

REVIEW

The role of the medial frontal cortex in the development of cognitive and social-affective performance monitoring

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Abstract

Adolescence is a time of many cognitive and social-affective changes that are important for rapid behavioral adjustment to a variety of environmental demands and social contexts. Performance monitoring is one of the most important processes for behavioral adjustment; it allows individuals to evaluate outcomes of actions and change behavior accordingly. Neuroimaging studies have demonstrated that dorsal and ventral subregions of the medial frontal cortex are differentially engaged in performance monitoring, depending on the cognitive or social-affective dimensions of a task. Based on a review of neuroimaging, ERP, and heart rate studies, the implications of these modality-dependent contributions are discussed for the development of performance monitoring in adolescence.

Descriptors: fMRI/PET/MRI, Cognition, Motivation, Children/Infants

Adolescence, which spans the life period between childhood and adulthood, is marked by many cognitive, affective, and social changes (Blakemore & Mills, 2014; Steinberg, 2008). Adolescence starts with puberty (also referred to as early adolescence), which is the period during which hormonal changes in brain and body start a cascade of changes in physical appearance and behavior. Puberty starts approximately around age 9–11 years, generally earlier for girls than for boys, and continues until the mid-teens (Dahl, 2004). Puberty is followed by a second phase of adolescence, during which adolescents develop further in terms of cognition, affective processing, and social orientation to eventually become adults with mature social goals (also referred to as mid- to late adolescence, ages 16–20 years). Whereas the beginning of adolescence is largely defined by biological changes, the end of adolescence is defined socially or culturally (Crone & Dahl, 2012; Dahl, 2004).

Performance monitoring plays a central role during adolescent development and is particularly important for rapid adaptation to a variety of changing social environments, such as forming new friendships, changing schools, and making future-oriented choices. The neural processes that are involved in the development of performance monitoring have been studied from a variety of perspectives, using cognitive learning tasks (Hajcak, Moser, Holroyd, & Simons, 2006; Holroyd & Coles, 2002) and social-affective feedback tasks (Fareri & Delgado, 2014; Somerville, Heatherton, &

Kelley, 2006). A key brain region for performance monitoring is the medial prefrontal cortex (mPFC) and its connections, which has been implicated in a wide range of performance-monitoring contexts (van Noordt & Segalowitz, 2012). A central question concerns whether different aspects of performance monitoring follow different neurodevelopmental trajectories, which has implications for understanding how adolescents learn, navigate, and adapt to a complex and changing social world.

This review will describe the role of the mPFC in the development of cognitive and social-affective performance monitoring. The mPFC area is large and heterogeneous, and meta-analyses based on neuroimaging studies performed in adults have demonstrated that subregions along the dorsal to ventral axes have different connections to other prefrontal cortex regions (van Noordt & Segalowitz, 2012). Some reports have argued that these networks are contributing to dissociable components of performance monitoring (Amodio & Frith, 2006; Flagan & Beer, 2013; Van Overwalle, 2009), whereas others have argued for an integrated view of mPFC as a region reflecting common operations across cognitive and affective domains (Shackman et al., 2011; Shenhav, Botvinick, & Cohen, 2013). This review will discuss the role of these mPFC subregions in relation to the development of cognitive and social-affective performance monitoring in adolescence. The results of this review will be discussed in relation to the changes in adolescent brain function as a sensitive period for cognitive and social-affective development.

Subregions in the mPFC and Their Role in Performance Monitoring

The mPFC, which consists of the medial parts of superior, middle, and orbital frontal cortex, ranges across a set of Brodmann areas (8/32/24/9/10/25) (Flagan & Beer, 2013). Studies in the adult lit-

