monitor whether the peer was observing their performance (see 7.1.1 for a more detailed discussion of how this might have contributed to the differences in developmental patterns).

Even though there was no developmental difference in the peer audience effect on performance, the fMRI analysis demonstrated that adolescent and adult activations in the relational-integration network were differentially modulated by a peer audience. Several regions within this network - a right inferior frontal cluster, a right parietal cluster, bilateral occipito-temporal clusters and a bilateral preSMA cluster - showed increased activation during relational reasoning when adolescents thought they were being observed compared to when they were alone. These regions showed the opposite pattern in adults, i.e. a decrease in activation (although note that the adult effects did not survive Bonferroni correction). This suggests that, while adolescents and adults showed a similar behavioural audience effect, the underlying neural mechanisms appear to differ.

In previous studies, activation patterns during peer observation differed according to the age of the participants (Chein et al., 2011; A. R. Smith, Steinberg, et al., 2014; Somerville et al., 2013). When adolescents (14 - 18 years) were deciding whether or not to take a risk in a driving game, they activated reward-related regions (OFC and VS) more in the peer-present relative to the alone condition, while young adults (19 - 22 years) did not show this modulation (Chein et al., 2011). It was suggested that peers might affect sensitivity of reward-related regions in the context of risky decision-making in adolescents more than in adults (Chein et al., 2011; A. R. Smith, Steinberg, et al., 2014). In the context of this high-level reasoning task, neural activation in the task-related network was differentially modulated in adolescents and adults. In adolescents, activation was increased in several regions in the task-related network. In adults, activation was decreased in these regions (although the effects did not survive Bonferroni correction). While the audience by age group interaction seemed to be driven by the adolescent increase in activation in reward-related regions during a risky driving task (Chein et al., 2010), the data in the current study suggest that adolescents and adults show different patterns of modulation of the fronto-parietal network. Thus, developmental differences in the peer audience effect on neural activation have now been observed both in the context of risky decision-making and a reasoning task.

In the fMRI study of Chein et al. (2011) actual peers were present and interacted with the participant via an intercom from the control room. The current study employed a peer audience manipulation in which participants were told that they would be observed and evaluated by a peer, whom the participant never met. Similar manipulations of peer conditions, in which participants were led to believe that they interacted with virtual peers, received peer feedback or were observed by virtual peers, have been employed in various previous fMRI and eye-tracking studies (for examples Guyer et al., 2009; Jones et al., 2014; Moor et al., 2010; Sebastian et al., 2011; Silk et al., 2012; Somerville et al., 2013). The behavioural and neuroimaging results in the current study demonstrate that the peer audience manipulation was successful; however it would be interesting to investigate whether these peer audience effects are dependent on the familiarity and physical presence of the peer. Similar to previous fMRI studies investigating peer influence effects, (Chein et al., 2011; A. R. Smith, Steinberg, et al., 2014; Somerville et al., 2013) the current study included two levels of the Audience factor, i.e. a Peer versus an Alone condition. This design does not allow the conclusion that the observed audience effects were specific to the presence of peers. Future studies – comparing a Peer to a Non-Peer to an Alone condition – should assess the specificity of this audience effect (see also 7.2.4).

As described in the introduction, adolescents show increased levels of autonomic arousal compared to children and adults, when they think they are being observed by a peer via a camera in the scanner (Somerville et al., 2013). One theory in the social psychology literature suggests that audience effects might be driven by increased arousal in the presence of an audience (Zajonc, 1965). Consequently, differences in the peer audience effect in adolescents and adults might be due to differences in autonomic arousal in the presence of a peer audience. Ito et al. (2011) showed that in adults, autonomic arousal was elevated across all levels of a working memory task in the presence of an evaluative, expert audience relative to alone (although this social condition additionally had a competitive component). In contrast, only in the most difficult condition (3-back), participants' performance was impaired, and NIRS data showed that prefrontal activation was increased in the 3-back condition relative to baseline. This suggests that audience effects in high-level tasks might not be mediated by arousal (at least directly), but instead the authors suggest a 'cognitive factor' leads to the performance decrease. However, NIRS does not allow sufficient spatial resolution to localize whether the increase in activation was within or outside the working memory network. Here, the analysis was restricted to the relational-integration network in order to test whether a peer audience modulates relational reasoning activation. The current study demonstrated that being observed by a peer influenced the recruitment of several of these fronto-parietal regions, showing that the audience effect modulates activation within the high-level task network.

It is only possible speculate about the cognitive mechanisms underlying the observed audience effect pattern in the current experiment. The increase in activation in the relational-integration network in the presence of a peer audience in adolescents might be associated with attentional distraction by the peer observation. Compared with adults, adolescents might be more preoccupied by what the peer thinks about them and thus show greater attentional distraction. Attentional distraction might lead to greater RT variability, consequently RT variability for the Peer and the Alone condition were compared. There was no effect of Audience on RT variability across the whole sample or between Age groups, which suggests that the audience effect might not be associated with attentional distraction in the current paradigm.

### 6.4.4 Conclusion

While previous studies have suggested that the presence of peers appears to influence activation in reward-related regions, the current study revealed that the presence of a peer audience modulates activation in the neural network associated with relational reasoning. Future studies should target the specific mechanisms underlying peer audience effects. It would be interesting to investigate the role of autonomic arousal for peer audience effects, since previous studies have found heightened arousal in adolescents in a peer context (Somerville et al., 2013). Furthermore, a potential contribution of cognitive load effects or attentional distraction might shed light on cognitive mechanisms.

