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Review article

Emotional control, reappraised

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ABSTRACT

We are frequently challenged with situations requiring the control of our emotions, often under substantial time-pressure and rapidly changing contextual demands. Coping with those demands requires the ability to flexibly and rapidly switch between different emotional control strategies. However, this ability has been largely neglected by current neurocognitive models on emotional control. Drawing on the decision-making literature, we propose that rapid switching between alternative emotional control strategies requires the concurrent evaluation of unchosen (counterfactual) options. This model explains how an individual can adaptively change emotional control behavior to meet contextual demands and shifting goals. We propose that the neural implementation of this emotional control mechanism relies on the anterior prefrontal cortex (aPFC/lateral frontal pole), given its known role in monitoring alternative options during cognitive decision-making tasks. We reappraise meta-analytic evidence showing consistent aPFC involvement during emotional control when monitoring of alternative emotional control strategies is required, and when alternative emotional actions have high value. We conclude with emphasizing the clinical and evolutionary implications of this new framework on emotional control.

1. Introduction

We are frequently challenged with complex, ever-changing situations requiring the dynamic control of our emotions. Emotion regulation (or: emotional control) refers to all conscious and non-conscious regulatory strategies by which the physiological, behavioral or subjective component of an emotional response is altered or controlled (Ochsner and Gross, 2005). Cognitive emotion regulation strategies include altering the perception of an emotional stimulus (e.g. distraction), its affective evaluation (i.e. cognitive reappraisal) or its associated behavioral response (e.g. emotional action control) (Ochsner et al., 2002; Ochsner and Gross, 2005; Roelofs et al., 2009). Crucially, the effectiveness of these different emotional control strategies depends on contextual and personal demands (Aldao, 2013; Sheppes et al., 2014, 2011; Sheppes and Levin, 2013). Therefore, adaptive emotional control requires the ability to flexibly switch between different emotion control strategies, especially in unfamiliar and rapidly changing situations when the best course of action is uncertain (Bonanno and Burton, 2013; Levy-Gigi et al., 2016; Sheppes et al., 2014, 2011; Sheppes and Levin, 2013). Yet, this ability has remained largely neglected in current neurocognitive models on emotional control (Etkin et al., 2015; Morawetz et al., 2017).

We aim to extend current neurocognitive accounts of emotional control, taking the ability to evaluate and generate alternative emotional control strategies into account. This model explains how an individual adaptively changes emotional control behavior to meet personal or contextual demands. Drawing on the decision-making literature, we propose that alternative scenarios, not directly guiding ongoing behavior, are concurrently evaluated to achieve control while the emotional experience unfolds. We consider the neural implementation of this emotional control model, for which we provide theoretical and meta-analytic evidence, and conclude with discussing its clinical and evolutionary implications.

2. Current neurocognitive models of emotional control

One of the current dominant neurocomputational models of emotional control was proposed by Etkin et al., (2015), who conceptualized emotional control in the context of reinforcement learning (Sutton and Barto, 1998), in which decisions on emotional control strategies are made to achieve a desired emotional state. According to general reinforcement learning models, behavioral choices are based on

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predictive values of actions and stimuli, which can be adaptively adjusted in case discrepancies between actual and predicted rewards or punishments arise, thereby reinforcing behavior that optimizes rewards and minimizes punishments (Sutton and Barto, 1998). During emotional control, behavior is aimed at achieving a desired emotional state (i.e. predicted outcome) by employing an emotional control strategy, such as distraction and reappraisal. The effectiveness of the chosen emotional control strategy is evaluated based on discrepancies between the expected and actual emotional state (i.e. prediction errors). Prediction errors thus signal that the chosen emotional control strategy did not result in the desired emotional outcome, because the desired emotional state was either not obtained (i.e. negative prediction error) or exceeded (i.e. positive prediction error) (Etkin et al., 2015).

