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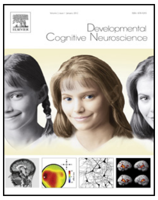

Neurocognitive bases of emotion regulation development in adolescence

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A R T I C L E I N F O

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A B S T R A C T

Emotion regulation is the ability to recruit processes to influence emotion generation. In recent years there has been mounting interest in how emotions are regulated at behavioural and neural levels, as well as in the relevance of emotional dysregulation to psychopathology. During adolescence, brain regions involved in affect generation and regulation, including the limbic system and prefrontal cortex, undergo protracted structural and functional development. Adolescence is also a time of increasing vulnerability to internalising and externalising psychopathologies associated with poor emotion regulation, including depression, anxiety and antisocial behaviour. It is therefore of particular interest to understand how emotion regulation develops over this time, and how this relates to ongoing brain development. However, to date relatively little research has addressed these questions directly. This review will discuss existing research in these areas in both typical adolescence and in adolescent psychopathology, and will highlight opportunities for future research. In particular, it is important to consider the social context in which adolescent emotion regulation develops. It is possible that while adolescence may be a time of vulnerability to emotional dysregulation, scaffolding the development of emotion regulation during this time may be a fruitful preventative target for psychopathology.

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1. Introduction

Emotion regulation has been broadly defined as the monitoring, evaluation and modifying of emotional reactions in order to accomplish goals (Thompson, 1994). This can include both implicit emotion regulation, i.e. processes which occur automatically and largely outside conscious awareness and occur at very early stages of the emotion regulation process, and explicit emotion regulation, which involves using conscious strategies to modify emotional responses (Gyurak et al., 2011). Fully functional emotion regulation requires the ability to recognise the emotional significance of perceived stimuli, to appreciate the need for regulation, and then to select and implement an appropriate strategy (Sheppes et al., 2015). As such, it requires the co-ordination of multiple high-level processes including executive functions (Kesek et al.,

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2009) and in some cases social cognitive skills such as perspective taking.

Adolescence (approximately spanning the ages 10–19; Sawyer et al., 2012) is of considerable interest from an emotion regulation perspective for several reasons. Developmentally, this period is associated with significant biological and physical changes, a growing need for independence, academic and employment pressures and fluctuating social relationships (Casey et al., 2010). These challenges are often accompanied by increased emotional reactivity and stress. As will be discussed in more detail below, it has been hypothesised that ongoing brain development renders adolescents less able to successfully regulate their emotions, putting them at greater risk for anxiety and stress related disorders (Powers and Casey, 2015). Indeed the period of adolescence has been associated with an increasing incidence of internalising and externalising symptoms (Lee et al., 2014; Paus et al., 2008; Spear, 2000). This suggests that adolescents may be particularly vulnerable to emotional dysregulation, although it is worth noting that, as with adults, it can be difficult to distinguish whether these behaviours result from poor regulation, increased affective responses, or both.

Cognitively, high-level executive and social processes needed for emotion regulation, including working memory, inhibitory control, abstract thought, decision making and perspective taking, all undergo development during adolescence (e.g. Blakemore and Robbins, 2012; Dumontheil, 2014; Sebastian et al., 2010a; Somerville and Casey, 2010). Development of these cognitive processes appears to be underpinned by structural and functional development at the neural level, particularly in the protracted development of parts of prefrontal cortex and the remodelling of connections between prefrontal and limbic regions (see below). Simultaneously, adolescents are learning to negotiate increasingly complex social contexts (Sebastian et al., 2010a; Vartanian, 2000). It is possible that the interactions between these neurocognitive processes and social pressures could contribute to the observation that aspects of adolescent emotional processing and regulation development appear to follow a non-linear trajectory. In turn, this may at least partially explain increased emotional volatility and risk taking at this stage of life relative to both adulthood and earlier childhood (Casey and Caudle, 2013). Adolescence may therefore be a critical phase for the development of adaptive emotion regulation, with long-term consequences for future regulatory success and mental health. It has been suggested that adolescence is a period of heightened learning and flexibility (Casey et al., 2008; Steinberg, 2005). It could therefore be a critical phase for the development of adaptive emotion regulation strategies and in turn the implementation of interventions. Targeting this window of opportunity could have positive long-term consequences for mental health (Wekerle et al., 2007).

This review will present mounting behavioural and neural evidence on the development of implicit and explicit emotion regulation in adolescence, and will highlight potential research directions. We will first briefly discuss the structural development of brain regions involved in the detection, expression and regulation of emotion across adolescence (see Blakemore, 2012; Giedd, 2008; Giedd and Rapoport, 2010; Lenroot and Giedd, 2006; Paus, 2005 for more comprehensive reviews of adolescent structural brain development). We will then review human behavioural and neuroimaging data investigating the development of different aspects of emotion regulation, ranging from automatic implicit emotional control (e.g. the ability to filter out emotional information via attentional control mechanisms) through to explicit and effortful strategy use. This section of the review will broadly follow the Process model of emotion regulation (e.g. Gross, 1998), and the recent Extended Process model (Sheppes et al., 2015). fMRI evidence suggests that, while conceptually quite different, there may be continuities in the way these implicit and explicit processes are instantiated at the neural level (e.g. Drabant et al., 2009). It is worth noting that due to the existence of other comprehensive reviews in the field (Blakemore and Robbins, 2012; Casey and Caudle, 2013; Steinberg, 2008) we will not cover risky decision-making, although emotion regulation abilities doubtless play a role here.

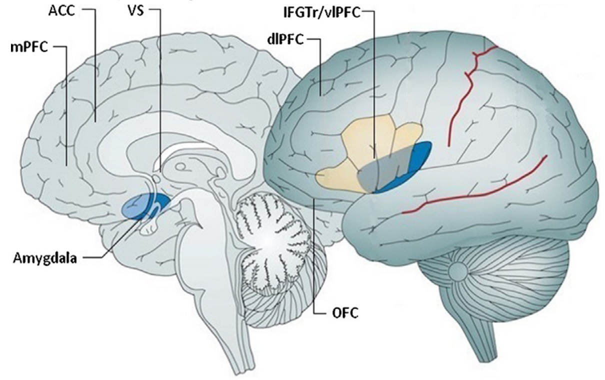
2. Adolescent brain development: relevance to emotion regulation

Adolescence is characterised by a period of heightened emotional reactivity, instability and risk-taking. Several studies using self-report questionnaires have found hypersensitivity to peer rejection and peer influence in adolescents relative to adults and children (Kloep, 1999; Larson and Richards, 1994; O'Brien and Bierman, 1988). Moreover, in a longitudinal study it was found that average emotional states over a week became more negative across early adolescence but this decline in emotions ceased by late adolescence (18 years of age) (Larson et al., 2002). Stability of daily emotional states also increased with age. Increased emotional reactivity has also been demonstrated in behavioural studies where experimental ostracism has been manipulated. In one study, overall mood was found to be significantly lower after ostracism in the adolescent group and state anxiety was higher in the young adolescent group (12–14 years of age) but there were no differences between conditions on either measure for adults (Sebastian et al., 2010a). Adolescents also place a higher emphasis on rewards, particularly social rewards, compared to adults which may make the perceived benefits outweigh the perceived risk (Reyna and Farley, 2006; Steinberg, 2008).

Over the past few decades, neuroimaging studies have begun to suggest that ongoing structural and functional brain development during adolescence may contribute to adolescent-specific behaviours. Evidence suggests that structural brain development in brain regions subserving emotion regulation continues into adulthood (Paus et al., 2008). For example, the prefrontal cortex (PFC), is central in the generation and maintenance of emotion regulation strategies (Ochsner and Gross, 2008; and see below). Subdivisions of the PFC most implicated in emotion processing and regulation include the dorsolateral (dlPFC), ventrolateral (vlPFC) and ventromedial regions (vmPFC) (Kalisch, 2009; Ochsner and Gross, 2008; see Box 1). Development of the PFC is particularly protracted, with reductions in cortical grey matter volume, density and thickness continuing into adolescence and even into the third decade of life (Gogtay et al., 2004; Shaw et al., 2008).