# CHAPTER 7: GENERAL DISCUSSION

## 7.1 Summary of findings

*Adolescence is often characterised as a period of heightened sensitivity to peer influence (Brown, 2004; Gardner & Steinberg, 2005; Steinberg & Monahan, 2007) as well as a period of increased levels of risk-taking (Boyer, 2006; Eaton et al., 2010; Steinberg, 2008). While these two behavioural patterns have been investigated in observational and questionnaire-based studies for several decades, only recently have they been systemically examined in experimental settings. Of particular interest has been the interplay between increased levels of risk-taking and heightened sensitivity to peer influence. Behavioural and neuroimaging studies have demonstrated that risky- and reward-related decision-making seems to be particularly influenced by the presence of peers during adolescence and that the presence of peers modulates activation in reward-related regions (Chein et al., 2011; Gardner & Steinberg, 2005; Haddad et al., 2014; L. O'Brien et al., 2011; Reynolds et al., 2013; A. R. Smith, Chein, et al., 2014; A. R. Smith, Steinberg, et al., 2014; Weigard et al., 2014). In light of these findings this thesis sought out to address three main research questions: 1) Do increased levels of sensitivity to peer influence in adolescence extend beyond the effects on risky- and reward-related decision-making to peer audience effects on high-level and low-level cognitive task performance? 2) Are there developmental differences in the behavioural sensitivity to conform to others' music preferences and in the neural correlates of social influence between adolescence and adulthood? 3) In the context of a non-affective task (in the absence of peers or emotions), what are the developmental trajectories of the impacts of risk and valence on risky decision-making during adolescence? In the following three sections, experimental evidence regarding these questions will be summarised and integrated.*

### 7.1.1 Developmental changes in peer audience effects

The studies described in **Chapters 4 and 5** investigated developmental changes in the effect of the presence of a peer audience on performance in a high-level cognitive task (relational reasoning, **Chapter 4**) and low-level cognitive task (visual discrimination, **Chapter 5**). While previous studies have only compared a peer-present condition to an alone condition, the studies in **Chapters 4 and 5** additionally included a non-peer condition: participants performed the tasks either alone, in the presence of an evaluative experimenter or in the presence of an evaluative friend. As previous studies in adults (C. F. Bond & Titus, 1983; Guerin, 1993) have suggested that the direction of the audience effect might depend on the difficulty of the task, both studies also included a simple (**Chapter 4**: Low-relational; **Chapter 5**: Low-noise) and a complex (**Chapter 4**: High-relational; **Chapter 5**: High-noise) task level.

In **Chapter 4**, adolescents' (aged 10.6 - 17.8 years) but not adults' relational reasoning performance was sensitive to the presence of a peer audience. These audience effects in adolescents were further dependent on the age of the participant, the identity of the audience and the task level. In young adolescents (aged 10.6 - 14.2 years), relational reasoning accuracy was impaired in the presence of the friend relative to the presence of an experimenter in the Low-relational trials only. In mid-adolescents (aged 14.9 - 17.8 years), both accuracy and RT were impaired in the presence of the friend relative to experimenter across both relational reasoning task levels. In contrast, the study in **Chapter 5** found no evidence for developmental changes in peer audience effects in the object oddity task. The only audience effect found in this visual discrimination task was an increase in RT in the presence of the experimenter relative to being alone (and a marginally significant increase relative to the friend being present) in High-noise trials.

With **Chapter 4** demonstrating that adolescents relative to adults showed increased sensitivity to peer audience effects on performance in a relational reasoning task, **Chapter 6** examined developmental changes in the effect of a peer audience on the recruitment of the relational integration neural task network. Similar to the study of Somerville et al. (2013), the study in **Chapter 6** employed a minimal, virtual peer manipulation: participants were told that they would be observed and evaluated by an unfamiliar peer via a camera in the scanner. As in **Chapters 4 and 5**, the relational reasoning task included two task levels – a one-relational (Control) and a relational integration (Relational) condition. In this study, both adolescents' (aged 14.2 - 16.7 years) and adults' relational reasoning accuracy was impaired in the complex relational integration condition when participants believed they were being observed by the peer relative to being unobserved. Participants activated a typical fronto-parietal network during relational integration. Activation in several regions of this fronto-parietal task network was differentially modulated in adolescents and adults by the peer audience. Activation in these regions was increased in the presence of the peer audience in adolescents, but not in adults.

Evidence from the study described in **Chapter 4** suggests that mid-adolescents' relational reasoning performance (accuracy and RT) was impaired when being observed by a peer audience relative to a non-peer audience, while performance in adults was not influenced. However, the behavioural results from **Chapter 6** describe a comparable impairment in relational integration accuracy in both mid-adolescents and adults when being observed by a peer audience relative to being alone. In 6.4.3, a number of differences between the studies were discussed that might have contributed to these differing results: differences in time constraints to solve relational reasoning problems (self-paced (max. 40 s) versus 4 s), physical presence of a friend versus a minimal virtual peer manipulation and longer audience sessions (6.6 min) versus shorter audience blocks (34.4 s)). In addition to these differences, the audience conditions differed with respect to the instructions participants were given regarding the observer. In **Chapter 4**, participants were not given explicit instructions to pay attention to the peer observing them. In contrast, in the fMRI study in **Chapter 6**, participants were asked to pay attention to the camera light in order to know whether the peer was watching them or not, i.e. participants were explicitly instructed to think about the peer. Comparing the results from these two studies, adolescent performance was affected by a peer audience in both studies, while adult performance was only affected in the fMRI study. Speculatively, adolescents might be hyperaware of the presence of peers and might thus automatically and constantly think about the peer observing and evaluating them, resulting in performance changes in the presence of both types of peer audiences. In contrast, adults might be less preoccupied about being observed and evaluated by the peer and might only think about the peer when explicitly asked to do so. This interpretation would be consistent with the notion that adolescents are particularly sensitive to the presence of peers.