Within the context of reinforcement learning-based theories of emotional control, a distinction is made between model-free and model-based decisions (Etkin et al., 2015). For instance, fear inhibition processes (e.g. during extinction learning) and emotional conflict effects (e.g. in emotional Stroop tasks) have been suggested to reflect model-free reinforcement learning processes (Etkin et al., 2015), which is based on experienced prediction errors only (Daw et al., 2005; Lee et al., 2012). That is, behavior is guided in response to experienced prediction errors, not requiring a priori knowledge of the context and resulting in reinforcement of the choices with the greatest rewarding value. This strategy is computationally simple, but often inflexible. During model-based reinforcement learning, on the other hand, behavior is guided based on internal representations of the environment and is not completely driven by direct experience of the rewarding or punishing consequences of actions, making it more flexible but computationally more demanding than model-free reinforcement learning (Daw et al., 2005; Lee et al., 2012). Emotional control strategies such as cognitive reappraisal and distraction are examples of model-based emotional control, depending on internal models of the individual's emotional state and contextual information (i.e. which emotional control strategy was used in this situation in the past) (Etkin et al., 2015). Thus, according to this neurocomputational model on emotional control, the effectiveness of the ongoing emotional control strategy is continuously monitored and adjusted to achieve a desired emotional state (Etkin et al., 2015). In this review, we extend the model of Etkin et al., (2015), arguing that alternative emotional control strategies should also be concurrently monitored to enable an individual to decide when to switch to which alternative strategy when needed.

3. Emotional control requires monitoring alternative options

Crucially, the outcome of an emotional control strategy may vary in different contexts, requiring the ability to flexibly switch between different strategies to meet contextual demands (Sheppes et al., 2014, 2011). For example, Sheppes et al. observed that healthy individuals flexibly switched between different emotional control strategies, depending on emotional intensity of the situation. Upon stimulus presentation, participants were instructed to choose either reappraisal (i.e. reinterpret emotional stimulus to reduce its negative meaning) or distraction (i.e. disengage from emotional stimulus and think about something emotionally neutral) as emotional control strategy to reduce negative affect. It was found that reappraisal - which allows for emotional processing and adaptation - was employed in low intensity situations, whereas distraction was preferred in high intensity situations, which enables blocking the emotional information (Sheppes et al., 2014, 2011). It is crucial for human adaptive emotional behavior to determine when to switch to which alternative strategy, depending on personal and situational demands, such as stimulus intensity and context (Bonanno et al., 2004; Levy-Gigi et al., 2016; Sheppes et al., 2015). For example, regulatory flexibility has been associated with stress resilience in primary responders: repeated trauma exposure was associated with increased post-traumatic stress disorder (PTSD) symptom severity in fire fighters with low regulatory ability, but not in those with high regulatory flexibility (Levy-Gigi et al., 2016). Thus, this contextual switching ability is crucial for effective emotional control (Bonanno et al., 2004; Bonanno and Burton, 2013; Levy-Gigi et al., 2016; Sheppes et al., 2015). However, as it has been largely neglected by current neurocognitive models on emotional control, we aim to extend these models by taking the ability to evaluate and generate alternative emotional control strategies into account.

Drawing on the decision-making literature, we propose that contextual switching between different emotional control strategies could be explained by hierarchically articulated models, where a repertoire of strategies is considered (Koechlin, 2016, 2014). Those models imply that alternative (counterfactual) emotional control strategies, including those not directly guiding ongoing behavior, are concurrently evaluated to achieve emotional control (Boorman et al., 2011; Koechlin, 2016). That is, besides monitoring the effectiveness of the ongoing emotional control strategy, evidence in favor of several counterfactual emotional control strategies should be concurrently evaluated to enable an individual to adaptively change emotional control behavior to meet personal and contextual demands (Koechlin, 2016, 2014). Thus, to optimally infer when to switch to which alternative emotional control action, evidence in favor of multiple alternative emotional control strategies, which were previously used to guide behavior, should also be concurrently evaluated. This enables retrieval of an alternative course of action in case the ongoing behavior does not result in the expected outcome. Moreover, new emotional control strategies may be created based on internal models of previously learned behavior, given current action outcomes and external cues (Koechlin, 2016, 2014). Taken together, this decision-making framework on the evaluation and generation of alternative emotional control strategies may account for the human ability to flexibly adapt behavior to unknown and/or changing situations.

