

Affective Modulation of Cognitive Control: A Biobehavioral Perspective

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1 Introduction

A life well-lived depends on a delicate balance between immediate and delayed rewards, between convenience and effort expenditure, and between letting go and hanging on. By keeping higher goals in mind, people may choose to resist an excess of leisure in favor of personal growth, for example, or permit themselves to give in to the pleasure of a well-earned vacation. That is, throughout life, people need to flexibly adapt their efforts to control their behavior.

The task of adapting one's efforts to varying life demands has been of longstanding interest to self-regulation researchers (e.g. Brehm and Self, 1989; Carver and Sheier, 1988; Duval and Wicklund, 1972; Kuhl, 1984). In more recent years, however, this topic has attracted increased attention among cognitive psychologists, who have become interested in the question how people adjust their levels of cognitive control to changes in task demands (Botvinick et al., 2001). Relatively to self-regulation research, cognitive control research has conducted more fine-grained analyses of active control processes in seemingly affectively neutral tasks that are somewhat artificial, but also subject to higher levels of experimental control. Despite these methodological differences, it is becoming increasingly apparent that self-regulation and cognitive control strongly overlap (e.g. Jostmann and Koole, 2007; Robinson et al., 2010)

One area in which cognitive control research is particularly converging with self-regulation research has focused on the affective modulation of cognitive control (e.g. Dreisbach and Goschke, 2004; van Steenbergen et al., 2009). Originally, most researchers thought of cognitive control as a 'cold' cognitive process that operates more or less independently of affective processes. Recent studies, however, have shown that cognitive control is strongly modulated by affective factors, such as reward, humor, and mood (e.g. Dreisbach and Fischer, 2012b; van Steenbergen et al., 2014). Moreover, there appears to be significant overlap in brain areas involved in cognitive control and affective processes

(Shackman et al., 2011). These new findings have great potential for not only informing cognitive control research, but also self-regulation research, which has traditionally paid more attention to emotion (e.g. Baumeister et al., 1994; Koole, 2009; Kuhl, 2000). To further exploit this potential, the present chapter will review recent research on the affective modulation of cognitive control.

In the following paragraphs, I set the stage with a brief discussion of modern research on cognitive control and control adaptation processes. Next, I turn to theories about affect and cognitive control and effort, and how these would predict affective modulation of control adaptation. This is followed by a review of recent empirical findings concerning the hedonic marking of cognitive control, and the effects of emotions, affect, stress, and stress-related psychopathology on cognitive control adaptation. I further review recent neuroimaging studies that hint at a possible neural mechanisms that supports hedonic regulation. Finally, I summarize my main conclusions and consider implications of this work for understanding the biobehavioral foundations of self-regulation.

1.1 Cognitive control and adaptation

One central issue that experimental psychologists have been examining since the 1950s is how humans are able to focus their attention on relevant information and shield it against distraction from irrelevant information. This process, referred to as executive function or cognitive control, is thought to originate from prefrontal neural systems that orchestrates goal-driven behavior and self-control (Norman and Shallice, 1986; see also Broadbent, 1958; Posner and Snyder, 1975; Shiffrin and Schneider, 1977).

Cognitive control is typically investigated with laboratory tasks assessing response times, such as the classical Stroop task (Stroop, 1992). The latter task requires participants to name the ink of color words, whereas the word itself should be ignored. When the name of a color (e.g., "blue," "green," or "red") is printed in a color not denoted by the name (e.g., the word "green" printed in red ink instead of green ink), people are typically slower to name the colors and tend to make more errors compared to when the color of the ink matches the name

of the color. This so-called “Stroop” effect shows that controlled processing usually cannot completely overcome the automatic tendency to read the word (Cattell, 1886; Macleod, 1991). Because the efficiency of focused attention in the Stroop task determines performance, this paradigm is a valuable tool to investigate the dynamics of cognitive control under the influence of modulating factors, such as affect and motivation. Similar measures can be obtained with other laboratory conflict tasks, such as the flanker task (Eriksen and Eriksen, 1974) and the Simon task (Simon, 1969).