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erature have demonstrated that cognitive performance monitoring relies on a dorsal mPFC region, specifically the presupplementary motor area (pre-SMA) and dorsal anterior cingulate cortex (dACC) (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004) (see Figure 1). In these studies, participants typically have to make a single or binary choice when presented with a stimulus, which is followed by performance feedback, which can have a positive valence when the choice is correct or negative valence when the choice is incorrect. Event-related potential (ERP) studies have shown that processing errors is associated with a negative ERP response even before feedback is presented (the error-related negativity, ERN, which peaks approximately 80–100 ms after an error is committed), and the source of this ERP component is estimated in the dACC (Carter & van Veen, 2007; Holroyd & Coles, 2002). A second negative ERP response is observed in response to performance feedback (the feedback-related negativity, FRN; also referred to as medial frontal negativity, MFN, which peaks approximately 250 ms after the feedback is presented). There is a debate with respect to whether the FRN/MFN responds to negative feedback (Segalowitz et al., 2010), reflects a reward-related positivity that is absent on negative feedback (i.e., nonreward) trials (Foti, Weinberg, Dien, & Hajcak, 2011), or responds to saliency of feedback irrespective of valence (Santesso, Dzyundzyak, & Segalowitz, 2011). The source of the FRN has been estimated in both the dACC (van Noordt & Segalowitz, 2012) and in the basal ganglia (Foti et al., 2011), consistent with the hypothesis that this potential reflects activity of phasic increases and decreases in midbrain dopamine systems, which signal to the dACC that outcomes are better or worse than expected (Holroyd & Coles, 2002).

Consistent with these findings, fMRI studies showed that, in adults, processing of negative feedback relative to positive feedback is associated with increased activation in the pre-SMA/dACC (Holroyd et al., 2004; Zanolie, Teng et al., 2008), and the neural response is larger when the negative feedback is unexpected (Zanolie, Van Leijenhorst, Rombouts, & Crone, 2008). This activity is often accompanied by activation in the lateral parts of the prefrontal cortex, and together these areas have been implicated in the implementation of behavioral adjustment (Carter & van Veen, 2007; Kerns et al., 2004). The “warning system” function of the dorsal mPFC also occurs in more affective domains, such as when individuals experience negative affect or pain, suggesting that the signals that are responsible for triggering adaptive control, or the need to update response sets in order to avoid negative consequences of choices, are processed in the dorsal mPFC independent

of domain (Shackman et al., 2011). Together, these studies led to the hypothesis that the dorsal mPFC monitors when outcomes are worse than expected and when there is a need to adjust behavior accordingly.

The more ventral parts of the mPFC (Figure 1) are generally engaged when the outcomes of actions are signaling reward or positive feedback in uncertain environments, for example, when learning the outcome of a gamble or a probabilistic choice (Blakemore & Robbins, 2012). In typical gambling experiments, individuals are presented with an uncertain choice, where one option may lead to a greater reward but has a higher probability of losing, whereas the other option may lead to a smaller reward with a smaller probability of losing. Several studies have reported that receiving rewards after uncertain choices results in activity in the ventral mPFC and the ventral striatum (Clark, Lawrence, Astley-Jones, & Gray, 2009; Delgado, 2007; Haber & Knutson, 2010). Together, these findings were interpreted to suggest that the ventral mPFC represents a convergence zone where affective information of the ventral striatum is updated and coded in terms of reward value (Ernst & Fudge, 2009).

The ventral part of the mPFC is also often implicated in receiving social-affective feedback (Flagan & Beer, 2013). In a pioneer study, Somerville et al. (2006) compared the effects of social evaluation feedback by presenting information about being liked or disliked by another peer. Crucially, participants could first make a prediction about whether they anticipated that they would be liked or not, depending on a pre-session where their picture was judged by peers on a first impression. Being liked (i.e., receiving positive feedback) relative to being rejected (i.e., receiving negative feedback) resulted in increased activation in the subgenual ACC, the most ventral part of the mPFC (see Figure 1) (see also Gunther Moor, van Leijenhorst, Rombouts, Crone, & Van der Molen, 2010; Guyer, Choate, Pine, & Nelson, 2012). These findings are consistent with the hypothesis that the subgenual ACC represents motivational influences on social cognition. Specifically, Flagan and Beer (2013) suggested that the subgenual ACC has a bottom-up influence on social cognition and has connections with the ventral mPFC, which is thought to mediate top-down influence on social evaluation by facilitating or controlling an activated motivational state.

Taken together, the mPFC seems to be consistently involved in performance monitoring, in the context of monitoring errors or receiving feedback on prior actions. However, there is a differentiation in the extent to which subregions of the mPFC are responding to cognitive error/negative feedback, which engages mostly the dorsal mPFC, or social-affective reward feedback, which engages mostly the ventral mPFC. These different contributions and their developmental trajectories can have implications for understanding how adolescents navigate a changing social world, given that this is a time of natural learning and adaptation (Blakemore & Mills, 2014; Crone & Dahl, 2012).