4. The aPFC encodes alternative options

At the neural level, the process of monitoring alternative options has consistently been attributed to the anterior prefrontal cortex (aPFC) or lateral frontal pole (Boorman et al., 2011, 2009, Koechlin, 2016, 2014; Mansouri et al., 2017). This prefrontal area has been associated with higher-order cognitive functions which require maintaining representations of alternative courses of action in mind (i.e. 'cognitive branching') (Koechlin and Hyafil, 2007), such as prospective memory (Burgess et al., 2011; Umeda et al., 2011; Volle et al., 2011), relational reasoning (Bunge et al., 2009; Hartogsveld et al., 2017; Vendetti and Bunge, 2014), multitasking behavior (Dreher et al., 2008; Roca et al., 2011) and arbitrating between model-based and model-free reinforcement learning (Lee et al., 2014). Evidence for the role the aPFC in monitoring counterfactual choices comes from functional MRI (Badre et al., 2012; Daw et al., 2006), EEG (Cavanagh et al., 2012) and transcranial magnetic stimulation (TMS) (Zajkowski et al., 2017) studies, showing aPFC involvement during decisions to explore alternative options. During voluntary decision-making, the aPFC accumulates evidence in favor of switching to alternative actions and communicates with the mid-intraparietal sulcus (mid-IPS) for the actual switching (Boorman et al., 2009). Notably, when presented with two alternative options, the aPFC accumulates evidence in favor of the best alternative option, increasing linearly with increasing reward probabilities of the best alternative. On the other hand, aPFC activity decreased linearly with increasing reward probabilities of both the current action and the other alternative, hence taking into account the costs of switching to the best alternative option (Boorman et al., 2011). In sum, accumulating evidence indicates that the aPFC is crucial in encoding value of the best counterfactual option, thereby enabling efficient switching to that option in the future (Boorman et al., 2011, 2009; Mansouri et al., 2017; Rushworth et al., 2011).

In this review, the aPFC is defined as the lateral part of the frontal pole (See Fig. 1). The frontal pole entails the anterior-most part of the

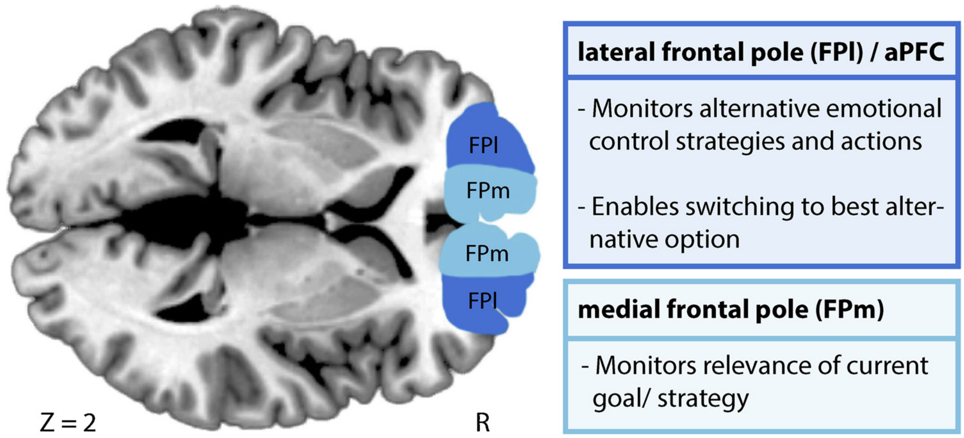

Fig. 1. Schematic illustration of the anterior prefrontal cortex (aPFC) and medial frontal pole.
Throughout this review, the anterior prefrontal cortex (aPFC) is defined as the lateral part of the frontal pole (FPl), which consists of a lateral and medial (FPm) subdivision. The aPFC (or lateral frontal pole) is suggested to monitor alternative emotional control strategies, which enables switching to the best alternative option. The medial frontal pole has been suggested to monitor relevance of the current behavioral goal or strategy.

prefrontal cortex (Öngür et al., 2003). Compared to other hominoids, the human frontal pole is largest, both in total size and relative to total brain volume (Semendeferi et al., 2001). Furthermore, extensive connections of the frontal pole with higher-order association areas (Semendeferi et al., 2001) are suggested to support domain-general processes (Ramnani and Owen, 2004). Positioned at the highest level of the rostral-caudal prefrontal hierarchy (Badre and D'Esposito, 2009), the most abstract and complex levels of human cognitive control are attributed to the frontal pole (Koechlin, 2016; Koechlin and Hyafil, 2007; Ramnani and Owen, 2004). The human frontal pole consists of a lateral and a medial subdivision, each with distinct cytoarchitecture, function and connectivity patterns (Bludau et al., 2014; Neubert et al., 2014). According to a comparative parcellation study of the ventral prefrontal cortex, connectivity profiles of the lateral frontal pole (or aPFC) have no obvious homologue in macaques (Mars et al., 2016; Neubert et al., 2014), supporting the idea that this prefrontal region may be uniquely human (Koechlin, 2011; Neubert et al., 2014). It has been suggested that, whereas the primate medial frontal pole monitors the relevance of the current goal or behavioral strategy (i.e. allowing for undirected exploration of alternative strategies when internal or external contingencies change), the lateral frontal pole (or aPFC) developed in humans to support the monitoring of multiple alternative tasks or goals and switching to the best alternative (i.e. directed exploration) (Mansouri et al., 2017).