Only a small number of experimental studies (see 1.6.2.1.2 for details) have compared peer influence effects in adolescents and adults (Chein et al., 2011; Gardner & Steinberg, 2005; A. R. Smith, Steinberg, et al., 2014). When comparing a peer-present to an alone condition, these studies have demonstrated that adolescents relative to adults showed increased levels of risk-taking in a car-driving simulation as well as a heightened activation in the VS when making go or stop decisions or when receiving monetary rewards. The presence of peers has also been found to increase adolescent risk-taking in a wheel-of-fortune type gamble and the balloon analogue risk task (see 1.6.2.1.2; Reynolds et al., 2013; A. R. Smith, Chein, et al., 2014) as well as adolescent preferences for immediate rewards in delay-discounting paradigms (L. O'Brien et al., 2011; Weigard et al., 2014). These latter studies did not compare the peer influence effects found in the adolescent group to an adult group. Consequently, it is not clear whether adolescents are also more sensitive to peer influence in these tasks in comparison to adults. In addition, a recent study suggested that developmental differences in peer influence effects on risky decision-making between adolescents and adults are dependent on whether peers merely observe the participant or advise on whether to choose the risky or safe option (Haddad et al., 2014). However, these studies have provided robust evidence that adolescent choice behaviour is affected by peers across a range of different risk-taking and reward-related decision-making tasks. The results from the studies in **Chapters 4 to 6** extend these findings. Adolescents also displayed an increased sensitivity to the presence of a peer audience on performance in a relational reasoning task relative to adults in **Chapter 4** and showed greater activation in the fronto-parietal task network during evaluative peer observation in **Chapter 6**, while adults did not. This suggests that increased levels of sensitivity to peer influence in adolescence extend beyond the effects on risky- and reward-related decision-making to peer audience effects on high-level cognitive task performance. However, this developmental pattern of peer audience effects seems to be dependent on the type of task and the characteristics of the peer. Adolescents did not demonstrate greater sensitivity to peer audience effects than adults in the low-level perceptual task in **Chapter 5**. As discussed in 5.4, these differences might be due to the differing levels of cognitive load in the relational reasoning task and the object oddity task. In addition, the motivational salience to perform well in the tasks might explain differences in the developmental pattern of the peer audience effects: adolescents might be more concerned about being evaluated in their cognitive abilities in the relational reasoning task (i.e. worrying whether their friend thinks they are 'stupid') relative to being judged on their visual discrimination abilities. Thus, the developmental pattern of peer audience effects might be dependent on the cognitive load, motivational salience, the type of peer audience and whether the instructions explicitly orient the participant's attention towards the peer audience. Future studies are required to systematically investigate the impact of cognitive load and motivational salience on peer audience effects during adolescence.

The findings from **Chapters 4 to 6** are also interesting in light of different models of brain development discussed in 1.3. The dual-systems model proposes a maturational gap between earlier developing subcortical affective systems and a protracted development of prefrontal control regions (Casey et al., 2008; Somerville et al., 2010; Steinberg, 2008). In contrast, the

Crone and Dahl model suggests that cognitive control systems are not simply insufficiently developed during adolescence, but instead that the cognitive control systems are more flexibly recruited in dependence on the motivational salience of a context and thus highly adaptive to different social contexts and new environments (Crone & Dahl, 2012). The context of different physically present audiences in **Chapter 4** – i.e. a peer versus non-peer audience – affected adolescents' (particularly mid-adolescents') relational reasoning performance, while adult performance was not affected. Consistent with the Crone and Dahl model, adolescent performance in a complex cognitive control task was thus found to be dependent on the social context. Furthermore, as suggested earlier in this section, the developmental differences between peer audience effects found in the relational reasoning task in **Chapter 4** and the perceptual discrimination task in **Chapter 5**, might be due to different levels of motivational salience to perform well in the two tasks. A dependency of the recruitment of cognitive control processes on the motivational salience is also in line with the Crone and Dahl model. Finally, **Chapter 6** also demonstrated that the recruitment of regions in a typical cognitive control network was increased in adolescents during evaluative peer observation, while this was not the case in adults. Consequently, consistent with the Crone and Dahl model of brain development, **Chapters 4 to 6** provide both behavioural and neuroimaging evidence that cognitive control processes in adolescence seem to be flexibly recruited in dependence on the social context and the motivational salience of a situation.

Social facilitation effects comprise both audience effects and co-actor effects (i.e. individuals performing the same task as the participant) (Guerin, 1993; Zajonc, 1965). However, as it is difficult to disentangle the impacts of competition and rivalry from other more general co-actor effects, this thesis focused on the analysis of the development of peer audience effects during adolescence. In most classroom settings, adolescents perform tasks either at the same time as their peers (co-actor effects) or while being implicitly or explicitly evaluated by peers or teachers (audience effects). The results from **Chapters 4 and 5** suggest that adolescents' relational reasoning performance (especially mid-adolescents' performance) in comparison to adults' performance, is impaired in the presence of peers relative to the presence of non-peers. This developmental effect was not found for a low-level perceptual task. Transferring these results to an educational context would suggest that mid-adolescents may benefit particularly from the presence of a teacher (or another non-peer) compared to the presence of a peer, when performing or learning high-level cognitive tasks. This might be less important when performing lower-level cognitive tasks. To achieve this effect, it may not be necessary to physically separate peers from each other when complex tasks are learned or performed, but creating spaces (for example semi-open cubicles) in which students can work without feeling observed by their peers but still be under the supervision of the teacher. While it is important that students can learn and work in environments that optimally support their acquisition of skills, it is also equally important that adolescents learn how to excel in tasks while being observed and evaluated by their peers. Ideally, educational settings would create a balance between the two environments, thus allowing adolescent students to become proficient in the task itself, but similarly creating situations which stimulate adolescents' learning to excel in tasks while being in the presence of evaluative peers.