These reductions are thought to index a maturational process. One theory is that they correspond to synaptic pruning, i.e. the elimination of redundant synapses (Blakemore, 2008). Post-mortem studies have shown that synaptic density gradually increases during childhood, peaks in early adolescence, and then reduces by roughly 40% during adolescence and early adulthood before stabilising, following an inverted-U shaped pattern (Huttenlocher and de Courten, 1987). This synaptic pruning in adolescence fine-tunes the remaining connections into specialised functional networks, which might result in more efficient cognitive processing (Blakemore, 2008). However, others have suggested that a reduction in the number of synapses during adolescence is unlikely to have such a large effect on cortical volume as measured by MRI, as cortical grey matter contains numerous cellular elements including neural cell bodies, axons, dendrites, glial cells and blood vessels. Instead, grey matter decline may reflect an artefact of increased myelination of intra-cortical axons (Bourgeois and Rakic, 1993; Paus, 2005; Paus et al., 2008). Unfortunately, methodological limitations make it difficult to directly link developmental change in the living brain as measured with structural MRI with changes in the underlying cellular anatomy.

Box 1: Brain regions associated with emotion regulation and discussed in the current review (adapted from Blakemore, 2008)



Regions shown (clockwise from top left) are medial prefrontal cortex (mPFC), anterior cingulate cortex (ACC), ventral striatum (VS), dorsolateral prefrontal cortex (dlPFC), inferior frontal gyrus triangularis (IFGTr)/ventrolateral prefrontal cortex (vlPFC), orbitofrontal cortex (OFC) and amygdala.
Subcortical regions:

- **Amygdala**: a collection of nuclei that has vast connectivity with several regulatory regions. Ventral and dorsal pathways connect the amygdala to prefrontal brain regions such as the medial and lateral OFC, as well as ACC and dlPFC (Bracht et al., 2009; Johansen-Berg et al., 2008). It has been linked to both learning and expressing the fear response (LeDoux, 2000) as well as determining saliency of emotional stimuli (Adolphs et al., 2005).
- **VS**: connectionally associated with limbic structures, such as the amygdala, hippocampus, midline thalamus, and certain areas of the PFC. It is linked with emotional and motivational aspects of behaviour and is particularly involved in the processing and anticipation of rewards (Schultz, 2006).

Cortical regions:

- **dlPFC:** associated with cognitive control processes, i.e. coordinating thoughts and actions in accordance with overarching internally represented goals. These processes are implicated in emotional control, particularly the down-regulation of negative emotion (Davidson et al., 2000).
- **IFGTr/vlPFC:** activity in this region is evident when reducing subjective negative affect during effortful regulation. These functions may result from interactions with dissociable neural regions, particularly the amygdala and VS (Mitchell, 2011). The vlPFC is also thought to play a critical role in inhibitory control for both emotional and non-emotional stimuli (Elliott and Deakin, 2005; Rubia et al., 2003).
- **mPFC:** integrates inputs from the midline thalamus, basolateral amygdala, and ventral hippocampus (Hoover and Vertes, 2007) related to attention, cognition, emotion, and memory (Vertes et al., 2007). The mPFC is particularly involved in social cognitive processes including Theory of Mind and understanding social emotions (Blakemore, 2008).
- **ACC:** has extensive bidirectional connections with dorsolateral, orbitofrontal, and insular regions of the cerebral cortex. ACC activation is increased during emotional and cognitive executive functions, suggesting it is a neural relay structure where these influences impact response behaviour (Gasquoine, 2013).
- **OFC:** associated with signalling the expected rewards/punishments of an action and is therefore important for adaptive learning (Schoenbaum et al., 2011). The OFC shares extensive reciprocal connections with the amygdala as well as the striatum, particularly ventral reward-related areas (Barbas, 2007).

Subcortical and limbic regions are heavily involved in emotion generation and regulation, and also show developmental change during adolescence. For example, the amygdala increases in volume between the ages of 7.5 and 18.5 years (Schumann et al., 2004). Moreover the amygdala has vast connectivity with several regulatory regions, for example ventral and dorsal pathways connect the amygdala to prefrontal brain regions such as the medial and lateral orbitofrontal cortices, as well as anterior cingulate cortex (ACC) and dlPFC (Bracht et al., 2009; Johansen-Berg et al., 2008). Structural connections between these regions continue to mature during adolescence, resulting in greater top-down control, and strengthening pathways that are called upon routinely (Gee et al., 2013). This improved connectivity is largely a result of a linear increase in white matter volume and density in adolescence; however, this decelerates into adulthood (Giedd et al., 1999; Ostby et al., 2009; Tamnes et al., 2013). Developmental changes in white matter are thought to reflect ongoing axonal myelination, increasing the efficiency of neurotransmission between brain regions (although see Perrin et al., 2009, for a discussion on sex differences in the maturation of white matter; specifically they found age-related increases in axonal calibre in males and increased myelination in females, suggesting a more complex developmental picture).

Together, these structural findings show that regions of the brain involved in emotion generation and regulation continue to develop during adolescence and beyond, and that adolescence may represent a time of particular plasticity for functions underlain by these circuits. They also show that structural development does not always occur linearly over time within brain areas, with quadratic and cubic trajectories often evident (e.g. Mills et al., 2014; Shaw et al., 2008), nor does it occur uniformly across multiple brain regions. Instead, we see that different brain regions that network together to implement emotion processing and regulation develop at different rates within the same individual, with connectivity between these regions also in flux. It has been suggested that this may have functional consequences, particularly for socioemotional processing and behaviour during adolescence, when the bulk of this development occurs. It should be noted however that we currently know relatively little about how the very well-characterised structural brain development occurring during adolescence influences brain function and subsequently behaviour.

Nonetheless, several testable models of links between adolescent brain and behaviour have been suggested. For example, several researchers have posited a ‘developmental mismatch’ or ‘imbalance’ between neural systems supporting emotional reactivity and regulation such that during adolescence the development of prefrontal regions lags behind that of limbic structures such as the amygdala, ventral striatum (VS) and orbitofrontal cortex (OFC) (e.g. Casey et al., 2008; Somerville and Casey, 2010; Steinberg, 2008). As a result, during the time lag in functional maturity between prefrontal and limbic regions, adolescents are less effective at regulating their own emotions and are more affected by emotional context (e.g. peer influence) when making decisions. Most recently, the ‘Triadic Systems Model’ (Ernst, 2014), has been developed, which posits an imbalance between three key systems: PFC (involved in regulatory control), striatum (involved in approach behaviours) and amygdala (involved in avoidance). Unlike the dual-system models mentioned above, it highlights the importance of both approach and avoidance and proposes different patterns of functioning within these three systems during adolescence relative to adulthood. These differences can be quantitative, with different age groups engaging regions more strongly or extensively than other age groups, and/or qualitative, with a shift in dependence on one set of brain regions to another. Moreover the model posits that the three systems mature along different timelines, and that this asynchrony, combined with less mature connectivity across brain regions, may be implicated in adolescent risk taking.

While these models all have in common the idea that behaviour indicative of poor emotion regulation in adolescence is due (at least in part) to the relative immaturity of the PFC and its connections relative to regions involved in more basic emotional responses, this notion has been criticised (Pfeifer and Allen, 2012). Contrary to these models, several studies have not consistently found heightened amygdala responses to emotional stimuli during adolescence (McRae et al., 2012; Pfeifer et al., 2011; Vasa et al., 2011). Moreover studies have shown that heightened VS responses are associated with adaptive functioning such as decreases in risky behaviour, increased resistance to peer influence and reductions in negative affect following social exclusion (Pfeifer et al., 2011; Masten et al., 2009). Additionally, diminished VS (and increased prefrontal) responses to reward anticipation and outcome have been associated with lower daily self-reported positive affect and higher depression in typically developing adolescents (Forbes et al., 2010). The developmental mismatch models therefore may oversimplify the link between adolescent brain development and behaviour.

One way in which these models have been refined and developed is with the integration of hormonal factors. For example Crone and Dahl's (2012) model suggests that pubertal hormone changes influence the limbic system, which contribute to social and affective changes. These social and affective influences interact with cognitive-control systems that can lead to flexibility in the engagement of frontal cortical systems in adolescents, depending on the motivational salience of the context. The interaction of these two processes is generally adaptive and developmentally appropriate to the learning demands of adolescence. However, some situations – perhaps through interactions between individual risk factors and risk environments – can contribute to negative consequences such as substance misuse or depression.