5. The aPFC encodes alternative emotional control strategies and actions

According to the literature reviewed above (Section 4), the process of monitoring evidence in favor of alternative options has been consistently attributed to the aPFC (Boorman et al., 2011, 2009; Mansouri et al., 2017; Rushworth et al., 2011). However, this notion on aPFC functioning has remained limited to the cognitive decision-making domain. Here, we investigate whether there is evidence in the neuroimaging literature for a domain-general role of the aPFC in monitoring alternative options, also underlying the regulation of emotions and emotional actions.

5.1. Alternative emotional control strategies

Consistent with the notion that the aPFC can play a role in emotional control, several coordinate-based neuroimaging meta-analyses found aPFC activity during cognitive emotion regulation tasks (Kalisch, 2009; Morawetz et al., 2017). Surprisingly however, the aPFC is typically not discussed in neuroimaging studies on emotion regulation, which emphasize involvement of frontoparietal and dorsal midline cortices during implementation of cognitive emotional control strategies (Braunstein et al., 2017; Buhle et al., 2014; Frank et al., 2014; Kanske et al., 2011; Kohn et al., 2014; Morawetz et al., 2017; Vanderhasselt et al., 2013). However, in a recent meta-analysis on emotion regulation, converging activation was found in the left aPFC (BA10) during cognitive reappraisal (N = 80 studies) (Morawetz et al., 2017). Although this notion was not part of their conclusion, a fair proportion of the studies (N = 18 studies, 22.5%) contributed to this observation.

In order to reappraise this observation, a researcher blind to our hypothesis subdivided the cognitive reappraisal studies included in the meta-analysis of Morawetz et al. (2017) into (1) studies with room for alternative strategies and (2) studies instructing a single emotional control strategy. This categorization was implemented to test the hypothesis that only during the ecologically valid situation when multiple emotional control strategies are possible, the aPFC is implicated in monitoring the unchosen emotional control strategies. In the studies allowing for alternative strategies, participants were provided with multiple reappraisal strategies (i.e. take the perspective of a detached observer, imagine the scenes are unreal and reinterpret the scenes), or were asked to reinterpret the outcome, meaning or situation of the depicted scenes into more positive terms. Both instances allow for considering alternative strategies and/or interpretations. In the single strategy studies, on the other hand, participants were instructed either to take the perspective of a detached observer, or to reinterpret the stimulus in a specific way (i.e. think about the long-term consequences of using a substance) (See Supplementary Table S1 for classification of studies).

Coordinates of the same contrasts considered in the meta-analysis of Morawetz et al. (2017) were fit into two separate coordinate-based quantitative meta-analysis: one on studies with room for alternative strategies (N = 42 studies, 585 foci) and one on studies with a single strategy (N = 35 studies, 419 foci). We conducted these meta-analyses with GingerALE 2.3.6 (http://brainmap.org/ale) (Eickhoff et al., 2009; Turkeltaub et al., 2002), using a cluster-level threshold of $p < 0.05$ and a cluster-forming threshold of p-uncorrected < 0.001 to correct for multiple comparisons. Finally, we performed a subtraction analysis (Eickhoff et al., 2011) to examine differences in meta-analytic activations between studies with room for alternative strategies vs those instructing a single strategy. As this contrast analysis was computed on clusters surviving multiple comparisons correction for the two separate meta-analyses, we used a threshold of p-uncorrected < 0.01 (5000 threshold permutations) and a minimum volume of 100 mm^3 to ensure stringent thresholding while avoiding inflation of negative results (Sokolowski et al., 2017). Data and results of these meta-analyses are available from the Donders Institute for Brain, Cognition and Behaviour repository at http://hdl.handle.net/11633/di.dccn.DSC_3023000.00_749.