However, it is important to note that the current findings need to be further validated by studies with larger and more diverse samples. The generalizability of the current studies to educational contexts is limited due to several reasons and thus future studies are required to extend the current results. *Firstly*, the studies in **Chapters 4 to 6** did not test for audience effects in educational settings or on educational tasks per se. Relational reasoning is a cognitive capacity that allows drawing analogies and is thus critical for children's learning and has also been found to be associated with academic achievements, such as mathematics performance, reading and academic knowledge (Ferrer et al., 2009; Krawczyk, 2012). Thus, while these links between relational reasoning and academic performance suggest that similar peer audience effects may be found in educational tasks, future studies should specifically investigate this for example by assessing the effect of a peer audience on solving mathematical equations, learning new vocabulary or reading comprehension. Furthermore, the current studies investigated the effect of a single evaluative observer on performance. In classroom settings, the audience will usually be larger and also consist of a mixture of non-peers (teachers) and peers (class-mates). It would be interesting to investigate whether these multiple audiences show additive effects and whether the presence of a non-peer audience may balance potentially detrimental peer audience effects on high-level cognitive task performance. In addition, the current studies focused on peer audience effects and thus cannot inform how collaborative or competitive peer contexts influence performance. *Second*, the current studies included female participants only. As suggested in 4.4, developmental differences in peer audience effects may be larger in females than in males. Thus, future studies with a larger sample including both sexes should assess whether developmental differences are affected by sex or whether the current results can be generalized to female and male students. The restriction to a female sample also means that the current findings are only applicable to single-sex educational contexts and thus calls for further studies measuring the influence of different-sex peers on performance. *Third*, individual differences may also contribute to the direction and magnitude of the audience effects. Individual resistance to peer influence scores were not related to the extent to which an individual participant's performance was influenced by a peer audience in **Chapter 4**. However, it would be interesting to investigate whether individual differences in fear of social evaluation may be related to the magnitude of the peer audience effects. If the developmental effects are driven by a subgroup of adolescents who are particularly sensitive to social evaluation, this group may particularly benefit from educational environments that allow them to study in the absence of their peers. Furthermore, individual differences in task proficiency may affect whether a task is simple or complex for a participant and thus influence the direction of the audience effect. The average IQ of the participants in the current studies was relatively high and thus task proficiency of the current samples may not generalize to an average IQ sample. However, the participants in

**Chapters 4 and 6** showed performance impairments in the relational reasoning tasks in the presence of a peer audience, suggesting that the tasks were complex for the current samples and thus should also be complex for a population with a wider range of cognitive abilities. The general direction of the effect should consequently also replicate in an average IQ sample and may actually be more pronounced (if average task proficiency was lower). Future studies could assess whether different levels of task proficiency are indeed related to different directions in peer audience effects. This could further inform education as to which students may particularly benefit from a non-peer audience relative to a peer-audience.

### 7.1.2 Developmental changes in the neural correlates of social influence

The study described in **Chapter 3** investigated the development of social influence effects on music song valuation and the neural correlates of social influence in adolescence and adulthood in a music choice task. The behavioural analysis of this study assessed individuals' tendencies to change their music song valuation (post-scan versus pre-scan ratings) in line with the preferences of an alleged group of music experts. The imaging analysis tested the neural correlates of agreement or disagreement with music experts on song choice, of the receipt of a token for the preferred relative to the alternative song and of the modulation of the latter by the music experts' preferences.

The study demonstrated that in terms of their behaviour adolescents (aged 14.2 - 16.7 years) and adults were similarly influenced in their music song valuation by the music experts. Adolescents and adults activated the bilateral VS more when receiving a token for the preferred song relative to the alternative song. Both adolescents and adults also showed greater activation in the right VS, as well as in the bilateral temporal lobes (more extended activation in the right hemisphere), when the music experts agreed with participants' song choices relative to when they disagreed. Moreover, in both age groups there was a negative correlation between the activation in a right posterior temporal cluster during agreement versus disagreement with the music experts' preferences and the behavioural tendency to adjust music song valuations in line with the music experts. In other words, participants who were more influenced by the music experts, showed a greater conflict signal in the right posterior temporal cluster (i.e. activation in the disagreement versus agreement contrast). The only age effect found in this study was a four-way interaction between Object outcome, Review outcome, Age group and the behavioural sensitivity to social influence ($B_{inf}$) in a left VS cluster. In adolescents, the behavioural sensitivity to social influence was positively correlated with the neural modulation of reward activation in this left VS cluster by the music experts' opinion, while adults showed the opposite pattern.

*Firstly*, these results suggest that adolescents and adults showed very similar tendencies to adjust their music song valuations in line with the music experts, as well as very similar activation patterns when receiving feedback about the music experts' choices. In a previous study, which employed a version of Asch's line paradigm, adolescents (aged 11 - 13 years) displayed a higher level of conformity to three peers in a social pressure condition than adults, with intermediate levels of conformity in 15 - 17-year-olds (see 3.4.1; Costanzo & Shaw, 1966). In the study of **Chapter 3**, participants were led to believe they viewed music preferences from a group of young music experts (whose photos and descriptions were chosen so that both adolescents and adults would view them as similar-aged to themselves). In addition to several differences between the two studies discussed in 3.4.1, the fact that physically present school-peers exerted the social influence in the study of Costanzo & Shaw (1966) relative to approximately similar-aged, but unfamiliar, virtual music experts, might explain the differing results in the two studies. Speculatively, adolescents might only show greater conformity than adults if the others exerting social influence are sufficiently salient, for example familiar or popular peers (see 1.6.1 for the latter). A potential impact of popularity, familiarity and physical presence of peers should be examined in future studies.