One important function of cognitive control is to adapt the cognitive system to situational demands (Kahneman, 1973). Because energy is limited, people typically invest effort only proportionally to the demands at hand (Ach, 1935; Brehm, 1999; Hillgruber, 1912), and such adaptation has been observed in physiological measures of effort mobilization (Gendolla and Richter, 2010). Notably, similar adaptation also occurs on a trial-to-trial level in conflict tasks that use a mixed presentation of incompatible and compatible stimuli (see Figure 1A). Here, the conflict of the immediately preceding trial typically results in an adjustment in performance indicative of an increase in cognitive control (Egner, 2007; Gratton et al., 1992). Specifically, as shown in Figure 1B (left panel) the Stroop effect is smaller on trials that follow incompatible (conflict) trials than on trials that follow compatible (no-conflict) ones. This sequential congruency effect has often been dubbed “conflict adaptation”, and is thought to reflect an adaptation in cognitive control driven by the conflict in the previous trial (Botvinick et al., 2001; Egner, 2007; Gratton et al., 1992; for alternative views see Hommel et al., 2004; Mayr et al., 2003; Schmidt, 2013).

Conflict monitoring theory (Botvinick et al., 2001) has proposed that adaptations in cognitive control originate from signals involving a conflict monitor localized in the medial parts of the prefrontal cortex, in particular the anterior cingulate cortex (ACC). The ACC is thought to signal the need for additional control to other more lateral regions in the prefrontal cortex that implement subsequent top-down control (Botvinick et al., 2001; Botvinick et al., 2001; cf. Berlyne, 1960). More recent work has shown that trials involving difficulty without

conflict also trigger behavioral adjustments, as observed in tasks that use words that are difficult or easy to read (Dreisbach and Fischer, 2011). It is thus likely that signals from the ACC indicating differences in task difficulty or disfluency are sufficient to drive adaptations in cognitive control. In this chapter, I will therefore use the term "control adaptation" or "adaptive control" to refer to adaptations in cognitive control in response to changes in task demands.

1.2 Theories about affect and cognitive control

It has long been recognized that focused attention is not only needed in situations of cognitive demands and conflict, but that it should also be mobilized when coming across dangerous situations where habitual actions are maladaptive (Baddeley, 1972; Norman and Shallice, 1986). Cognitive control adaptations might thus be driven by negative affective signals in general, of which conflict and demands are just a special case. Indeed, the idea that negative states modulate attention has a long tradition in psychology. For example, a link between negative affect and increased attentional focus has been suggested by theorists such as Easterbrook (1959), Derryberry and Tucker (1994), Schwarz (1990) and Fredrickson (2001), and it has been proposed that these changes reflect an effect of top-down control processes (Rowe et al., 2007; Vanlessen et al., 2013).

However, studies that have directly tested whether negative affective valence produces a sustained increase in attentional focus and cognitive control have provided mixed findings. Whereas the visual scope of attention has been found to be modulated by affective states when using the Navon task or detection tasks that involve neural measures of visual processing (Gasper and Clore, 2002; Rossi and Pourtois, 2012; Schmitz et al., 2009; Vanlessen et al., 2013), evidence for a similar affective tuning in conflict tasks is less consistent. Although some studies observed that, compared with positive affect, negative affect increase sustained cognitive control and thus reduces the main interference effect (e.g., the Stroop effect), other studies have not observed such direct effects (e.g. Chajut and Algom, 2003; Bruyneel et al., 2013; Martin and Kerns, 2011; Rowe et al., 2007; van Steenbergen et al., 2011). In addition,

recent work has also suggested that affective tuning effects are more context-specific than previously thought (Huntsinger, 2012). Moreover, some researchers have suggested that motivational intensity rather than affective valence drives attentional tuning (Kuhl, 2000; Kuhl and Kazen, 1999; Gable and Harmon-Jones, 2008; Gable and Harmon-Jones, 2010). Which affective dimensions determine attentional breadth is an issue currently under discussion (cf. Friedman and Forster, 2010; Friedman and Forster, 2011; Harmon-Jones et al., 2011) and outside the scope of this chapter.

1.3 A new approach: Testing effects on control adaptation

In a more recent line of research, we have investigated the modulation of *dynamic adaptation* in cognitive control rather than the direct modulation of the interference effect itself. Changes in control adaptation may occur when affective states introduced in the task modulate emotional responses that were triggered by the task demands. Such indirect modulation might influence the strength of adaptive control as measured in trial-to-trial adjustments. As illustrated in Figure 2B, such indirect effects on control adaptation can be dissociated behaviorally from direct effects on base levels of control. In other words, instead of a general reduction of the interference effect which would reflect an enhanced sustained or base level of interference control (Figure 2B mid panel), increased control adaptation is indexed by a reduced interference effect following a previous conflict trial only (Figure 2B right panel).