In line with our hypothesis on the role of the aPFC in encoding counterfactual options, significant left aPFC activity was found during

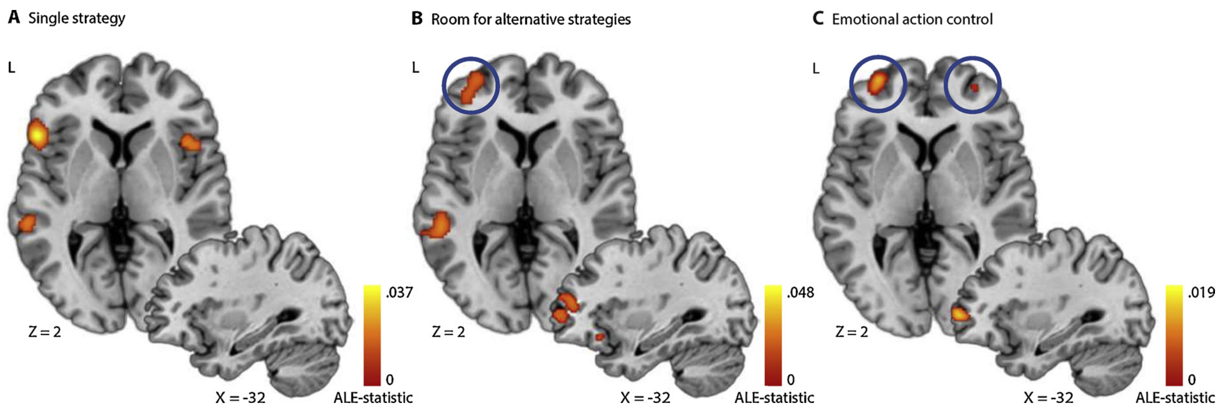

Fig. 2. aPFC encodes alternative options during emotional control.
The studies included in the meta-analysis of Morawetz and colleagues (2017) were classified into (A) those instructing a single strategy and (B) those with room for alternative strategies. This classification shows significant aPFC activation during reappraisal (vs control conditions) when alternative strategies are available. (C) Significant bilateral aPFC activity is also found when (high value) automatic emotional actions need to be monitored during emotional action control, based on 8 fMRI studies on emotional action control. Coordinates are given in MNI stereotaxic space.

emotional control in studies with room for evaluating alternative emotional control options (BA10, Center of mass MNI xyz = −34, 49, 7; see Fig. 2B and Supplementary Table S3 for all results of the meta-analyses). On the other hand, when participants performed a single emotional control strategy and had little room to consider alternative options, no significant aPFC activity was found (See Fig. 2A). Furthermore, when directly contrasting these meta-analytic activations using a subtraction analysis, we observed two clusters of left aPFC activity in studies with multiple strategies compared to those instructing a single strategy (1. BA10, Center of mass MNI xyz = −34, 56, −2 and 2. BA10 Center of mass MNI xyz = −36, 50, 12). Thus, these meta-analytic findings suggest the aPFC is implicated in emotional control, especially when the tracking of different emotional control strategies is required. In line with this suggestion, a previous behavioral emotion regulation study found that subjects who used more emotional control strategies switched more often between available strategies (Aldao and Nolen-Hoeksema, 2013). Our meta-analytic finding of aPFC activity may therefore reflect the monitoring of and switching between emotional control strategies. However, this possibility needs to be tested empirically, for example by systematically altering the number of alternative strategies, or by instructing participants to monitor evidence in favor for alternative strategies. Notably, in line with our meta-analytic evidence, a previous meta-analysis on cognitive emotion regulation studies found aPFC activity during ‘late’ reappraisal processes, which arguably involve maintaining the emotional control strategy in working memory, monitoring regulation success and monitoring alternative strategies (Kalisch, 2009).

5.2. Alternative emotional actions

Further support for the role of the aPFC in emotional control comes from studies investigating the neural control over automatic action tendencies, which typically require decisions on whether to approach or avoid an emotional stimulus. When automatic action tendencies to approach positive and avoid negative stimuli (Frijda, 1986; Lang et al., 1990) interfere with goal-directed behavior, these automatic action tendencies need to be controlled in favor of the opposite actions (Kaldewaij et al., 2017; Roelofs et al., 2009; Volman et al., 2011b). Neural control over emotional actions involves the aPFC and adjacent vlPFC (Radke et al., 2015; Roelofs et al., 2009; Volman et al., 2011a, 2011b), in line with results of a quantitative meta-analysis in eight emotional action control studies (BA10, left: MNI xyz = −30, 58, 4, right: MNI xyz = 32, 54, 8; See Fig. 2C). Although goal-directed control over automatic action tendencies is crucial for human flexible behavior, simply suppressing those tendencies might not suffice. In rapidly changing and uncertain contexts, it may be equally important to simultaneously encode accumulating evidence in favor of alternative actions. Overriding automatic action tendencies may have detrimental consequences (i.e. approaching an angry person may result in a fight), and considering alternative actions would enable rapid switching when needed (i.e. avoid the angry individual if a fight is imminent). Notably, evidence indicates that the best alternative option has a special status in the aPFC: the aPFC does not encode all alternative strategies equally (Boorman et al., 2011). The involvement of the aPFC in emotional action control might result from the contribution of this region in monitoring evidence in favor of the best alternative action or alternative task sets.