The Development of Cognitive Performance Monitoring

Cognitive performance monitoring is often studied in the context of executive control functions, which refer to those abilities that allow one to work with relevant information online for the purpose of obtaining a future goal (Zelazo, Craik, & Booth, 2004). Developmental studies have shown that there are important behavioral improvements across childhood and adolescence in executive functions, particularly in children’s ability to monitor, evaluate, and adjust behavior according to changing environmental demands.

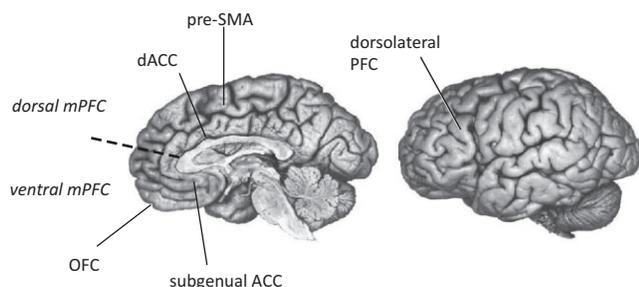


Figure 1. Display of anatomical and functional subregions within the medial frontal cortex implicated in performance monitoring. PFC = prefrontal cortex; mPFC = medial prefrontal cortex; ACC = anterior cingulate cortex; dACC = dorsal anterior cingulate cortex; pre-SMA = presupplementary motor area; OFC = orbitofrontal cortex.

Performance monitoring can be signaled by internal signals that are activated when one notices that an error is committed, or by external signals, such as signals from the environment (van Noordt & Segalowitz, 2012).

Internal monitoring of actions has been extensively studied in the ERP literature, by focusing on the ERN. Studies that have compared the ERN in speeded reaction time tasks across development have reported that the ERN is present, but small, in children between ages 3–7 years (Grammer, Carrasco, Gehring, & Morrison, 2014), 5–7 years (Torpey, Hajcak, Kim, Kujawa, & Klein, 2012), 7–9 years (Richardson, Anderson, Reid, & Fox, 2011), and 10–12 years (van Meel, Heslenfeld, Rommelse, Oosterlaan, & Sergeant, 2012), and becomes larger between late childhood (10–12 years) and early adulthood (Santesso, Segalowitz, & Schmidt, 2006; van Meel et al., 2012; Wiersma, van der Meere, & Roeyers, 2007), with continued changes between late adolescence and adulthood (Ladouceur, Dahl, & Carter, 2007; for a review, see Tamnes, Walhovd, Torstveit, Sells, & Fjell, 2013). These findings have been complemented by heart rate analyses, which have also demonstrated that heart rate slowing following an error increases between childhood and early adolescence (ages 8/9–12 years) with continued development until early adulthood (Crone, Jennings, & Van der Molen, 2004; Crone, Somsen, Zanolie, & Van der Molen, 2006). These studies have been interpreted to suggest that error monitoring, purportedly controlled by the dorsal mPFC, develops gradually during adolescence.

In terms of external feedback monitoring, there are marked behavioral age-related improvements in the ability to rapidly adjust behavior following cues or feedback that signal a change of rules on the Wisconsin Card Sorting Task (Huizinga, Dolan, & van der Molen, 2006), task switch paradigms (Crone, Ridderinkhof, Worm, Somsen, & van der Molen, 2004), and learning tasks (Eppinger, Mock, & Kray, 2009; van den Bos, Guroglu, van den Bulk, Rombouts, & Crone, 2009). These improvements are more pronounced during childhood and early adolescence (8–12 years), but continued improvement is observed in early to mid-adolescence (12–15 years) (Huizinga et al., 2006). These behavioral changes seem to be associated with a developmental improvement in filtering relevant, informational performance feedback for future behavioral adaptation. The evidence for this hypothesis comes from the following fMRI and ERP studies.