*Second*, the findings of **Chapter 3** suggest that the theory of adolescent hyper-responsiveness to rewards might be too simplistic. While a number of studies has provided evidence for increased VS activation in response to rewards during adolescence (Barkley-Levenson & Galván, 2014; Ernst et al., 2005; Galván et al., 2006; Galván & McGlennen, 2013; Geier et al., 2010; Padmanabhan et al., 2011; Van Leijenhorst, Moor, et al., 2010; Van Leijenhorst, Zanolie, et al., 2010), others have found no difference in VS activation between adolescents and adults (Bjork et al., 2004, 2010; Galván & McGlennen, 2013; Van Leijenhorst, Zanolie, et al., 2010) or even decreased VS activation in adolescents relative to adults (Bjork et al., 2004, 2010; Geier et al., 2010). These differing results might be attributable to different paradigms and rewards that have been employed as well as different trial phases (reward assessment, anticipation or receipt) analysed. Further studies are required to disentangle under what circumstances adolescents display increased levels of activation to rewards.

*Third*, previous studies have demonstrated that typical reward-related regions are also involved in the processing of social rewards (Bhanji & Delgado, 2014; Davey et al., 2010; Fareri & Delgado, 2014; Rademacher et al., 2010; Spreckelmeyer et al., 2009). If adolescents are generally hyper-responsive to rewards, they might also show elevated VS responses when processing social rewards. In line with this, one previous study demonstrated that adolescents, relative to children and adults, show greater VS responses to happy faces (versus rest) (Somerville et al., 2011). In the study in **Chapter 3**, adolescents and adults displayed no significant difference between levels of activation in the right VS when music experts agreed with the participant's song choice. This indicates that the theory of adolescent hyper-responsiveness might not generalize to social stimuli per se. However, speculatively, adolescents might show greater responses to socially rewarding feedback if physically present peers or familiar peers had provided feedback. This could be investigated in future studies.

### 7.1.3 Developmental changes in risky decision-making in adolescence

The study described in **Chapter 2** examined the development of the impacts of risk and valence on risky decision-making in a non-affective task during adolescence. This was investigated in a monetary gambling task, which has previously demonstrated that adult decision-making is independently influenced by the valence and the risk of a choice (Wright et al., 2012). Previous studies have shown different developmental trajectories for risk-taking in affective ('hot') versus non-affective ('cold') contexts during adolescence (Blakemore & Robbins, 2012). The study in **Chapter 2** specifically aimed to investigate the impacts of risk and valence in the absence of affective components to examine their developmental trajectory without studying their potential interaction with emotion.

The study revealed that adolescent (aged 11 - 16 years) choices were influenced by risk, such that adolescents were risk-averse (i.e. they made fewer riskier than safe decisions), and by valence, such that fewer riskier choices were made for losses than for gains. These two decision variables independently influenced adolescent choices. The impacts of risk and valence on choice behaviour found in **Chapter 2** are thus similar to those described by a previous study in adults (Wright et al., 2012). Finally, the influences of risk and valence on choice behaviour showed different developmental trajectories: the impact of risk remained stable in adolescents aged 11 to 16 years, while the impact of valence decreased with age. In other words, younger adolescents were more biased away from the riskier option by losses relative to gains.

In the study of **Chapter 2** participants made risky decisions involving real monetary gains and losses, i.e. their final payments were dependent on the choices made during the experiment. The use of real monetary incentives is crucial from a neuroeconomical perspective to allow extrapolating behaviour in experimental conditions to 'real world' choices (Glimcher & Fehr, 2013; V. Smith, 1976). However, in developmental studies this approach is problematic, as the subjective value of money is likely to differ between age groups (Barkley-Levenson & Galván, 2014; Galván & McGlennen, 2013). While some studies have employed primary reinforcers (e.g. sugar water versus salt water) or have attempted to control for the subjective value in a monetary gambling paradigm (Barkley-Levenson & Galván, 2014; Galván & McGlennen, 2013), the difference in subjective value between adolescents and adults might introduce a confound in experimental designs employing monetary reinforcers. Consequently, the study in **Chapter 2** only included adolescent participants and investigated the development of the impacts of risk and valence during adolescence. However, the comparison of the results from this study, together with a previous study in adult participants (Wright et al., 2012), shows that adolescents and adults are similarly influenced in their choices by the impacts of valence and risk (although a comparison of the magnitude of this effect between the two samples is not possible).

Many experimental studies have aimed to understand the causes of heightened levels of real-world risk-taking behaviour in adolescence, such as risky driving, drug abuse or unsafe sex. The peak in adolescent risk-taking seems to be only replicated in experimental conditions when risk-taking is measured in an affective context. While these studies have been important for our understanding of adolescent risk-taking, the development of other impacts on risky choices might have been masked when studied in affective contexts. Consequently, the findings from **Chapter 2** advance the developmental risk-taking literature by providing evidence that in the absence of an affective context, the impact of risk on choices remains stable during adolescence, while the impact of valence decreases. This developmental stability of risk-taking in a non-affective context is also in line with the predictions of the Crone and Dahl model of brain development (for details see 1.3), which suggests that the recruitment of cognitive control processes in adolescents is dependent on the motivational salience of the context (Crone & Dahl, 2012). Specifically, it was suggested that heightened adolescent risk-taking is promoted by an increased salience of obtaining social status and an increased tendency to seek intense affective experiences. Thus in the absence of these context-dependent factors, i.e. in non-affective situations, risk-taking would not show a peak in adolescence. This is exactly what the current study shows. Future studies could now investigate how the impact of risk and valence on risky choices further interact with an affective context, e.g. when emotions are at stake or peers are present.