Typically, in cognitive neuroscience, a cognitive function is first well-characterised by behavioural experiments. Models based on these are then further tested using neuroscientific techniques to characterise the neural bases of these functions and refine cognitive models where possible. In the study of adolescent emotion regulation, research has followed a different paradigm. The discoveries in the past 15 years or so regarding ongoing and uneven neural development during adolescence have led to a revival of interest in the development of the functions underpinned by these regions. Functional neuroimaging studies have been used to investigate isolated emotion regulatory functions during adolescence, but until recently behavioural work on adolescent emotion regulation has been surprisingly scarce (Adrian et al., 2011). Luckily, this is now changing as the neuroimaging studies have provided a context for behavioural research (therefore the discussion of studies in this review will follow this sequence). Moreover, adolescent emotion regulation research is also beginning to benefit from the large body of practical and theoretical work on adult emotion regulation to have emerged over the past two decades. Below, influential adult models of emotion regulation are discussed in order to provide a framework for data addressing the development of emotion regulation during adolescence.

3. Models of emotion regulation: relevance to adolescence

There are many strategies for regulating emotional responses, and the most prominent approach to organising these has been to focus on the time point at which regulatory processes are brought to bear on emotion-evoking situations. The "process model" of emotion regulation (Fig. 1a) theorises that emotion generation and appropriate regulatory processes unfold in a particular sequence over time (Gross, 1998, 2014). The first two processes – situation selection and situation modification – both help to shape the situation to which an individual will be exposed. A situation that is emotionally salient gives rise to early emotional reactivity (i.e. intense involuntary reaction to an emotional situation, coupled with a generation of emotional responses such as attentional bias and heightened physiological responses). This emotional reactivity tends to be implicit in nature and therefore occurs before conscious awareness. As awareness increases, the individual actively selects which situation they will place themselves in and modifies its emotional impact (e.g. by shortening exposure time). Situation selection is commonly seen in psychopathology, e.g. where an individual with social anxiety disorder avoids social situations to regulate their emotions (Wells and Papageorgiou, 1998). Attentional deployment is then used to focus attention away from aspects of the situation that provoke undesired emotions. The emotional situation is then explicitly appraised and evaluated, either by engaging in cognitive change such as reappraisal (i.e. reinterpreting the meaning of the situation to reduce its negative impact) or response modulation, which refers to direct attempts to influence physiological, experiential or behavioural emotional responses once they already have been elicited. For example, exercise and relaxation techniques may be used to decrease physiological and experiential effect of negative emotions (Oaten and Cheng, 2006). One of the most researched forms of response modulation is expressive suppression, which entails inhibiting emotional expressions (Gross, 2002). The process model also contains a feedback loop, recognising that emotional responses can modify the situation that gave rise to the response in the first place, and suggesting that the emotion generation process can occur recursively, is ongoing, and dynamic (Gross and Thompson, 2007). The processes identified in this model can be thought of as existing on a continuum from implicit to explicit emotion regulation: as awareness of emotional reactivity increases, regulation becomes more explicit. However, it is difficult to pinpoint the threshold at which regulation becomes explicit, as this likely varies between individuals and contexts.

It has been noted, however, that while the process model focuses mainly on implementation success (or failure) of particular emotion regulation strategies, adaptive emotion regulation actually involves a broader repertoire of skills, including flexible strategy selection (e.g. Bonanno and Burton, 2013). This has led to the recent development of an 'extended process model' (Gross, 2014; Sheppes et al., 2015, see Fig. 1b). This posits that emotion regulation occurs in three stages: (1) Identification, in which an emotional state is identified and the decision over whether or not to regulate this is made; (2) Selection, in which an appropriate regulatory strategy is selected and (3) Implementation, in which the strategy is implemented (corresponding to the original process model). Each stage involves perception of the state of the world, valuation as to whether this is positive or negative, and then action based on the valuation stage. For example, at the Identification stage, an individual might perceive that they are experiencing a negative emotion, evaluate that this exceeds a given threshold of negative affect and that regulation is required, and therefore decide to take action to select an appropriate strategy. This then feeds into the Selection stage, where the full range of regulatory strategies are perceived and evaluated, and appropriate action is taken.

When taken in relation to models of adolescent brain development, the extended process model raises several questions. At each stage, does the perception–valuation–action cycle unfold in the same way as in adults, or are there developmental differences? It might be posited, for example, that if social approval is particularly rewarding (Blakemore and Mills, 2014), a hedonic state elicited in the presence of peers may not trigger the valuation of a need to regulate in the Identification stage. Equally, however, adolescents might be hypothesised to show immaturities at the Selection stage. A wide range of regulatory strategies have been identified (see Table 2 for a list of explicit/deliberate strategies), but adolescents may not have access to the same range as adults,

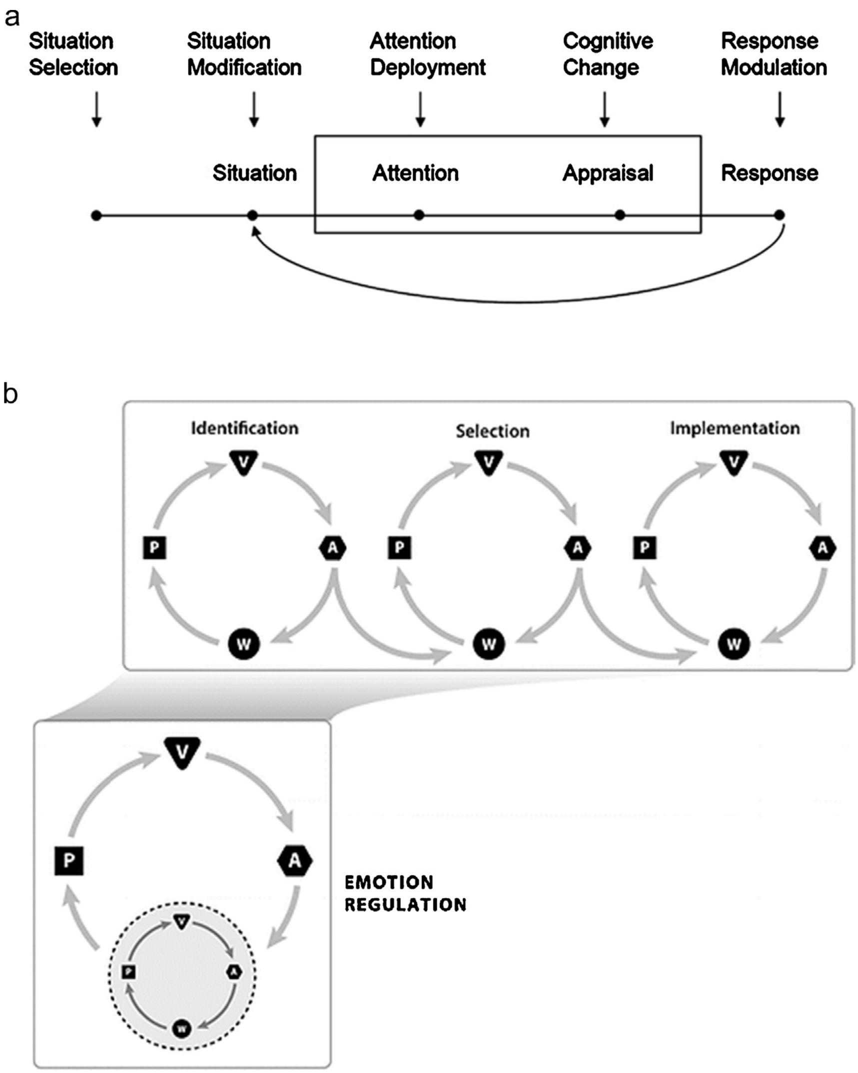


Fig. 1. (a) The process model (Gross and Thompson, 2007) posits that each of the four points in the emotion generation process can be subjected to regulation. From this approach, the process model suggests five different aspects of emotion regulation (situation selection, situation modification, attention deployment, cognitive change and response modulation) that correspond to the regulation of a particular point in the emotion generation process. Reprinted with permission from Guilford Press and J. Gross. (b) The extended process model of emotion regulation. (a) The World (W) gives rise to Perception (P). When valued as either negative or positive, these Valuations (V; known as emotions) give rise to Actions (A) that can change the state of the World. The model classifies three stages of emotion regulation: identification (which involves deciding whether to regulate emotions or not), selection (which involves deciding which strategy to use), and implementation (which involves implementing the chosen strategy). This may change the first-level Valuation system. Reprinted with permission from G. Sheppes.

either because they are unaware of particular strategies, because they have not had sufficient practice in using them, or because certain strategies require advanced executive function (Hofmann et al., 2012) and/or social cognition (Gross, 2014) skills, which continue to develop during adolescence. If these skills are not fully developed, adolescents may not be able to select from the range of strategies available to adults, or may select a strategy that they are unable to implement effectively. Executive function development may also impact the ability to switch flexibly from one strategy to another during Selection, if the original strategy proves ineffective.