The neural correlates of performance monitoring by external signals have been studied using fMRI by examining neural responses following positive and negative performance feedback when children and adolescents perform cognitive learning tasks. It is known from the adult literature that the dACC/pre-SMA (parts of the dorsal mPFC) are active when individuals receive negative performance feedback (Holroyd et al., 2004; Zanolie, Teng et al., 2008). Several developmental fMRI studies have demonstrated that activation in the dACC/pre-SMA following negative feedback increases between childhood and early adolescence (Crone, Zanolie, Van Leijenhorst, Westenberg, & Rombouts, 2008; van den Bos et al., 2009; van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008). For example, Crone et al. (2008) asked individuals of three age groups (8–11 years, 14–15 years, and 18–25 years) to perform a rule-learning task that was based on the principles of the Wisconsin Card Sorting Task. Participants were asked to sort stimuli in one of four locations and received performance feedback after each sort. Participants had to use trial-and-error learning to find the correct sorting rule, and after this rule was applied for a variable number of trials, it changed unexpectedly. Developmental comparisons showed that the pattern of activation

in ACC/pre-SMA changed between ages 8–11 years and 14–15 years, such that 8–11-year-olds activated this region for all types of negative feedback, whereas 14–15-year-olds and 18–25-year-olds activated this region specifically after unexpected negative feedback signaling a rule shift. Developmental increases in neural activity following negative feedback were also observed in the dorsolateral prefrontal cortex (DLPFC), and this region showed a more protracted development with continued changes between mid-adolescence and adulthood (see also van den Bos et al., 2009; van Duijvenvoorde et al., 2008).

A recent study by Peters et al. (2014) aimed towards examining the exact time point at which the neural pattern to negative feedback reached adult levels by including participants of each age group between ages 8 and 17 years (i.e., 10 age groups). Using a rule-searching task with deterministic feedback, participants had to use positive and negative feedback to find the correct location for different stimuli. Peters et al. (2014) found that the developmental pattern in learning from negative feedback, and associated activity in dACC/pre-SMA and DLPFC following negative feedback, increased until age 14, after which it stabilized (Peters et al., 2014). There were strong brain-behavior correlations, showing that this network was involved in performing the task well, but there was also unique activity associated with age-related changes. These neural patterns of protracted development in dACC/pre-SMA and DLPFC have been observed in a variety of executive control paradigms, such as studies examining response inhibition and working memory (for a review, see Bunge & Wright, 2007) and can therefore be interpreted as the maturation of a cognitive learning process.

A specific hypothesis, which was derived from the neuroimaging studies on performance monitoring, was that young children are less able to distinguish between the informational value conveyed by feedback, which would lead to developmental changes especially when the feedback is invalid or ambiguous. This interpretation finds support in a study that made use of ERPs and heart rate analyses. Eppinger et al. (2009) compared 10–12-year-old children and 19–24-year-old adults on a probabilistic learning task in which feedback could be valid (contingent upon performance), partly valid (80% contingent upon performance), or invalid (not contingent upon performance). They found that the FRN was deviant in children compared to adults especially in the partly invalid condition. Similar results were observed in a study that compared 9–11-year-old children, 13–14-year-old adolescents, 20–30-year-old adults, and 65–75-year-old adults using a feedback-learning task. The FRN was largest in young children and declined with increasing age, and the FRNs to positive and negative feedback did not differentiate for children but did differentiate for the adolescents and adults (Hammerer, Li, Muller, & Lindenberger, 2011). These findings are consistent with studies that used heart rate slowing as an index of performance monitoring, in which it was also found that 8–12-year-old children already show a strong heart rate response to valid negative feedback (Crone et al., 2006), but failed to distinguish between valid and invalid feedback (Crone, Jennings, & van der Molen, 2004; Van Duijvenvoorde, Jansen, Griffioen, Van der Molen, & Huizinga, 2013).