The basic assumption of this line of research is that demanding situations trigger a negative, aversive state (cf. Botvinick, 2007; Proulx et al., 2012). Ideas along these lines go back to the classic ‘law of least effort’ (e.g. Gibson, 1900; Hull, 1943), which states that organisms tend to minimize the amount of effort they put into a task. Consequently, demands are typically evaluated as being costly and trigger avoidance behavior when possible (Botvinick, 2007). One of the functions of this demand-driven negative affective state may be to guide future behavioral optimization, such as the improvement of control in order to avoid future occurrence of conflict (van Steenbergen et al., 2009). That is, demands might become

hedonically marked (Lewin, 1935; Morsella et al., 2011; Winkielman et al., 2003), and the aversive state associated with demands might help to subsequently mobilize cognitive effort.

Affect introduced during demanding tasks is expected to modulate demand-driven effort mobilization in an affect-congruent way (cf. Cabanac, 1992). That is, positive affect might undo the negative state triggered by the demand, whereas negative affect might intensify it. Evidence for undoing effects comes from studies showing that positive affect counteracts cardiovascular aftereffects of negative affect (Fredrickson et al., 2000). Relatedly, mood states may carry diagnostic information (Schwarz and Clore, 1983) which determine how task demands are evaluated. The amount of effort mobilized may depend on these appraisals (Gendolla, 2000). Accordingly, negative affect increases the perceived task difficulty resulting in increased effort mobilization, albeit only as long as success is experienced to be possible and worthwhile (Gendolla, 2000; cf. Brehm and Self, 1989; Kahneman, 1973; Kukla, 1972). Control adaptation may thus go hand in hand with these changes in effort.

Figure 1B illustrates how affect might regulate the transient trial-to-trial adaptations typically observed in cognitive control tasks. If it is the aversive quality of a demand that drives the improvement of cognitive control observed following conflict, it should be possible to modulate such control operations using an affect induction. Accordingly, positive states may reduce conflict-adaptation whereas negative states increase it (see Figure 1B right panel, for an example of increased adaptation).

1.4 Hypothesized neural mechanism

At the neural level, affect might regulate cognitive control via subcortical areas modulating the prefrontal cortex (PFC) (Miller and Cohen, 2001). The need for allocating additional cognitive control may be signaled by medial parts of the PFC, in particular the ACC. According to conflict monitoring theory, conflict is detected in the ACC, which drives control adaptation by signaling the need for amplified goal-related processing to the lateral PFC (Botvinick et al., 2001). More recently, it has been shown that the ACC not only monitors information processing conflict and demands, but that it also responds to many events

involving negative affect, such as monetary loss, pain, negative feedback, and social rejection (Botvinick, 2007; Bush et al., 2000; Shackman et al., 2011). It is thus possible that affective modulation of control adaptation is supported via the neural integration of demand-related and affective-state signals in the ACC.

Preliminary evidence for the integrated coding of the conflict and affective signals in the ACC comes from studies measuring the so-called error-related negativity (ERN) in affective contexts. The ERN is a change in electrical brain potentials that occurs quickly after people have made a mistake. Localization studies indicate that the ERN likely originates from the ACC (Ridderinkhof et al., 2004) and might reflect the affective evaluation of performance errors (Hajcak, 2012). Several studies have shown that negative affect is associated with amplified ERNs (e.g. Aarts and Pourtois, 2010; Luu et al., 2000; Wiswede et al., 2009a) whereas positive affect is related to reduced ERNs (e.g. van Wouwe et al., 2011; Wiswede et al., 2009b). A similar modulation in the ACC during correct conflict trials might drive the modulation of adaptive control. That is, the ACC response to demands might be amplified in a negative affective context, which consequently increases control adjustments. Similar effects have been observed in a wide range of other palliative adaptations in response to changed task demands (Proulx et al., 2012).