The role of executive function and social cognition skills may also play an important role in the Implementation stage. For example, the strategy of reappraisal (cognitively changing one's interpretation of an emotion-eliciting situation) requires that executive functions such as working memory and verbal fluency are in place (Hofmann et al., 2012), but perhaps more importantly that individuals are able to take another person's perspective (Gross, 2014). If a teacher is short with a student, a classic reappraisal response would be to think that perhaps the teacher was just having a bad day. However, there is considerable evidence that the ability to take another person's perspective undergoes protracted development at both behavioural (e.g. Dumontheil et al., 2010) and neural (e.g. Pfeifer and Blakemore, 2012) levels. The following sections will review evidence for the continued development of emotion regulatory processes and their neural bases during adolescence, including the contribution of component executive and social skills where applicable. To date, the vast majority of research has focused on the Implementation stage, i.e. participants are given a strategy and the effectiveness of implementation is measured. However, where possible, reference to Identification and Selection will be made.

These sections will be broadly divided into implicit and explicit processes, as the paradigms used to investigate these are quite different. However, it is noted that this distinction may be too simplistic and that the boundaries between implicit and explicit emotion regulation are likely porous. For instance, Gyurak et al. (2011) proposed that implicit emotion regulation may develop from the habitual use of specific explicit strategies. For example, explicitly reminding oneself that an angry coworker had a bad day may over time lead to the same regulation process occurring implicitly, without awareness.

4. Implicit emotion regulation: neural bases and development in adolescence

Implicit emotion regulation is defined as "any process that operates without the need for conscious supervision or explicit intentions, and aims at modifying the quality, intensity, or duration of an emotional response" (Koole and Rothermund, 2011, p. 1). While this definition does encompass the automatic and habitual use of strategies generally considered explicit as discussed above, this section will focus on regulatory processes that occur at the very earliest stages of emotion perception and processing, and which occur even when individuals are unaware of feeling a subjective emotional response. Emotional stimuli capture our attention (see Carretié, 2014 for a review), particularly via the activation of limbic regions such as the amygdala, which initiates an orienting response to salient stimuli (Gamer and Büchel, 2009). This can be adaptive as such stimuli are particularly likely to require action (e.g. to avoid a dangerous situation), although a hallmark of disorders such as depression and anxiety is a tendency for exaggerated capture by negative and disorder-relevant stimuli (Eysenck and Derakshan, 2011; Williams et al., 1996). However, emotional stimuli in the environment are also often irrelevant, and interfere with our current goals. Regulatory processes typically involving prefrontal circuitry are therefore brought online automatically in order to downregulate limbic responses, particularly when the presentation of emotional stimuli has the potential to interfere with a concurrent executive task. A recent meta-analysis of interactions between emotional stimuli and cognitive control in adults highlighted the involvement of ACC, inferior frontal junction, dlPFC and posterior medial OFC (Cromheeke and Mueller, 2014).

It is therefore no surprise that executive functions are frequently relied upon during emotion regulation as one needs to remember goals, anticipate outcomes, and plan and execute responses (Zelazo and Cunningham, 2007). Accordingly, adult studies have shown that executive functions, such as greater verbal fluency, are associated with greater ability to down-and up-regulate emotions (Gyurak et al., 2009, 2012). A recent study investigating this in adolescence has found similar results. Using self-report questionnaires, Lantrip et al. (2015) found that better executive functions were associated with greater use of reappraisal, while reliance on suppression was associated with poorer executive functions such as poorer inhibitory control, problem solving and organisation skills. The findings suggest that the boundaries between executive functions and emotion regulation are quite porous, with executive functions subserving regulation of cognitive and well as emotional processes.

Consequently, tasks used to measure executive functions have also been adapted to assess emotion regulation. The go/no-go task is frequently used to study attention and inhibitory control. In this task, participants are required to either respond and press a button when certain stimuli appear (Go), or withhold their response when a particular target stimulus appears (No-Go). As Go trials are more common, the task measures one's ability to inhibit a prepotent response. When participants perform this task in the presence of emotional stimuli (e.g. when the no-go stimulus is emotional) greater implicit emotion regulation is required as emotion interferes with cognitive control (i.e. the stopping response). Therefore, slower reaction times on Go trials, or greater false alarm rates (responding on No-Go trials) indicate poorer emotion regulation performance.

Another task that measures inhibitory control and attentional bias is the Stroop test (Stroop, 1935) in which participants are required to name the colour of ink in which an item is printed, while attempting to ignore the item itself. Research has continuously found that it takes participants longer to name the colours when the base items are antagonistic colour names than when they are rows of meaningless stimuli (van Maanen et al., 2009). An adaptation of this is the emotional Stroop task where participants name the ink colour in which emotional and neutral words are written. Emotional words, particularly negative words most salient to an individual (e.g. cleanliness-related words in obsessive compulsive disorder), capture attention and lead to reaction time interference relative to neutral stimuli (see Williams et al., 1996 for a review). Like the go/no-go task, implicit emotion regulation here is defined as the ability to maintain cognitive control in the presence of emotional words.

Several functional neuroimaging studies have been conducted using variations of these tasks (summarised in Table 1) to investigate the neural bases and developmental trajectory of implicit emotion regulation in adolescence. For example in a variation of the go/no-go task, Hare et al. (2008) (Table 1) found that children (aged 7–12) and adolescents (aged 13–18) were slower than adults when responding to fearful target ('go') faces, implying that they were less efficient at overriding affective interference compared with adults, particularly when asked to override what might be considered a prepotent response to avoid (as opposed to approach) fearful faces. Neurally, adolescents showed exaggerated amygdala activity relative to both children and adults across target and non-target expressions (although this exaggerated response habituated with repeated exposure to the stimuli), providing evidence of a non-linear developmental trajectory of amygdala response, possibly in line with 'developmental mismatch' accounts.

This study has been followed up by several behavioural and fMRI studies examining adolescent development in more detail. Tottenham et al. (2011) used a version of this task with 100 participants aged 5–28. Emotion regulation performance was defined as the false alarm rate on no-go trials using emotional face stimuli, since these trials required inhibitory control to be performed in the presence of emotion. More generic cognitive control was defined as false alarm rate on neutral no-go trials. Both emotion regulation and cognitive control improved with increasing age, but importantly the discrepancy between the two decreased with increasing age, i.e. adults showed a smaller difference in performance in withholding responses in the presence of emotion relative to neutral faces than did children or adolescents.

An fMRI study using a variant of this go/no-go task with only appetitive (happy face) and neutral calm face cues found that the false alarm rate on no-go 'happy' trials relative to no-go neutral trials was disproportionately greater for adolescents (aged 13–17) than for either children (aged 6–12) or adults (18–29) (Somerville et al., 2011). This adolescent-specific performance dip was paralleled by heightened activity in the VS, an area involved in the processing and anticipation of rewards (Schultz, 2006). Conversely, activation in the inferior frontal gyrus (IFG; typically activated during inhibitory control (e.g. Aron et al., 2004), decreased with increasing age for no-go relative to go trials, and was positively correlated with overall no-go false alarms. Connectivity analyses between IFG and striatum also showed age differences: children showed reduced functional coactivation between these regions on happy no-go relative to happy go trials, compared with adolescents and adults, while adolescents showed increased coactivation between dorsal and VS relative to both children and adults. The neural mechanisms at play during adolescence seem to support the models discussed above: when required to regulate behaviour, adolescents may be driven disproportionately by subcortical signalling, (which shows a non-linear, inverted U-shaped response with age), in the presence of a functionally immature prefrontal regulatory system.

Table 1
Studies investigating the development of implicit emotion regulation.