Taken together, studies examining performance monitoring based on internal error monitoring and processing negative feedback have consistently shown that the ability to monitor errors and distinguish between feedback types develops in childhood and adolescence. That is to say, between childhood and adolescence, there is an increase in capacity for internal performance monitoring (i.e., monitoring errors). In addition, between childhood and ado-

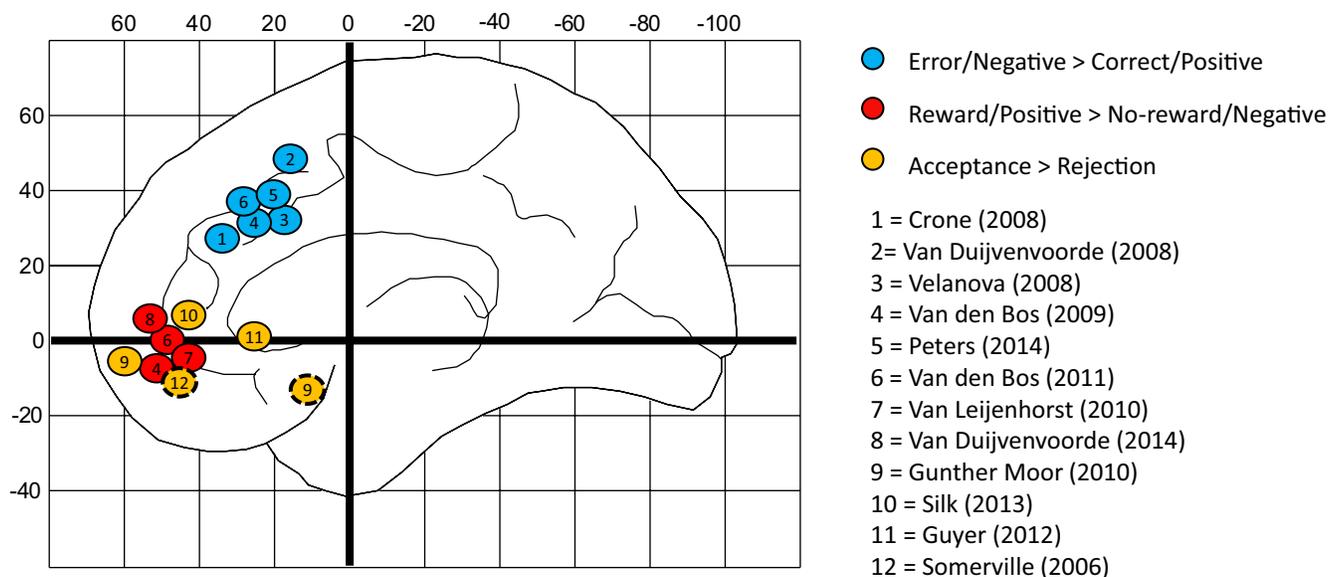


Figure 2. Activity in medial PFC for the comparisons error/negative feedback > correct/positive feedback, reward/positive feedback > loss/negative feedback, and social acceptance > social rejection feedback. This meta-analysis is based on developmental fMRI studies on performance monitoring, which have reported activation in dorsal and ventral mPFC. Dashed lines represent activation based on adults only. The selected studies are described in more detail in the online supporting information.

lescence, adolescents become more successful in filtering informative value of feedback, thereby learning to use feedback more efficiently. This development is accompanied by changes in activity patterns in dorsal mPFC (specifically dACC/pre-SMA) (see Figure 2 for an overview of these findings), and lateral prefrontal cortex (Peters et al., 2014). These findings have been attributed to changes in executive functions and protracted development of the dorsal mPFC and lateral prefrontal cortex (Hammerer & Eppinger, 2012).

The Development of Social-Affective Performance Monitoring

Social-affective performance monitoring is often studied by examining how individuals process feedback after making choices with uncertain outcomes for monetary gains or social rewards. Adolescence is well known for its rise in risky behavior, specifically in the domain of sensation and fun seeking (Steinberg et al., 2008). Developmental studies using experimental risk-taking paradigms have reported that risky and disadvantageous choices are mostly present at young ages (8–10-year-olds) and decrease during adolescence (Crone & van der Molen, 2004; Van Duijvenvoorde, Jansen, Bredman, & Huizenga, 2012; Van Leijenhorst et al., 2010), although some studies have reported an initial rise in risk taking in early to mid-adolescence followed by a decrease in risk taking (Burnett, Bault, Coricelli, & Blakemore, 2010; Figner, Mackinlay, Wilkening, & Weber, 2009). Moreover, risky behavior increases in the presence of peers, more so for adolescents than for adults (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011; Gardner & Steinberg, 2005). These behavioral findings lead to the hypothesis that adolescents may be more sensitive to the rewarding aspects of sensation seeking and social interactions.