The possibly opposing influences of demands and positive affect might reflect some compensatory effects at a neurotransmitter level. For example, Holroyd and colleagues (Holroyd et al., 2008; Holroyd and Coles, 2002) have suggested that negative and positive events interact via dopamine modulation, which drives ACC activity. Conversely, there is evidence suggesting that the ACC sends feedback signals down to the midbrain, via the striatum – the input structure of the basal ganglia (BG) – to inhibit dopamine neurons (Frank, 2005). Moreover, animal studies have shown that both the striatum and the pallidum – the BG output structure – are involved in positive states. In particular, regions within the ventral striatum (VS) and ventral pallidum (VP) comprise so-called "hedonic hotspots", which generate hedonic states in animals when stimulated depending on opioid signaling (Haber and

Knutson, 2010; Kringelbach and Berridge, 2009). We have hypothesized that affective influence on adaptive control is supported by neural interactions between these hedonic hotspots and the ACC (cf. Botvinick et al., 2009; Haber and Knutson, 2010; Heimer et al., 1982).

2 Review of Empirical Findings

2.1 The hedonic marking of cognitive conflict

Although there is quite some evidence that processing fluency becomes hedonically marked (e.g. Morsella et al., 2011), researchers have only recently started to study whether conflict as elicited in cognitive control tasks also elicits negative affect. Using a variant of the affective priming task, Dreisbach and Fischer (2012a) have introduced congruent and incongruent Stroop color-word primes before an affective target. They found that incongruent Stroop color-words facilitated the evaluation of negative targets. This data thus support the idea that conflict stimuli are automatically evaluated as negative events which then facilitates the evaluation of negative targets and slow down the evaluation of positive targets.

In a follow-up study, Fritz and Dreisbach (2013) have demonstrated that Stroop color-word primes also affect the spontaneous judgments of subsequent affective neutral stimuli. Here it was observed that neutral target stimuli were more frequently judged as negative after conflict than after nonconflict primes. This study thus provides converging evidence for the idea that Stroop conflict is associated with negative evaluation.

Studies from other labs have focused on avoidance behavior possibly triggered by cognitive conflict. In line with data showing that participants avoid cognitive demands (Kool et al., 2010), it has been shown that participants systematically avoid choosing a task with a high proportion of conflict trials (Schouppe et al., 2013). Higher urge to quit following incongruent trials has also been reported (Lynn et al., 2012).

Schouppe and colleagues (Schouppe et al., 2012) have suggested that in standard conflict tasks pressing a response button associated with the correct target could actually be

qualified as an approach response. If conflict triggers avoidance actions, it is therefore possible that the typical slowdown observed on incongruent trials might reflect an incompatibility between the elicited avoidance tendency and the required approach response. If this is true, the compatibility effect would be reduced when participants use an avoidance response. This was indeed what their data showed, especially for Stroop trials inducing stimulus conflict.

Additional evidence for the affective marking of conflict comes from studies using psychophysiological measures of affect. For example, many studies have shown that conflict processing across different tasks is associated with elevated levels of arousal as measured with galvanic skin response (GSR) and pupil dilation (Brown et al., 1999; Laeng et al., 2011; Siegle et al., 2004; Siegle et al., 2008; van Bochove et al., 2013; van Steenbergen and Band, 2013; van Steenbergen et al., 2013). Such findings suggest that elevated emotional arousal might be an important characteristic of conflict processing, in particular because trial-to-trial effects in arousal closely mirror similar behavioral patterns of control adaptation (van Steenbergen and Band, 2013).

We have suggested that it is likely that only certain types of emotional arousal – such as those combined with a negative valence (cf. Thayer's (1989) conception of 'tense arousal') drive improved control and adaptation effects (van Steenbergen et al., 2011; van Steenbergen and Band, 2013). However, facial corrugator muscle activity, an established physiological marker of negative valence that responds to aversive stimulation (e.g. Larsen et al., 2003) and cognitive and physical effort (e.g. Boxtel and Jessurun, 1993; Cacioppo et al., 1985; de Morree and Marcora, 2010), has been shown to be insensitive to conflict, at least when measured in a Simon task (Schacht et al., 2010). Thus, further investigation is warranted.

Taken together, recent studies have shown to provide substantial evidence for the idea that conflict becomes hedonically marked. Effects of conflict were observed in measures of negative evaluation, avoidance behavior, and physiological measures of arousal. Future studies have to investigate whether physiological measures of affective valence are also sensitive to conflict.

2.2 Effects of short-term affect on adaptive control

Although there is now accumulating evidence for the idea that conflict processing elicits aversive affect, this does not necessarily prove a causal role for affect in producing control adaptations. Demonstrating a causal role of conflict-driven aversion requires experimental manipulation; If negative valence drives conflict-driven control adaptations, such adaptation should be countered by a manipulation that undoes the affective consequence of conflict (van Steenbergen et al., 2009).