Study	Participants	Paradigm	Behavioural results	Neuroimaging results
Hare et al. (2008)	60 (30F) participants; Children aged 7–12; Adolescents aged 13–18; adults aged 19–32	Emotional go/no-go task using fearful, happy and calm facial expressions	Children and adolescents had longer RTs than adults when responding to fearful go trials	Adolescents vs. children and adults showed greater amygdala activity across go and no-go trials (fMRI)
Tottenham et al. (2011)	100 (49F) participants; 53 children aged 5–12; 24 adolescents aged 13–18; 23 adults aged 19–28	Emotional go/no-go task using fearful, sad, angry and happy facial expressions	False alarm rate to emotional no-go stimuli was higher than it was to neutral no-go stimuli for all groups, but the difference decreased with increasing age	N/A
Somerville et al. (2011)	62 (31F) participants; 18 children aged 6–12; 19 adolescents aged 13–17; 25 adults aged 18–29	Emotional go/no-go task using happy and calm facial expressions	False alarm rate on no-go happy trials relative to no-go neutral trials was greater for adolescents than for either children or adults	Adolescents vs. children and adults showed greater ventral striatum activity. PFC recruitment positively correlated with overall accuracy and decreased with increasing age for no-go vs. go trials. Adolescents vs. children and adults showed greater ventral-dorsal striatal co-activation for happy no-go vs. go trials (fMRI)
Cohen Kadosh et al. (2014)	60 (30F) participants; 30 early adolescents aged 11–12; 30 late adolescents aged 17–18	Emotional go/no-go task variant (Overlap task) using fearful and angry facial expressions. Go trials indicated by green fixation cross, no-go indicated by red. Participants decide which of two lines presented either side of a central face was horizontal	Young vs. late adolescents had slower RTs on fearful go trials. No age differences for either go or no-go accuracy	N/A
Cohen-Gilbert and Thomas (2013)	100 (50F) participants; 20 children aged 11–12; 20 early adolescents aged 13–14; 20 adolescents aged 15–16; 20 young adults aged 18–19; 20 adults aged 20–25	Go/no-go task where letters were presented at the center of IAPS images depicting negative, positive, or neutral scenes	RTs were longer for negative trials across all age groups Adolescents aged 13–14 and girls aged 15–16 had lower accuracy on no-go trials in the presence of negative images vs. other age groups	N/A
Perlman and Pelphrey (2011)	20 (11F) children aged 5–11; 25 (12F) adults aged 19–41	Go/no-go point loss task to induce negative emotion	N/A	After points were lost (emotion regulation required) amygdala activation increased in adults, but decreased in children Effective connectivity between ACC and amygdala increased with ER demands and increased with age (fMRI)
Lewis et al. (2006)	58 (30F) participants aged 5–16. Age span subdivided into six periods of 2 years each	Go/no-go point loss task to induce negative emotion	Accuracy improved and response time decreased with age	Increased response associated with inhibitory control (the N2 component) in adolescents but not children in response to point loss. No-go N2 amplitudes were greater than go N2 amplitudes following the emotion induction at all ages. No-go P3 (inhibitory) amplitudes were greater than go P3 amplitudes and they decreased with age, whereas go P3 amplitudes remained low (ERPs)
Sebastian et al. (2010b)	35 (all F) participants; 19 adolescents aged 14–16; 16 adults aged 23–28	Emotional Stroop task using rejection-themed words	Adolescents vs. adults made more errors across the whole task	Adults showed greater right ventrolateral PFC response to rejection vs. neutral/acceptance words. Adolescents showed a greater response in this region to acceptance vs. rejection and no difference to rejection vs. neutral (fMRI)
Veroude et al., 2013	74 (39F) participants; 38 late adolescents aged 18–19; 36 young adults aged 23–25	Cognitive and emotional Stroop task	Trend towards larger emotional interference RTs in late adolescents vs. young adults	Young adults showed greater activation in the dorsomedial PFC, left IFG, left middle temporal gyrus, precuneus and middle cingulate vs. late adolescents during negative words (fMRI)
Ladouceur et al. (2009)	60 (32F) participants; Children aged 8–10; Young adolescents aged 11–13; older adolescents aged 14–17; and adults aged 18–27	Emotional face *N*-back task	Age negatively correlated with RTs on 2-back trials in the presence of fearful distracters, but only across participants high in trait anxiety	N/A

In each of the above studies, the emotional content of the stimuli was relevant for task performance, i.e. participants at least needed to be able to distinguish between emotional and calm faces before making a go vs. no-go decision, if not overtly recognise the precise emotion displayed. Facial expression recognition continues to develop in adolescence, with the ability to categorise different expressions developing at different rates; for example, categorisation of happy faces develops earlier than fear (Durand et al., 2007; Thomas et al., 2007). This factor may at least partially contribute to developmental differences seen in this version of the emotional go/no-go task, or influence the results in an unpredictable manner. There have been a couple of recent studies that have instead looked at inhibitory control in the context of task-irrelevant emotion.

Sticking with facial expression stimuli, Cohen Kadosh et al. (2014) used an emotional go/no-go task variant known as the Overlap task (Bindemann et al., 2005; Table 1) to compare groups of early (aged 11–12) and late (aged 17–18) adolescents. On go trials, the young adolescent group was disproportionately slowed by fearful faces relative to happy and neutral faces, as compared with the late adolescent group. This was interpreted as indicating poorer attentional control in the presence of fear in early adolescence, possibly underlain by continuing maturation of dlPFC. It could be that this group were more likely to have their attention captured by the fearful faces; or that they had more difficulty disengaging from these faces once attention had been captured. Another possible interpretation is that arousal caused by the fearful faces interfered with the decision-making component of the task (i.e. right/left decision), even if attention was appropriately allocated. Interestingly, unlike the emotional go/no-go task discussed above, no age differences were seen for either go or no-go accuracy, perhaps suggesting that age differences in inhibitory control during adolescence are less apparent when emotion is task-irrelevant. This interpretation is supported by a recent study which directly compared go/no-go task versions where emotion was relevant vs. irrelevant in participants aged 6–25, and found that only task-relevant emotion had a strong effect on inhibition (Schel and Crone, 2013).

However, it could also be that the development of inhibitory control in the presence of emotion during adolescence is particularly subtle and follows a non-linear trajectory, rendering it necessary to sample relatively large numbers of participants across the adolescent age range in order to see development. This approach was taken in a recent study by Cohen-Gilbert and Thomas (2013) ($N = 100$) which employed a go/no-go task in which task-relevant letters were presented at the centre of task-irrelevant background images portraying negative, positive, neutral or scrambled scenes. Slower reaction times were found across all age groups for negative trials. However, lower accuracy on no-go trials in the presence of negative images was seen specifically in adolescents aged 13–14 years (and in girls aged 15–16). Thus, negative emotional inputs appear to disrupt regulatory efforts more easily in early-mid adolescence even when the emotional information is not directly relevant to the task. A shortcoming of using this type of stimuli is that the images are visually less well-matched as compared to facial stimuli. Nonetheless age-related developments in emotion-related inhibitory control measured by this task show parallels with behavioural and neuroimaging data discussed above for the emotional go/no-go task in which emotion is task-relevant. It is interesting to speculate as to why task-irrelevant emotion impacted inhibitory control in this task but not others. Possibly negative pictures and scenes are more emotionally arousing than negative facial expressions; alternatively, the use of finer grained age distinctions enabled subtle age differences to emerge.

Another approach to studying the development of inhibitory control in the context of emotion is to induce emotional states in participants. In one developmental fMRI study, 20 participants aged 5–11 and 25 adult controls engaged in a go/no-go task in which they gained and lost points towards a desired prize (Perlman and Pelphrey, 2011). The task was designed such that participants lost all of the points they had previously won, in order to induce negative emotions of frustration. Five-to-11-year-olds and adults displayed distinct patterns of ACC and amygdala activation when emotion regulation was required; for example, children showed reduced amygdala response when recovering from emotional frustration, while adults showed the reverse pattern. Connectivity analyses showed that as frustration (and thus regulation demands) increased, effective connectivity between the ACC and amygdala also increased. Importantly, this connectivity increased with age in the children, suggestive of ongoing neural maturation underlying this process between childhood and early adolescence. This study did not specifically explore development on this task across adolescence. However, Lewis et al. (2006) (Table 1) conducted an event-related potential (ERP) study using a similar task with 58 participants aged 5–16 years. They found an increased response associated with inhibitory control (the N2 component) in adolescents but not children in response to a negative emotion induction (point loss). These findings suggest that differing cortical regions are involved in emotion regulation as children mature into adolescence.

In early- and mid-adolescence, peer relationships are particularly salient: individuals show an increased sensitivity to acceptance and rejection by peers (Brown, 2004; Nelson et al., 2005; Sebastian et al., 2010a), and an increase in awareness of others' opinions (Parker et al., 2006; Vartanian, 2000). On the basis of this, Sebastian et al. (2010b) used a rejection-themed emotional Stroop task with fMRI, and found that mid-adolescents (aged 14–16) showed attenuated right vlPFC responses relative to adults during the processing of rejection-related words compared with neutral and acceptance words. This finding is in line with the above theories suggesting that prefrontal regulatory regions continue to develop between mid-adolescence and adulthood. Emotion was task-irrelevant and the requirement to regulate emotion was implicit. However, it is possible that this task tapped into immaturity in prefrontal mechanisms that contributes to hypersensitivity to rejection in adolescence; particularly, as will be seen below, there is considerable overlap in the prefrontal regions recruited during implicit and explicit social rejection tasks.