## 7.2 Methodological considerations

### 7.2.1 Generalizability of results

Due to significant sex differences in functional and structural brain maturation during adolescence (Guyer et al., 2009; Herting et al., 2012; Mills et al., 2014; Raznahan et al., 2011), the studies in this thesis included female participants only. In addition, observational and questionnaire-based studies have also demonstrated sex differences in the resistance to peer influence (Berndt, 1979; Steinberg & Silverberg, 1986), public self-consciousness (Rankin et al., 2004), fears of negative peer evaluations (La Greca & Lopez, 1998; La Greca & Stone, 1993; Rudolph & Conley, 2005) and the importance of peer approval for self-esteem (S. F. O'Brien & Bierman, 1988). Consequently, to maximise the homogeneity of the sample and thus reduce potential noise due to sex differences, the samples in this thesis comprised female participants only. This approach means that the findings in this thesis can only generalize to females. Future studies with larger samples of both male and female participants, could include sex as a between-subject factor in the analysis. This would allow testing whether the developmental patterns found in this thesis are further modulated by sex or whether they generalize to both males and females. Furthermore, the peer audience effects found in **Chapters 4 to 6** are also only applicable for same-sex peer relationships and it remains to be studied whether evaluative observation by a different-sex peer would result in more or less pronounced effects on performance.

The majority of participants forming the adolescent samples in this thesis attended academically selective schools. To match adolescent and adult participants in terms of their educational background, most adult participants were university graduates. This recruitment approach was chosen to maximise sample homogeneity and to optimize the ability to detect developmental changes. However, this specific educational background and the relatively high IQ of the samples in this thesis, limit the generalizability of the findings (see 7.1.1 for how this may limit the generalizability to educational contexts). Future studies are required to determine whether the findings of this thesis are specific to the current samples or whether they can be replicated in a sample with a wider range of general cognitive abilities.

As with the majority of developmental studies in adolescence, the studies in this thesis defined the adolescent groups by chronological age rather than by puberty status. This allowed an easier comparison of the current results to the literature. Crucially, **Chapters 3 to 6** aimed to compare adolescents to an adult group and puberty as the main developmental measure would not allow to capture developmental changes that are occurring after the end of puberty. While pubertal status and chronological age are correlated with each other, puberty onset can vary by 4 - 5 years in healthy individuals (Blakemore et al., 2010; Parent et al., 2003). This may introduce variability in the data if only chronological age is measured. Consequently, future studies should collect data about pubertal development. While many developmental studies have suggested links between puberty-related hormonal changes and brain development, only recently have studies started to investigate this relationship. These studies have found evidence for associations between pubertal development as well as sex hormone levels with changes in both brain structure (Goddings et al., 2014; Herting et al., 2014, 2012; Menzies, Goddings, Whitaker, Blakemore, & Viner, 2015) and function (Forbes, Phillips, Silk, Ryan, & Dahl, 2011; Goddings, Burnett Heyes, Bird, Viner, & Blakemore, 2012; Op de Macks et al., 2011). In addition, these studies have demonstrated that some of the developmental changes were solely explained by chronological age, while others were accounted for by pubertal developmental. The current studies in this thesis cannot differentiate between these two developmental effects; consequently, some of the developmental changes reported in this thesis may be driven by puberty. Future studies should disentangle the effects of chronological age and puberty in the developmental changes found in this thesis.

### 7.2.2 Cross-sectional age-comparisons

A particular challenge in the design of experiments that compare adolescent and adult behaviour and neural correlates is to know whether the experimental tasks themselves are matched in terms of arousal, salience or performance between age groups. In order to minimize the influence of potential baseline differences in adolescents and adults on the effects of interest, all experimental factors but age were manipulated as within-subject factors. In addition, if inherent differences in the salience of tasks between adolescents and adults are likely, limiting the sample to adolescent participants can reduce the risk of potential artefacts of task-related salience. This approach was adopted in **Chapter 2**, due to the likely differences in the subjective value of money between adolescents and adults.

**Chapters 4 to 6** investigated whether the manipulations of interest, i.e. the presence of a peer audience, affected task performance in adolescents and adults. Baseline differences in task-related arousal or salience between adolescents and adults may influence the degree to which a peer audience affects performance. With regard to the performance measures collected, i.e. accuracy and RT, no age differences were found in **Chapters 4 to 6**. This suggests that, at least with regard to accuracy and RT, the tasks were matched in adolescents and adults. However, age differences in arousal or salience when performing these tasks may not be captured by these performance measures. Consequently, future studies measuring autonomic arousal are required, in order to fully control for potential differences in task-related arousal.

### 7.2.3 Magnetic resonance imaging approaches

Interpreting fMRI data is prone to reverse inference, a process of reasoning in which the engagement of a specific cognitive process is inferred from the activation of a brain region or set of regions (Poldrack, 2006). For example, a region (e.g. the insula) that has previously found to be activated during a specific cognitive process (e.g. experiencing feelings of love) might be activated in a specific task contrast (e.g. viewing videos of ringing iPhones). Applying reverse inference might lead to the conclusion that the activation found in the task contrast demonstrates the occurrence of this cognitive process (i.e. activation of the insula when viewing videos of an iPhone means that participants love their iPhone, Lindstrom, 2011). This kind of inference is particularly problematic if a region such as the insula, which is one of the most frequently reported regions in fMRI studies (Chang, Yarkoni, Khaw, & Sanfey, 2013), is known to be activated by a large number of cognitive processes. Reverse inference would only be valid if a region of interest would exclusively respond to a cognitive process. Consequently, reverse inference will only provide very limited evidence that a cognitive process might be involved when a region with low selectivity is activated (Poldrack, 2006).