In a first attempt to demonstrate this effect, we (van Steenbergen et al., 2009) have introduced short-term positive affect immediately following conflict trials in a flanker task. We hypothesized that a positive state introduced immediately after the conflict trial would counteract the aversive quality of conflict and subsequent control adaptation. In the task we presented, participants were shown happy, sad or neutral smiley faces that signaled an unexpected monetary gain, loss or no gain/loss immediately following a response to the flanker trial. In line with predictions, the arbitrary feedback between trials affected subsequent control adaptations: Standard control adaptation effects were found in the loss and neutral conditions, whereas no adaptation was observed in the gain condition (van Steenbergen et al., 2009). Consistent with the notion that effortful situations are aversive (Botvinick, 2007), this finding thus suggests that incompatible trials trigger a negative affective state that, unless neutralized by a positive event such as a monetary reward, increases adaptive control. A follow-up study using EEG replicated this modulation in behavioral adaptation (van Steenbergen et al., 2012a).

However, more recent studies from other labs have shown that it is highly unlikely that positive affect *sui generis* counteracts control adaptation. Note that in our work, feedback was presented independently of the actual response made by the participants. In contrast, a study by Stürmer and colleagues (Sturmer et al., 2011) that presented feedback contingently on performance in a Simon task observed that performance-contingent reward increased control adaptation. In another study by Braem and colleagues (Braem et al., 2012), it was also found

that performance-contingent reward increased control adaptation. Taken together, these studies suggest that in contrast to the decreased control adaptation observed following random reward, performance-contingent reward actually increases control adaptation.

To account for the improved conflict-adaptation effect following performance-contingent reward, it has been suggested that reward might enhance cognitive control (Sturmer et al., 2011). It is also possible that reward signals reinforce task-specific representations and the response, which accounts for both increased conflict adaptation and increased conflict-driven task switch costs observed following reward (Braem et al., 2012). Differences in motivation rather than affect might also be important (Braem et al., 2012; van Steenbergen et al., 2012a). In a recent review of these conflicting findings, Dreisbach and Fischer (2012b) have speculated that the positive affective reaction produced by random gains is different from the affective reaction triggered by successful task performance. According to this account, successfully overcoming conflict might involve an intrinsic reinforcement signal (Satterthwaite et al., 2012) which is further enhanced by external performance contingent reward (Braem et al., 2012). On the other hand, non-contingent random reward might actually counteract this signal, as it might convey information that task performance is not a value by itself.

However, independent of these reward effects, high-arousing stimulation might also modulate control adaptations. This was demonstrated in a recent study by Padmala and colleagues (Padmala et al., 2011). These authors used arousing negative pictures, such as mutilated bodies, presented as arbitrary stimuli in between Stroop trials. The data showed that these negative pictures (in comparison to neutral pictures) prolonged reaction times and reduced control adaptation. Their data are in line with the suggestion that arousing stimuli may bias attention and expend or divert resources needed for control implementation (Pessoa, 2009; cf. Schwarz, 1990). Indeed, manipulation of task load (without emotional stimuli) have also been observed to reduce adaptation effects (Fischer et al., 2008; Soutschek et al., 2013). Notably, a very recent study by Braem and colleagues (Braem et al., 2013a) suggests that this

effect might depend on trait punishment sensitivity. In this study, performance-contingent punishment was shown to increase control adaptation in low punishment sensitive participants (as measured by the Behavioral Inhibition System scale), whereas high punishment sensitive participants instead showed prolonged conflict-driven reaction times in the absence of increased adaptation. Thus, high-arousing stimuli that compete for shared resources may bias attention away from the main task which might result in reduced control adaptation.

To summarize, some data suggest that short-term positive affect can counteract control adaptation. However, motivation and arousal are also likely to play an important role in the adjustment of cognitive control. Future studies are needed to understand and dissociate the influence of these effects of affect, motivation, and arousal and their possible interactions.

2.3 Effects of sustained affect on adaptive control

We have recently also started to investigate how sustained affect – as opposed to short-term affect, i.e. emotions - induced prior to the conflict task modulates adaptive control. The Mood Behavior Model (MBM) predicts that hedonic tone in sustained affective states such as mood modulates the appraisal of demand-related effort mobilization (Gendolla, 2000). Along the same lines, we have hypothesized that adaptive cognitive control is also mobilized proportional to the level of experienced task difficulty (van Steenbergen et al., 2010). Thus, control adaptations might be stronger when participants are in a negative mood in comparison to a positive mood.