An emotional variant of the Stroop task has also been used to investigate the development of prefrontal control in late adolescence (ages 18–19) compared with early adulthood (23–25 years; Veroude et al., 2013). Adults activated dorsomedial PFC and precuneus to a greater extent than late adolescents in the presence of negative stimuli (e.g. 'death') compared with neutral words (e.g. 'chair'). While the right vlPFC (inferior frontal gyrus) region identified above as showing age differences in the rejection-themed emotional Stroop did not differentiate between age groups in response to emotional stimuli in this study, left inferior frontal gyrus did show reduced activation in the late adolescents in a non-emotional contrast. This study demonstrates that the maturation of regulatory mechanisms involved in the implicit processing of emotional (and non-emotional) information continues even between late adolescence and the early twenties. This time period (approximately 18–23: 'emerging adulthood') is receiving increasing empirical attention in efforts to link identity and role change occurring at this time with continuing neural maturation.

While inhibitory control has so far received the most empirical attention in relation to implicit emotion regulation, there is also evidence for ongoing development of interactions between working memory and emotion processing. Ladouceur et al. (2009) (Table 1) used an emotional *n*-back task in which participants viewed a continuous stream of items and determined whether each item matched the stimulus presented *n* stimuli before, in the presence of flanking emotional or neutral faces. In this behavioural study, performance of participants (aged 8–27 years) was examined on trials with neutral and fearful faces as emotional distracters and varying in working memory load (i.e., 2-back versus 0-back condition). Age was negatively correlated with reaction times on 2-back trials in the presence of fearful distracters, i.e. participants became faster with age. However, this effect only held across participants high in trait anxiety. The role of individual differences in emotion regulation and relevant traits during adolescence is discussed in more detail in Section 6 in relation to psychopathology.

Together, these behavioural and neuroimaging studies illustrate specific implicit emotion regulation processes that continue to develop from childhood through adolescence and into adulthood, and deliver insights into their neurocognitive developmental trajectories. Reaction time and accuracy data across tasks show general improvement in the ability to resist interference by emotion between adolescence and adulthood (e.g. Cohen Kadosh et al., 2014; Tottenham et al., 2011) however, some studies have found evidence of a non-linear trajectory, with increased interference in mid-adolescence compared with earlier childhood (e.g. Cohen-Gilbert and Thomas, 2013). Neuroimaging evidence is suggesting that the mechanisms underlying these effects are largely in line with developmental mismatch and triadic model accounts of adolescent development. Studies have shown increased limbic responses to emotional stimuli (e.g. Hare et al., 2008), reduced prefrontal control (e.g. Sebastian et al., 2010b; Veroude et al., 2013), and altered or reduced connectivity between these systems (e.g. Somerville et al., 2011) during adolescence. Thus, there is considerable evidence that the ability to filter out emotional stimuli entering the processing stream in a 'bottom-up' manner (Gyurak et al., 2011) in pursuit of a goal continues to mature throughout adolescence. The following section will examine whether similar evidence is available for the development of explicit regulatory processes.

5. Explicit emotion regulation

Explicit emotion regulation strategies require conscious effort during initiation, and some level of monitoring during implementation (Gyurak et al., 2011). As discussed above, explicit strategies of cognitive reappraisal (reinterpreting emotion-eliciting scenarios in a more positive light) and expressive suppression (reducing the outward display of an emotional reaction) have received the most empirical attention, both in adolescence and in emotion regulation research in general. In a recent study by Lantrip et al. (2015) although it was found that reappraisal use was associated with better executive functions in a group of adolescents (aged 12–18), there were no age related differences in strategy use. However, the sample size of this study was relatively small ($N = 70$) in comparison to a longitudinal study of 1128 adolescents (Gullone et al., 2010). Using a similar self-report method Gullone and colleagues found that suppression use decreases between the ages of 9 and 15. Suppression is generally considered a maladaptive strategy, with reliance on this strategy associated with reduced ability to repair negative moods and decreased experience of positive affect (Gross and John, 2003). Therefore, this reduction in use in this age range makes theoretical sense, as individuals gain the experience and underlying executive and social skills to develop alternative strategies (John and Gross, 2004).

By the same logic, we would predict that use of the more adaptive reappraisal strategy would increase over this time; however, evidence to date has been mixed. Contrary to predictions, Gullone et al. (2010) found an overall decrease in the self-reported use of this strategy in everyday life between the ages of 9 and 15. However, results using a lab-based reappraisal paradigm suggest development in the ability to successfully use reappraisal, at least when instructed to do so (Silvers et al., 2012). Forty-four participants aged 10–23 viewed negative and neutral IAPS pictures and rated their current strength of negative affect on a 4-point scale when either instructed to 'look' at the picture and give their natural response, or 'decrease', i.e. use reappraisal as trained prior to the experiment. Regulation success was defined as percentage decrease in self-reported negative affect on 'decrease' trials relative to 'look' trials for negative stimuli, and was found to improve with age, following both linear and quadratic trends. It is worth noting significant methodological differences between these two studies that could explain the discrepant findings, including different age ranges, sample sizes and operationalisations of reappraisal (frequency vs. success). Studies which combine self-reported and experimental measures of reappraisal use and success across the adolescent age range are therefore needed (see Box 2 'Outstanding Questions'). While there is research on adults investigating this, there are still many confounds involved such as the different methods used and the timescales in which frequency and success are measured. More research is needed to assess real-world sampling of emotion regulation success over longer time periods both in adults and adolescents (see McRae, 2013, for a discussion on future directions).

Neuroimaging studies of explicit emotion regulation strategies in adolescence have recently begun to investigate age differences in both spontaneous and instructed regulatory processes. In a study by McRae et al. (2012) participants aged 10–22 years completed a reappraisal task similar to that reported by Silvers et al. (2012) above, whilst undergoing fMRI. A linear increase in cognitive reappraisal ability was found with age (in line with Silvers et al., 2012) and this was accompanied by a concomitant age-related

Box 2: Outstanding research questions

- Why do some studies of implicit emotion regulation suggest a linear pattern of development in adolescence, and others a non-linear pattern? Does it depend on the specific task, the sample age range, or both?
- How exactly are these linear and non-linear effects related to structural and functional brain development?
- How does performance on implicit measures of emotion regulation relate to the use of explicit strategies during adolescence? Is the same underlying neural circuitry involved? Do these abilities develop together, does one precede the other, or are they relatively independent?
- How does the neurocognitive development of related skills during adolescence such as mentalising and linguistic ability contribute to the use of particular emotion regulation strategies?
- What is the relationship between spontaneous use of emotion regulation strategies in adolescence and the ability to use specific strategies when instructed?
- Can the extended process model be applied to adolescents? At each stage, does the perception-valuation-action cycle unfold in the same way as in adults, or are there developmental differences?
- Which of the diverse array of emotion regulation strategies available (see Table 2) do adolescents actually use most in everyday life, and does this change over the course of adolescence?
- Are there particular 'neural vulnerabilities' associated with poor emotion regulation that might predict the onset of internalising or externalising symptoms?
- Can we improve adolescent emotion regulation with a view to preventing the onset or maintenance of internalising and externalising symptoms? If so, which aspects of emotion regulation training would be most fruitful, and would it be helpful to look at neural markers and use tools such as neurofeedback?

increase in left vlPFC. As discussed above, this brain region has been implicated in cognitive control processes in both emotional and non-emotional contexts, and is also associated with cognitive reappraisal in adults (Ochsner and Gross, 2005, 2008). When participants were not specifically asked to reappraise (i.e. during an unregulated emotional response) adolescents (aged 14–17 years) showed less activation in brain areas associated with social cognition, such as medial prefrontal, posterior cingulate and temporal regions than did either children (aged 10–13 years) or emerging adults (aged 18–22 years). However, these regions were activated to a greater extent during reappraisal (i.e. a regulated emotional response) in adolescents compared to the other age groups. The authors interpreted this as suggesting that adolescents may not automatically engage in these social cognitive processes during unregulated responding, but are able to do so when specifically instructed. However, these inferences should be treated with some caution. The study did not directly test whether social cognitive processes were indeed responsible for activation in these regions (although this is a reasonable assumption based on previous studies); and it is further unknown whether activation of these regions during passive viewing in the children and emerging adults truly constituted spontaneous regulation.