Neuroimaging studies have examined developmental differences in processing monetary reward and social rewards in separate studies. In terms of research on processing monetary rewards, prior

studies have dissociated between neural correlates of the decision process and neural correlates of outcome monitoring, in which outcomes are mostly presented as rewards and losses (Delgado, 2007; Galvan, 2010). The comparison of rewards and losses have shown that especially rewards result in elevated activation in the ventral mPFC (Blakemore & Robbins, 2012; Clark et al., 2009; Van Leijenhorst et al., 2010), as well as the ventral striatum (Delgado, 2007). These areas are known to have anatomical connections and are often interpreted as a reward network (Blakemore & Robbins, 2012). Developmental neuroimaging studies reported that especially the ventral striatum is more active in early (10–12 years) to mid-adolescence (14–15 years) than in adults, which has been interpreted in terms of elevated reward sensitivity in adolescence (Van Leijenhorst et al., 2010). For example, a study by van Leijenhorst et al. (2010) showed that adolescents (ages 12–16 years) had stronger reward-related activation in the ventral striatum than children (ages 8–10 years) and adults, and all age groups showed robust activity in the ventral mPFC following reward relative to loss. This effect has been reported in several studies and suggests hypersensitivity of this reward network in early to mid-adolescence (Galvan et al., 2006; Geier, Terwilliger, Teslovich, Velanova, & Luna, 2010; van Duijvenvoorde et al., 2014; see Figure 2).

The elevated response in the connections between ventral striatum and ventral mPFC was found not only in studies using simple gambling designs (van Duijvenvoorde et al., 2014), but also in studies where participants had to learn from reward outcomes in an uncertain environment. In a probabilistic learning task with rewards and losses, Cohen et al. (2010) showed that participants between ages 8–30 years all had robust activity in the ventral mPFC when receiving positive feedback (monetary gain) relative to negative feedback (no gain). In addition, Cohen et al. (2010) showed that adolescents (ages 11–19 years) had a stronger neural response in the ventral striatum to positive prediction errors, that is to say, to unexpected rewards, than children and adults (Cohen et al., 2010).

These findings were interpreted as a stronger dopaminergic response to rewards in mid-adolescence, which possibly aids in directing adolescents towards explorative learning (see also Van den Bos, Cohen, Kahnt, & Crone, 2012). It should be noted that these prior probabilistic learning studies also reported linear age-related changes (decreases or changes in connectivity) in ventral mPFC in relation to decision value, but not in response to feedback, suggesting that internal monitoring of behavior (i.e., monitoring choice values) may be represented differently than external action monitoring (i.e., feedback processing). This question should be addressed in more detail in future studies.

A second line of social-affective studies has focused on the neural responses to receiving social rewards in adolescence, specifically in the context of peer evaluation. Several developmental studies used the paradigm developed by Somerville et al. (2006) to study the neural response to feedback indicating whether or not a participant is being accepted by a peer. Adolescence is a time of major social reorientation during which adolescents spend more time with peers and peer evaluation becomes more important (Blakemore & Mills, 2014). For example, in mid-adolescence, adolescents report that peer evaluation affects their feelings of social worth more than when they were early adolescents (O'Brien & Bierman, 1988). Also, being excluded by a peer in an online laboratory game resulted in feeling lower mood and higher state anxiety in adolescence (Sebastian, Viding, Williams, & Blakemore, 2010). Thus, it was expected that social acceptance and social rejection is salient in adolescence.

Neuroimaging studies using the social evaluation paradigm developed by Somerville et al. (2006) in adolescents have reported a set of compelling findings. Consistent with findings in adults, receiving feedback about being accepted by a peer resulted in robust activity in the ventral mPFC (mostly in the subgenual ACC) in both adolescents and children (Gunther Moor, van Leijenhorst et al., 2010; Guyer et al., 2012). For example, Gunther Moor, van Leijenhorst et al. (2010) showed that, when participants could first make a guess about whether they would be accepted by a peer based on first impression (yes or no), followed by actual feedback from the peer (yes or no), the yes/yes answer resulted in strong activity in the ventral and subgenual ACC for participants aged 8–10 years, 12–14 years, 16–17 years, and 18–25 years (see Figure 2). There were no age differences in neural responses in the

ventral and subgenual ACC or other brain regions to being accepted, suggesting that this neural signature of feeling accepted is already present at a young age (but see Guyer et al., 2012, who reported age differences to being accepted in several other cortical and subcortical areas).