6. Phylogenetic perspective on the aPFC

Our model on the role of the aPFC in monitoring alternative emotional control strategies and actions can also be discussed from a phylogenetic perspective. The frontal pole has been suggested to have specialized in the hominid lineages (Semendeferi et al., 2001) and the lateral part (or aPFC) does not seem to have an obvious homologue in macaques (Neubert et al., 2014). Higher-order cognitive functions attributed to the frontal pole, such as abstract reasoning, were suggested to have developed late in the human lineage (Mithen, 1998). For example, non-human primates use less efficient strategies to solve higher-order relational reasoning problems (Penn et al., 2008), which may support expansion of these cognitive functions in the human lineage. Indeed, it has been suggested that the development of the prefrontal and posterior parietal cortices improved foraging choices in anthropoids, which eventually resulted in development of domain-general relational reasoning and problem-solving capabilities in humans (Genovesio et al., 2014; Passingham and Wise, 2012).

Interestingly, considering alternative long-term outcomes over immediate action outcomes enables the ability to systematically engage in prosocial activities and social tolerance, which has been suggested to be important for the development of cumulative culture in the human lineage (Hare, 2017; Hare and Tomasello, 2005). For instance, chimpanzees' inability to control their monopolistic attitudes towards rewards is a well-known factor contributing to the frequent breaches of cooperative efforts in their groups. More precisely, social tolerance systematically breaks down once rewards require turn taking (Hare et al., 2007; Melis et al., 2006), i.e. considering alternative long-term outcomes to the immediate action outcome. In this perspective, effective emotional control might contribute to the ability to systematically engage in prosocial activities, a fundamental condition for the development of cumulative culture (Whiten et al., 2017). Notably, the frontal pole has been implicated in social cognition (Moll et al., 2011, 2001; Roca et al., 2011), and human lesion studies consistently found socially inappropriate and less social behavior in patients with frontal pole and orbitofrontal lesions (Beer et al., 2006; Berlin et al., 2004; Damasio et al., 1994). Moreover, patients with frontal pole lesions not only showed impaired multitasking behavior, but also impaired social cognition on a theory of mind task (i.e. predicting beliefs and intentions of others), which was positively associated with extent of right frontal pole volume damage (Roca et al., 2011).

7. Relevance of the novel emotional control model for psychopathology

Various psychiatric disorders, such as major depressive disorder (MDD), anxiety disorders, PTSD and psychopathy, are characterized with impaired emotional control abilities (Aldao et al., 2010; Liberzon and Abelson, 2016; Rive et al., 2013; von Borries et al., 2012). Not surprisingly, currently available psychotherapies for these disorders, such as cognitive behavioral therapy (CBT), all focus on emotion regulation aspects. Crucially, however, diminished emotional control abilities in psychiatric disorders may additionally be characterized with the (in)ability to select or switch to optimal emotional control strategies (Kato, 2012; Sheppes et al., 2015). Given insufficient response to currently available psychotherapies (Bradley et al., 2005; Johnsen and Friborg, 2015), valuable insights could be gained by investigating the (in)ability to switch between emotional control strategies in psychopathology, and how to improve this ability within psychotherapy.