Studies have also looked at the development of reappraisal in the regulation of appetitive cravings for unhealthy foods (Silvers et al., 2014; Giuliani and Pfeifer, 2015). In a recent study, females aged 10–23 were asked to use reappraisal to reduce cravings (Giuliani and Pfeifer, 2015). Across all participants reappraisal engaged regions commonly activated during self-regulation such as the vlPFC and the ACC. While there was a lack of age-related changes in reappraisal success, activation in the right IFG was found to be positively correlated with age, suggesting that older participants may have needed to work harder to regulate their desires for unhealthy food. The authors state however that the age-related changes seen in the reappraisal of negative emotion may not be as pronounced in the reappraisal of food craving.

Given theories linking emotional behaviours in adolescence to maturational processes in underlying brain structure, it makes sense to examine the relationship between structural maturation and successful development of regulatory strategies. This approach was taken in a recent longitudinal study (Vijayakumar et al., 2014), in which 92 participants underwent structural scans at ages 12 and 16, and reported their usage of reappraisal and suppression at age 19. Greater cortical thinning in left dlPFC and vlPFC over the course of adolescence was associated with greater use of reappraisal at age 19, but only in female participants. The direction of the result is in line with the idea that cortical thinning indexes maturation (e.g. Shaw et al., 2008; Tamnes et al., 2013), and thus may underpin more efficient usage of regulatory processes reliant on these brain regions. While it is unclear why the effect was specific to females, the authors suggest that peak cortical thickness may have been reached by the first time point in females but not males, meaning that continuing increases in cortical thickness could have obscured in males the pattern that was observed in females. Studies of reappraisal in adults have also shown that females may recruit prefrontal regions to a greater extent than males (McRae et al., 2008): maturation of the prefrontal regions of interest studied here may therefore be of greater relevance for females than males.

As is the case for adult emotion regulation research, the majority of behavioural and neuroimaging studies in adolescents have focused on strategies that are most tractable for use in the laboratory, namely reappraisal and suppression. However, some researchers have argued that focusing on specific strategies may be problematic for understanding the everyday use of a broad range of explicit emotion regulation strategies (Aldao and Nolen-Hoeksema, 2013). One recent experience sampling study (Heiy and Cheavens, 2014) identified approximately 40 strategies that adult participants (aged 18–31) reported using over the course of the study for the regulation of both negative and positive states (summarised in Table 2). Indeed it is often necessary to regulate positive as well as negative states, e.g. one may wish to upregulate positive responses by savouring a recent happy experience, or conversely downregulate positive reactions if they are socially inappropriate, e.g. *schadenfreude*.

Experience sampling methods have been used for some time to investigate emotion regulation in adolescence. For example, Silk et al. (2003) asked adolescents (aged 12–15) to provide multiple reports about the intensity, lability, and strategies used to regulate their naturally occurring emotional experience throughout the day across one week. Adolescents also completed self-report measures of adjustment. It was found that adolescents who reported using disengagement (e.g. denial, avoidance, escape, or wishful thinking) or rumination strategies to regulate their emotions were associated with higher levels of depressive symptoms and externalising behaviours. It is worth considering whether it may be possible to incorporate aspects of this more ecologically valid approach with neuroimaging techniques to understand emotion regulation in typical adolescence. As will be seen in the following section, several studies have taken an important step in this direction, linking neural responses as measured in the laboratory with evidence of emotion regulation and dysregulation in everyday life in relation to psychopathology. As discussed above, adolescence is associated with increased emotional reactivity and the developmental trajectory of certain brain areas may render adolescents less able to regulate their emotions effectively, putting them at greater risk of internalising and externalising problems. Examples from the internalising (depression) and externalising (conduct problem) literature will be given in the following section.

6. Emotion regulation, the adolescent brain and adolescent psychopathology

6.1. Internalising symptoms

Psychopathology associated with internalising symptoms notably increases during the adolescent years (Lee et al., 2014; Paus et al., 2008). Major depressive symptoms rise drastically from around 2% in early adolescence (ages 13–15) to 15% in middle adolescence (ages 15–18) (Hankin et al., 1998). In addition, adolescents classified as having internalising problems such as depression have been shown to score highly on the use of maladaptive emotion regulation strategies such as self-blame and rumination, whilst obtaining low scores on reappraisal use (e.g. Garnefski et al., 2005). Recent neuroimaging studies have therefore attempted to shed light on mechanisms underlying poor emotion regulation in adolescent depression.

Neuroimaging studies of explicit emotion regulation in depressed adolescents have largely focused on reappraisal, where this group are known to exhibit behavioural deficits. Studies of instructed reappraisal in depressed adults have found reduced dlPFC response and reduced PFC–amygdala coupling relative to healthy controls (e.g. Erk et al., 2010), in line with findings in typical adults that successful reappraisal relies on the ability of regions including dlPFC, dACC and vlPFC to downregulate emotional responses in amygdala, VS and insula (Ochsner et al., 2012). However, to date, fMRI studies of reappraisal in depressed adolescents suggest a different pattern. Perlman et al. (2012) compared 14 adolescents with depression and 14 controls (aged 13–17) on a task requiring participants to either ‘maintain’ or ‘reduce’ emotional responses to negatively valenced images. During the ‘maintain’ condition, the authors found increased amygdala response and decreased PFC–amygdala connectivity in the depressed adolescents relative to controls, in line with predictions. However, this

Table 2
The range of explicit emotion regulation strategies used in everyday life by young adults (adapted from Heiy and Cheavens, 2014, with author permission). Experience sampling methods have shown that adolescents also use many of these strategies (e.g. Silk et al., 2003); although as yet it is unclear whether adolescents have access to the same breadth of strategies as adults, or how adolescents recognise the need for regulation and select particular strategies. It is possible that these processes may relate to neural maturation associated with underlying executive function and social cognitive skills.

Strategy	Strategy impacts negative or positive emotion	How strategy is used
Acceptance	Negative	I accepted the situation and/or my emotions
Behavioural activation	Negative and positive	I found an activity to keep myself distracted/I sought out activities and socialising
Benefit finding	Negative	I thought about how I could become stronger or learn from the situation
Broadening	Positive	I thought about all the good things that were happening in my life as well
Capitalising	Positive	I made a plan to make the good situation happen again
Consequences	Negative or positive	I thought about all the different things in my life that this situation would impact
Denial	Negative or positive	I just acted like the situation never happened
Exercise	Negative	I exercised
Emotional expression	Positive	I emphasised my emotions by showing them
Entertainment	Positive	I listened to upbeat music or watched a happy movie or show
Future focus	Positive	I concentrated on upcoming positive events in my life
Generalising	Negative	I thought about all the other things that have happened to me in addition to this
Minimising	Positive	I thought about how the situation was not really that great
Non-suicidal self-injury	Negative	I hurt (pinched/cut/burned/hit) myself
Other-blame/credit	Negative and positive	I thought about how the situation was someone else's fault/due to someone else
Perspective	Negative	I reminded myself that things could be worse
Positive refocusing	Negative	I thought of something pleasant instead of what had happened
Problem solving	Negative	I made a plan to make the situation better
Reappraisal	Negative or positive	I thought about the situation in a different way
Reminiscing	Positive	I reminisced about pleasant memories
Replaying	Positive	I replayed all the details of the event in my head
Reward	Positive	I treated myself to something special
Rumination	Negative	I thought over and over again about the situation and my feelings
Savouring	Positive	I tried to revel in the moment and concentrate on how good I felt
Self-blame/credit	Negative and positive	I thought about how my actions brought about this situation
Sleep	Negative	I went to sleep
Social support/sharing	Negative or positive	I found a friend or family member to talk to
Stimulus control	Positive	I avoided all negative thoughts and stressors
Substance use	Negative or positive	I smoked a cigarette/drank alcohol/got high
Suppression		
Expressive Suppression	Negative or positive	I controlled my emotions by not showing them
Emotional Suppression	Negative	I ignored my feelings and acted like the situation never happened at all

pattern did not hold for the 'reduce' condition: conversely, greater connectivity was found in depressed adolescents when instructed to 'reduce'. This suggests that dysregulation of PFC–limbic circuitry may contribute to adolescent depression under some circumstances (in this case the instruction to 'maintain'), but that this is not necessarily a constant marker in adolescent depression.