Even though acceptance feedback may be a strong marker for learning, it would be expected that the processing of social rejection feedback becomes more salient in mid-adolescence (Sebastian et al., 2010). Neuroimaging studies did not find differences in activation in relation to processing rejection feedback (Gunther Moor, van Leijenhorst et al., 2010; Guyer et al., 2012), but interesting evidence for this assumption comes from studies examining heart rate and pupil dilation responses to social rejection feedback. That is to say, Gunther Moor, Crone & van der Molen (2010) found that receiving rejection feedback (no) after anticipating you will be accepted (yes) resulted in pronounced heart rate slowing, approximately two to three heart beats after the rejection feedback was presented (Gunther Moor, Crone et al., 2010) (see Figure 3). When these heart rate responses were studied in 8–10-year-old children and 11–14-year-old adolescents, the results showed that the cardiac slowing was larger for adolescents than for children (Gunther Moor, Bos, Crone, & Van der Molen, 2014). These findings indicate that the monitoring of negative social feedback emerges in adolescence. Secondly, pupil dilation, which is an index of increased activity in cognitive and affective regions of the brain, was previously found to provide a larger response to peer rejection relative to acceptance in adolescence ages 9–17 years, with an age-related increase in pupil dilation to peer rejection (Silk et al., 2012; see Figure 3). Thus, there is evidence from psychophysiological measures that processing peer rejection feedback develops in adolescence.

An important question for the future will be to examine the interplay between neural responses to negative feedback (errors, negative performance feedback, losses, social rejection) and positive feedback (positive performance feedback, rewards, social acceptance) and the relation with activity in the dorsal and ventral mPFC. Possibly the strongest neural activity is observed for feedback, which is most informative for learning at a certain age, or in a specific developmental phase, which can be negative feedback in a cognitive learning paradigm (i.e., signaling a warning for updating behavior) but reward feedback in a social-affective learning

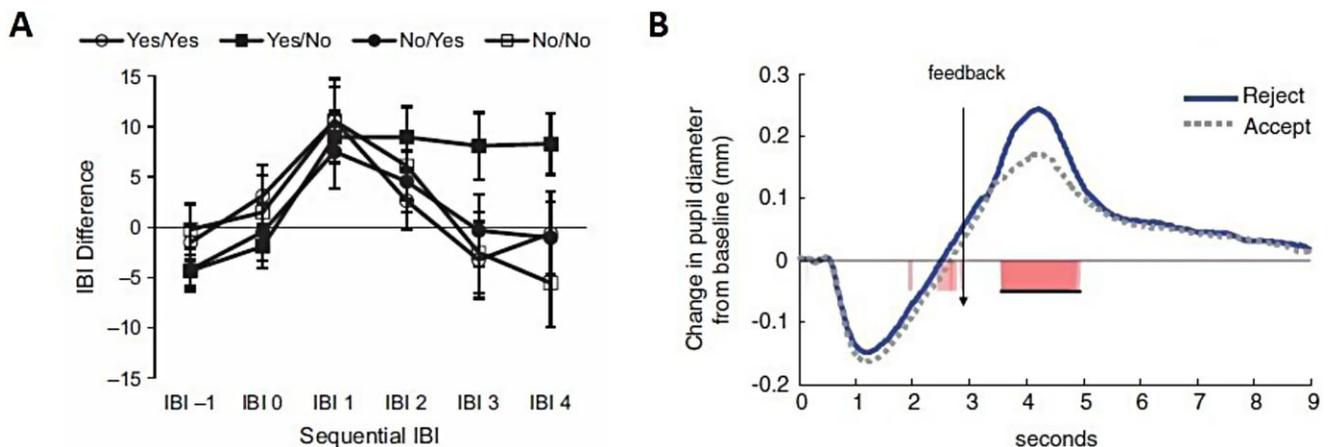


Figure 3. Heart rate and pupil dilation responses to social rejection. A: Heart rate slowing to peer rejection feedback in adults displayed in interbeat intervals (IBIs) (Gunther Moor, Crone et al., 2010). B: Pupil dilation to peer rejection in 11–17-year-old adolescents displayed in seconds (Silk et al., 2012).