Similarly, it is difficult to interpret an increase or decrease in activation when contrasting two task conditions in terms of the cognitive processes involved. For example, due to the lack of prior fMRI studies investigating audience effects, it was not clear whether peer audience observation in **Chapter 6** would evoke increased or decreased activations in regions of the fronto-parietal task network. Consequently, the interpretation of the Audience by Age group interaction pattern found in several regions of the fronto-parietal task network can only be speculative; particularly as the behavioural decrease in relational reasoning accuracy in the peer audience condition was not associated with the neural effect of the peer audience. As suggested in 6.4.3 increased activation in the fronto-parietal task network in adolescents might be associated with attentional distraction by the peer observation. However, this interpretation would need to be verified by future studies, which for instance assess whether a non-social distractor might evoke similar effects as the presence of a peer audience. Furthermore, it is still debated how a distractor affects task-related activation. In the face of a distractor, compensatory mechanisms might be engaged to maintain the level of task performance. FMRI studies investigating the effect of emotional distractors on task performance, have for instance demonstrated an increase in activation in task-related regions in the presence of emotional distractors (Wessa, Heissler, Schönfelder, & Kanske, 2013). In contrast, distractors might divert attention away from the task and lead to a deactivation in task-related regions, as has been found for other fMRI studies examining the effect of emotional distractors on task performance (Dolcos & McCarthy, 2006; Mitchell et al., 2008). The increase in activation in the fronto-parietal network found in adolescents might thus speculatively be interpreted as a compensatory mechanism, which might be effective in the simple Control condition but not sufficient in the complex Relational condition, leading to the observation of different patterns of peer audience effects in the behavioural and neuroimaging data.

This thesis focussed on the development of the behavioural and functional correlates of peer audience and social influence effects during adolescence. As reviewed in 1.2, the adolescent brain undergoes prolonged structural changes. Consequently, it would be interesting to investigate whether functional changes might be associated with structural changes. Future studies could for instance investigate whether the functional changes in peer audience effects on the neural correlates of relational reasoning between adolescence and adulthood observed in **Chapter 6**, might be related to structural grey matter changes. Although there was only limited evidence for functional changes in the neural correlates of social influence between adolescence and adulthood in **Chapter 3**, an analysis of structural changes might still be informative. A recent study demonstrated that the more adult participants were influenced by music experts in their valuation of the music songs (i.e. the greater their $B_{inf}$ values), the greater was their grey matter volume in the bilateral OFC (Campbell-Meiklejohn et al., 2012).

While there was no difference in $B_{inf}$ between adolescents and adults in the study of **Chapter 3**, the relationship between grey matter volume and $B_{inf}$ might still differ between adolescents and adults. Consequently, future studies should compare the relationships between $B_{inf}$ and OFC volume in adolescents and adults.

### 7.2.4 Design of peer conditions

What is common between **Chapters 4 to 6** is that they created peer audience environments in experimental settings. In **Chapters 4 and 5** similar-aged, same-sex pairs of friends took part in the study and in the peer audience condition participants were observed and evaluated by their friend. In contrast, the peer audience condition in **Chapter 6** was experimentally manipulated by telling participants that an unfamiliar, approximately similar-aged, same-sex peer would observe them via a camera in the scanner. Behavioural findings from the audience effect studies (**Chapters 4 and 6**) suggest that adolescents' relational reasoning performance relative to adults' performance might be more sensitive to a peer audience when a physically present friend is evaluating the performance relative to when an unfamiliar peer is allegedly watching via a camera in the scanner. It is not clear whether these differing results are due to the physical presence or the familiarity of the peer (in addition to several other differences between the studies – discussed in 7.1.1). However, studying the influence of 'real' peers in experimental settings might yield greater sensitivity to detect subtle developmental changes. Using real peers or friends allows creating a more ecological valid peer context. This is particularly important as it is challenging to translate the dynamics of real-life peer influence into experimental settings. For example, many risk-taking behaviours are likely to emerge in the 'heat of the moment' and these spontaneous decisions will be difficult to capture in laboratory paradigms. However, using virtual peers or confederates allows greater experimental control. Peer characteristics such as gender, age or popularity can be easily manipulated. In addition, the type of peer influence that is exerted on participants can also be manipulated, for instance whether a peer is risk-seeking or risk-averse or whether participants receive positive or negative peer feedback. Future studies could employ these manipulations to test the impact of different peer characteristics on peer audience or social influence effects.