Furthermore, our hypothesis on the role of the aPFC in monitoring counterfactual emotional control strategies has important implications for research on the neural correlates of (impaired) emotional control, both in healthy individuals, and in psychopathology. It suggests that neuroimaging findings on (deficient) involvement of different prefrontal areas in emotional control may depend on task instruction, i.e. whether alternative emotional control strategies are available or whether a single strategy is instructed. For example, during down-regulation of negative affect using detachment as single strategy, impaired amygdala down-regulation was found in MDD patients, compared to healthy controls (Greening et al., 2014), whereas prefrontal recruitment was similar in both groups (Greening et al., 2014; Rive et al., 2015). On the other hand, when multiple emotional control strategies were provided, relative over-recruitment of ventrolateral PFC activity (Johnstone et al., 2007), as well as reduced down-regulation of prefrontal default mode network nodes (Sheline et al., 2009) was observed in MDD patients during down-regulation of negative affect. Thus, conclusions on whether emotion regulation deficits in MDD are associated with impaired amygdala down-regulation (Greening et al., 2014), or increased prefrontal recruitment (Johnstone et al., 2007; Sheline et al., 2009), may depend on availability of counterfactual emotional control strategies during task performance. Additionally, we observed reduced aPFC activity in patients with borderline personality disorder and in aggressive delinquents, as well as reduced aPFC-amygdala functional connectivity in aggressive delinquents during approach avoidance tasks where the unchosen option has higher value (Bertsch et al., 2018; Volman et al., 2016). Thus, differences in the availability of alternative emotional (control) actions may have influenced previous findings, although the limited number of neuroimaging studies on emotional control in psychiatric patients prevented us from systematically reviewing this. Our hypothesis on aPFC involvement in emotional control underlines the importance to investigate the neural correlates of the contextual switching component of emotional control in psychopathology.

8. Conclusion

8.1. Implications

In this review, we extended the current neurocognitive account of emotional control by incorporating the ability to flexibly switch between different emotional control strategies, which is needed for optimal emotional control in unfamiliar and rapidly changing environments. We provided theoretical and empirical evidence that the aPFC is involved in emotional control, especially when monitoring of alternative emotional control strategies is required. Accounting for this contextual switching ability advances our understanding of emotional control, enabling us to investigate the ability to flexibly change and even generate new emotional control strategies when the ongoing strategy does not meet personal or contextual demands. Further, it has important implications for research on the neural correlates of emotional control, both in healthy individuals and psychiatric patients, indicating that task instruction (i.e. whether alternative regulatory strategies are available) may influence findings of prefrontal involvement during (ineffective) emotional control. Moreover, it suggests a domain-general role of the aPFC in encoding counterfactual task-sets, thereby pointing at the long neglected role of the aPFC in the affective domain.

8.2. Setting a research agenda

Although we provided converging evidence for the hypothesis on the role of the aPFC in encoding counterfactual emotional control strategies, some interpretational limitations need to be mentioned. First, our hypothesis on the role of the aPFC in monitoring alternative emotional control strategies should be empirically investigated, both in healthy participants and in psychiatric patients. For instance, it remains to be tested whether the involvement of the aPFC in emotional control indeed depends on the number of available emotional control options given contextual demands (Sheppes et al., 2014, 2011), and reflects monitoring of and/or switching between alternative emotional control options. Alternatively, it has been suggested that aPFC activity may reflect domain-general motivation to obtain a specific (emotional control) goal (Soutschek et al., 2018). However, the motivation to reduce negative affect was presumably comparable in emotion regulation studies instructing multiple strategies vs a single strategy, rendering this alternative explanation unlikely.

In addition, it remains to be investigated whether the aPFC activity reported in emotional control studies spatially overlaps with aPFC activity evoked during cognitive processes typically attributed to the aPFC, such as cognitive branching and relational reasoning (Koechlin and Hyafil, 2007; Vendetti and Bunge, 2014). We are currently investigating the spatial overlap between aPFC contributions to emotional control and relational reasoning. Another important issue for future research on the involvement of the aPFC in emotional control pertains to its changing contributions during human development. The aPFC continues to develop into late childhood and adolescence (Konrad et al., 2005; Shaw et al., 2008; Sowell et al., 2003; Travis et al., 2005), and it has previously been found that less mature adolescents showed less aPFC involvement during emotional action control, compared to more mature same-aged peers (Tyborowska et al., 2016). From an evolutionary perspective, the aPFC developed late in the human lineage (Semendeferi et al., 2001; Tsujimoto et al., 2011), possibly supporting the unique human ability to systematically engage in prosocial activities by considering long-term consequences. Whether aPFC involvement in monitoring alternative emotional control strategies also develops during childhood and adolescence in humans remains an open research question. Answering these outstanding questions will be important for understanding the human ability to flexibly adapt their emotional control strategies to ephemeral social environments, and to integrate the often juxtaposed domains of emotion and reasoning.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neubiorev.2018.11.003.

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