paradigm (i.e., signaling the salience of reward and social acceptance). In addition, even though this review focuses on general developmental patterns, prior studies have shown that activity in mPFC is sensitive to individual differences in temperament and personality (Santesso & Segalowitz, 2009; Segalowitz et al., 2012). Future studies should combine the different psychophysiological indices to get a better understanding of which neural responses are most sensitive to the task manipulations and can inform us about how adolescents learn in complex social environments.

Conclusion

Performance monitoring has been studied from different perspectives with tasks that focus on the cognitive or social-affective consequences of choices. Prior studies reported that the mPFC is a key brain region for performance monitoring, yet subregions within mPFC showed distinguishable contributions to performance monitoring depending on the informative value and valence of the feedback. The dorsal mPFC (dACC and pre-SMA), and its connections with the lateral PFC, is mostly implicated in negative feedback processing in a cognitive-learning context, signaling a warning signal for updating task sets (Holroyd & Coles, 2002; Zanolie, Teng et al., 2008), whereas the ventral mPFC and the subgenual ACC, and their connections to the limbic areas, show stronger responses to reward feedback in an affective and social context (Fareri & Delgado, 2014; Flagan & Beer, 2013). Studying the contributions of these separable brain networks from a developmental perspective provides a promising starting point for understanding the development of performance monitoring especially in adolescence, when there are high demands for navigating a complex and socially challenging world.

This review provides evidence from empirical studies that subcomponents of performance monitoring rely on separable contributions of the mPFC. Specifically, when monitoring is focused on learning from errors or negative feedback, there is a developmental increase in neural responses in dorsal mPFC (Crone et al., 2008; van den Bos et al., 2009) and the lateral PFC, an area with which the dorsal mPFC is thought to have strong connections (Carter & van Veen, 2007; Kerns et al., 2004). These developmental improvements are also observed for ERP and heart rate changes, which are associated with monitoring outcomes (Crone, Jennings

et al., 2004; Eppinger et al., 2009; Tamnes et al., 2013). In contrast, when monitoring is focused on processing positive outcomes, such as when receiving a reward after taking a gamble, this is associated with a neural response in the ventral mPFC, which is already strongly present in early adolescence (Van den Bos et al., 2012; Van Leijenhorst et al., 2010). Similarly, when receiving feedback from peers about being liked or socially accepted, this results in a neural response in the subgenual ACC, which is also strongly present in early adolescence (Gunther Moor, van Leijenhorst et al., 2010).

A recent study by Perkins, Welsh, Stern, Taylor, & Fitzgerald (2013) demonstrated that, when learning from errors in an interference task, topographical analysis of individual data patterns showed that adults recruited more dorsal/posterior parts of the ACC and mPFC, whereas younger children recruited more ventral parts of the ACC and mPFC. Moreover, performance was a strong predictor of the extent to which participants recruited more dorsal/posterior regions, such that better performance was associated with more activity in the dorsal mPFC. The authors interpreted these findings to suggest that children may perform interference tasks in a different way than adults (Perkins et al., 2013). This study highlights the importance of understanding strategy use across development and the role of performance differences. These questions should be followed up in future research where developmental trajectories of mPFC subregions are studied in relation to cognitive and affective context and performance.

The reviewed studies suggest a relative stronger focus on reward learning (affective and social) early in adolescent development to learning from errors and negative feedback later in adolescent development. One possibility is that this shift in learning from positive to learning from negative has evolutionary advantages given that adolescence is a time of exploration. Blakemore and Mills (2014) argued that monitoring social feedback is most likely crucial for successful social communication, and the changes and individual differences in adolescence can have strong implications for their social development. The way adolescents process feedback is possibly shaped in such a way that it helps them to navigate a complex social world and adjust quickly if necessary. Future longitudinal studies should reveal whether stronger neural responses to affective feedback are associated with positive development when growing into adulthood.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1: Experimental details of developmental studies displayed in Figure 2.