Another important aspect when designing the social condition factor is to create a suitable alone condition. It has previously been criticised that in many audience effect studies in adults, the experimenter remains present in the room during the alone condition, so that the participant is not actually alone (Guerin, 1993). With the exception of one study by Weigard et al. (2014), this remained a problem in the more recent peer influence studies with many studies not describing whether the experimenter left the testing room during the alone condition (Gardner & Steinberg, 2005; L. O'Brien et al., 2011; Reynolds et al., 2013). In the behavioural studies in **Chapters 4 and 5**, the experimenter left the room during the alone and friend-present condition. In previous behavioural studies investigating peer influence on risky decision-making the peer was encouraged to interact with the participant (Gardner & Steinberg, 2005; L. O'Brien et al., 2011; Reynolds et al., 2013). In contrast, the participant and her friend in the studies in **Chapters 4 and 5** were not allowed to interact. This was important in order to exclude the possibility that a performance impairment in the presence of the peer might simply be due to the participant being distracted by an interaction with the peer or that the peer might advise the participant on the relational reasoning or visual discrimination problems. In order to ensure that the participant and the peer were not interacting, a student was working in a distant corner of the room, facing away from the participant, throughout the experiment (i.e. the student was not able to observe participant's performance). Consequently, while their performance was not observed, participants were not completely on their own in the alone condition. In fMRI studies, participants are aware that the experimenter is operating and monitoring the fMRI scanner and thus it is difficult to create a condition in which the participant feels completely on their own (**Chapter 6**; Chein et al., 2011; Smith, Steinberg, et al., 2014). Finally, even if a participant is truly alone in the alone condition, they know that their responses will be eventually analysed by the experimenter, which might affect their choices or performance; although this is the case in all psychology or neuroscience experiments. These challenges in designing a 'real' alone condition might make it more difficult to detect developmental changes in peer influence effects.

Finally, another challenge when designing the social condition factor is to select an appropriate control condition to the peer present condition. The majority of peer influence studies have compared an alone condition to a peer condition (Chein et al., 2011; Gardner & Steinberg, 2005; L. O'Brien et al., 2011; A. R. Smith, Chein, et al., 2014; A. R. Smith, Steinberg, et al., 2014; Weigard et al., 2014). Only two studies have compared risk-taking behaviour in an alone condition to different peer conditions (Haddad et al., 2014; Reynolds et al., 2013). The study of Haddad et al. (2014) compared the effects of mere observation by three virtual, alleged peers to either risky or safe advice by these three peers. Reynolds et al. (2013) contrasted a condition, in which two familiar, physically present peers were instructed to encourage risk-taking (and their payment was dependent on the participant's level of risk-taking) to a peer condition, in which the peers merely observed and were not allowed to interact. However, previous studies have not compared the influence of peers to the influence of non-peers. Consequently, it is not possible to attribute peer influence effects specifically to the presence of peers in these studies. This is also a limitation of the Audience factor employed in the fMRI study of **Chapter 6**. However, in addition to a peer and an alone condition, the studies in **Chapters 4 and 5** also included a non-peer condition. The results of **Chapter 4** suggest that comparing a peer to a non-peer condition might be more sensitive to detect developmental changes than comparing a peer to an alone condition. Future studies that systematically vary the physical presence of a peer, the familiarity of the peer and the age of the observer, would disentangle what aspects of a peer are critical to produce peer influence effects. In addition, a peer who is physically present relative to a peer who is observing via camera may elicit greater arousal. Thus, future studies should obtain autonomic arousal measures to test whether varying arousal levels might affect peer audience or peer influence effects in general.

## 7.3 Conclusion

In the recent years, many studies in the developmental cognitive neuroscience field have focussed on the investigation of heightened levels of risk-taking in adolescence in affective contexts as well as the impact of peer influence on risky and reward-related decision-making. This thesis aimed to extend these findings. *Firstly,* it was demonstrated that examining risky choice behaviour in the absence of an affective context might be more sensitive to detect subtler developmental changes in the decision variables affecting risky choices during adolescence. *Second*, in an fMRI study, this thesis provided further evidence that the theory of adolescent hyper-responsiveness of the reward system might be too simplistic, calling for future studies to systematically investigate this phenomenon. This fMRI study also provided evidence that adolescent and adult tendencies to conform to the music preferences of a group of music experts were very similar, which was paralleled by similar neural correlates when receiving feedback whether the music experts agreed or disagreed with the participant's song choice. This suggests that adolescents do not show a generalized heightened sensitivity to conform to others' preferences, but instead this effect might be dependent on the identity of the others exerting influence or the object of social influence.

*Third,* this thesis also demonstrated that heightened levels of sensitivity to peer influence during adolescence relative to adulthood are not limited to risky- and reward-related decision-making. Instead, this developmental pattern seems to extend to peer audience effects on cognitive task performance. However, developmental changes in peer audience effects might be less pronounced than peer influence effects found in the domain of risky- and reward-related decision-making. The developmental pattern of peer audience effects found in the studies of this thesis seems to be dependent on the type of task that participants performed while being observed, the difficulty of the task and the characteristics of the peer forming the audience. A follow-up fMRI study demonstrated that observation by a peer audience differentially modulated adolescent and adult activations in the fronto-parietal task network. Future studies are required to further identify the cognitive mechanisms underlying these developmental differences.

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The following paper includes material presented in **Chapter 6:**

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## APPENDICES

### Appendix 3.1 Music Expert Description

Ben is a mash up DJ in London. He loves listening to and playing music. He owns a massive music collection from over 50 countries, but he also listens to the top 40 at work. He is an avid drummer and plays guitar. When DJing, he creatively mixes samples of anything from hip hop to the Beatles and describes his music taste as ‘eclectic but with a good ear for quality sounds.’


Rachel is always listening to music. She recently started as a music journalist, and reviews albums for big music magazines, and interviews up-and-coming artists. Because of her job, she often has access to new music before the general public. She prefers new and independent artists, but admits that she also listens pop music while ‘out and about’ in town and with friends.

Emily works as an intern for a music record company. She is constantly surrounded by music of all genres. Her job involves helping to sign new artists. Although she tends mostly to listen to the artists and bands that she works with, her musical tastes are not restricted to them – she also loves what she refers to as “old classics” as well as anything in the charts that can make her get up and dance!