A similar pattern of results was seen in an fMRI study using a more ecologically valid 'chatroom' task in which social stress is created by participants being rejected by virtual peers, relative to being accepted (Guyer et al., 2009). Adolescents are likely to encounter peer rejection in everyday life, and may show greater sensitivity to its effects than do adults (Sebastian et al., 2010a). It has further been argued that rejection may play a special role in the aetiology of adolescent depression, with reciprocal relationships developing over the course of adolescence between social rejection and depressive symptoms (Platt et al., 2013). Platt et al. (2015) instructed 15 depressed and 15 non-depressed adolescents aged 15–17 to either 'attend' or to 'reappraise' instances of social rejection. Both groups were able to implement reappraisal, reducing negative affect in response to rejection; however, the depressed group showed increased connectivity between right frontal pole and regions including amygdala and hippocampus, specifically during reappraisal. Together, the two extant studies of reappraisal in adolescent depression raise the possibility that mechanisms underlying poor emotion regulation may not be identical to those in adult depression. However to date there have been no studies directly comparing depressed adolescents and adults on emotion regulation abilities in the same sample. Platt et al. (2015) speculate that this increased connectivity during instructed reappraisal may reflect an ability for depressed adolescents to address their pre-existing emotion regulation deficits using cognitive strategies, and suggest that reappraisal training may therefore represent a particularly fruitful avenue for treating adolescent depression. This is an intriguing possibility, but will require additional studies with larger samples to confirm. Another possibility is that depressed adolescents need to engage regulatory mechanisms to a greater extent to achieve the same behavioural effect.

There have also been several studies which have looked at the neural bases of typical adolescent responses to peer rejection in the absence of an explicit instruction to regulate (Guyer et al., 2009; Masten et al., 2009; Sebastian et al., 2011), although participants are fully aware of being rejected and of the negative emotions generated, meaning participants may use explicit regulatory strategies spontaneously. One longitudinal fMRI study explored relationships between neural responses to social rejection and depressive symptoms one year later in 20 13-year olds (Masten et al., 2011). This study used the 'Cyberball' paradigm (Williams et al., 2000), in which participants play an online ball tossing game and are unknowingly systematically included or excluded at particular points during the game by the experimenter. Responses in the subgenual ACC predicted depressive symptoms at follow-up. This region was of particular interest given evidence that heightened activity here has been associated both with depressive symptoms (Saxena et al., 2003) and with heightened responses to peer rejection in typically developing adolescents (Masten et al., 2009). Future work could investigate whether instructed strategies such as reappraisal could influence the responsivity of this region in adolescent depression.

6.2. *Externalising symptoms*

While conduct disorder sometimes onsets before the age of 10 (childhood onset), the majority of externalising symptoms, which include physical aggression, theft, destruction of property and truancy, emerge during adolescence (Moffitt, 1993). Aggressive behaviour is often categorised as either reactive or proactive: reactive aggression refers to aggression triggered by external provocation or frustration, and is associated with poor executive function (Giancola et al., 1996) and impulsivity (Raine et al., 2006); whereas proactive aggression refers to aggression used instrumentally in pursuit of a goal, and is associated with psychopathic traits in adulthood (Patrick, 2001) and callous–unemotional traits in childhood/adolescence (Frick et al., 2003). Poor emotion regulation is thus particularly associated with reactive as opposed to proactive aggression (Eisenberg et al., 2010), although reactive and proactive aggression are moderately correlated and proactive aggressors often display low frustration tolerance.

Neuroimaging studies have only recently begun to investigate conduct problems in adolescence, and early studies in this area have not differentiated between subtypes (e.g. Herpertz et al., 2008). One study which did differentiate groups of adolescents with conduct problems on the basis of low vs. high levels of callous–unemotional traits found that low levels of such traits (i.e. those whose aggressive behaviour is more reactive in nature) were associated with amygdala hyperactivity in response to fearful faces presented implicitly, i.e. below the level of conscious awareness (Viding et al., 2012). This study illustrated inherent overreactivity in response to emotion at the very earliest levels of processing, suggested to be due to an attentional orienting response effect (Gamer and Büchel, 2009; Moul et al., 2012). This is likely to have downstream consequences that contribute to poorly regulated behaviour, since hypervigilance to threatening stimuli is a hallmark of many psychological disorders including anxiety (Richards et al., 2014) and post-traumatic stress disorder (Dalgleish et al., 2001), as well as reactive aggression (Dadds et al., 2006). However, this study did not target regulatory mechanisms specifically.

Sebastian et al. (2014) tested an overlapping sample of adolescents with conduct problems on an implicit emotion regulation task in which participants made a perceptual decision (is a blue dot present or absent?) in the presence of fearful or calm faces. Importantly, when the blue dot was present, it was either presented in the eye region of the face (a particularly salient region for interpreting fear cues: Adolphs et al., 2005) or elsewhere in the face. Adolescents with conduct problems and low callous–unemotional traits (reactive-aggressive subtype) were disproportionately slowed in making the dot/no dot decision in the presence of fearful eyes relative to typically developing controls; and slower reaction times in the presence of fearful eyes in this group were associated with increased left amygdala response. This group also showed increased neural responses during the presentation of fearful eyes in subgenual ACC and OFC relative to controls; two regions involved in directing attention to affective stimuli (Zikopoulos and Barbas, 2012) and integrating emotion and cognitive control (Pessoa, 2008). These findings suggest that emotion may disproportionately interfere with executive processes in adolescents with reactive-aggressive conduct problems, although future studies could additionally examine interactions between prefrontal and limbic circuitry to uncover more detail as to the mechanisms of poor implicit emotion regulation in this group.

If ineffective prefrontal-limbic control is important in the aetiology of reactive aggression, then we might predict that improvement in symptoms would be accompanied by improvement in cortical function. Lewis et al. (2008) investigated this hypothesis using the frustration-inducing emotional go/no-go task described in Section 4) in an ERP study with 27 participants aged 8–12 with mixed externalising an internalising symptoms and 15 typically developing controls. Participants completed the task before and after a 14-week community intervention involving elements of cognitive behavioural therapy and parent management training. Following treatment, children who showed behavioural improvement also showed a normalisation of their N2 ‘inhibitory control’ response, generated by ventral frontal regions, while non-responders did not. Interestingly, the normalisation seen was actually a reduction in N2 amplitude. The authors suggest that previously this group had relied on an inflexible, threat-focused regulatory style which generated a strong N2 response. While still preliminary, this study illustrates that interventions designed to reduce externalising and internalising symptoms may concomitantly help to normalise neural mechanisms tapped by implicit emotion regulation tasks. It is potentially interesting to ask whether the reverse would hold true, for example whether training neural circuits involved in implicit (or explicit) emotion regulation would lead to downstream positive consequences for behaviour.

7. Conclusions

The development of emotion regulation during adolescence has enjoyed a recent surge in interest, largely prompted by discoveries over the past 15 years or so regarding ongoing adolescent development of the cortical and subcortical circuitry underpinning regulatory processes. This review brings together models concerning the structural and functional development of the adolescent brain with models of emotion regulatory processes. It is likely that development continues to occur in processes underpinning all three stages of the extended process model, namely Identification, Selection and Implementation. However, the majority of behavioural and neuroimaging work to date has focused on Implementation. There is some evidence that both behavioural and neural responses during implicit emotion regulation tasks such as emotional go/no-go task variants develop in a non-linear manner, with mid-adolescents showing exaggerated responses to emotion compared with younger and older individuals. This would support models suggesting that non-linear structural brain development has consequences for brain function and adolescent behaviour. However, not all studies show this pattern, and it is unlikely that links between brain structure, brain function and behaviour will be straightforward. For example, even if brain and behaviour are shown to follow similar developmental trajectories for a given function, this does not necessarily mean that one trajectory causes the other (Pfeifer and Allen, 2012). Regarding explicit strategies such as reappraisal, some studies show an increase in the use of this strategy over adolescence, in line with theories suggesting that reappraisal use should increase as underlying executive, verbal and social cognitive skills develop. However, others suggest that instructed use may not be paralleled by increasing spontaneous use with age in everyday life. As there are still relatively few studies in the area, methodological differences across studies make it difficult to draw overall conclusions. These include whether emotion is relevant or irrelevant to task performance, whether particular strategies are instructed or not, how tasks are adapted for neuroimaging, and sample age range and size. As more empirical work becomes available, an important next step will be to synthesise evidence through the use of meta-analysis. Some outstanding research questions are listed in Box 2. Of most practical relevance will be work delineating relationships between the neural bases of emotion regulation and the emergence and prevention of psychopathological symptoms. The plasticity of the adolescent brain at this time could yield opportunities for positive intervention before symptoms escalate to clinical levels.

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