To test this prediction, in one of our studies (van Steenbergen et al., 2010) we have used an affect induction procedure in order to manipulate the participants' mood state. Critically, even though the MBM framework predicts affective valence (i.e., whether affect is positive or negative) effects only, this study investigated the impact of other affective factors as well. Since the work of Wilhelm Wundt (cf. Reisenzein, 1992), emotion researchers have been using dimensional descriptions to account for the wide variety of affective states. As a result, several different theoretical frameworks have emerged that describe affective states with

various dimensions and structures, including Russell's (1980) circumplex model, Watson and Tellegen's (1985) positive and negative affect distinction, Thayer's (1989) dissociation between tense and energetic arousal, and Larsen and Diener's (1992) description of eight combinations of pleasantness and activation. Recent psychometric studies have shown that all these models share a similar structure, which can be described with a Cartesian space that includes the dimensions valence and arousal (Yik et al., 1999). The valence or hedonic axis defines where affect is on a bipolar pleasant versus unpleasant dimension, whereas the arousal axis indicates the arousal or activation level on a low activation (sleep) versus high activation dimension.

Given these two fundamental dimensions, we investigated four groups of participants who underwent a standard mood-induction manipulation before performing a conflict-evoking flanker task. (cf. Jefferies et al., 2008). The four derived moods that were induced were anxiety (low pleasure, high arousal), sadness (low pleasure, low arousal), calmness (high pleasure, low arousal), and happiness (high pleasure, high arousal). In line with our prediction that negative affect would produce stronger conflict-driven adaptation effects, we observed ~~reduced~~ adaptive control for participants with low pleasure levels (anxious and sad participants) in comparison to participants with high pleasure levels (calm and happy participants). Notably, this effect was not accompanied or modulated by effects of arousal level; participants with high-activation moods (anxious and happy groups) did not show differences in adaptation effects in comparison with participants in low-activation moods (sad and calm groups) (van Steenbergen et al., 2010).

Using a similar approach, Kuhbandner and Zehetleitner (2011) recently investigated the effect of pleasure and arousal on performance in a visual pop-out distractor task. Consistent with our findings, they observed reduced control adaptation for the positive in comparison to the negative affect groups. However, unlike our results, they also observed a main effect of arousal on sustained cognitive control as measured with the interference effect. High-aroused participants were more sensitive to distraction than low-aroused participants. Using computational modeling, Kuhbandner and Zehetleitner (2011) further demonstrated

that these effects on control adaptation versus interference reflect independent effects on control adaptation versus base level of control.

We have also studied the effect of a more implicit manipulation of bodily states, probably associated with affective valence (Cacioppo et al., 1993; but see also Harmon-Jones and Allen, 1998). Here, we tested whether approach and avoidance body feedback as induced with an arm flexion versus extension also impacted control adaptation (Hengstler et al., 2014). In line with an affective valence account, approach was indeed associated with less control adaptation in comparison to the avoidance condition. In addition, independently of the effects on adaptation, the avoidance state also increased sustained control as indicated by a reduced interference effect (Koch et al., 2008; Koch et al., 2009). These findings thus suggest that motor feedback aspects of affect might play an important role in the modulation of adaptive control.

To summarize, across different manipulations of sustained affective states and across different tasks, it has been observed that the valence dimension of affect determines control adaptations: More negative affect was found to be associated with more control adaptation, whereas more positive affect was associated with less control adaptation. Motor feedback aspects of affect might play an important role in this modulation.

2.4 Effects of depression and stress on adaptive control

We have also started investigating the effects of depressive symptoms on control adaptation. Here we considered that—analogue to negative mood effects in healthy samples—dysphoria in remitted depressed individuals may similarly improve demand-driven behavioral adaptation. Enhanced demand-driven effort recruitment in depression has indeed been demonstrated in cardiovascular measures (Brinkmann and Gendolla, 2007).

To test the effects of depression on control adaptation, we have analyzed the effects of a pharmacological manipulation (Acute Tryptophan Depletion) in remitted depressed participants on control adaptation as measured in a Simon task. ATD is known to lower central serotonin levels, which increases depressive symptoms in vulnerable populations. Our

results confirmed predictions: ATD-induced depressive symptoms were associated with more control adaptation (van Steenbergen et al., 2012b).

It is important to note, however, that the effects of transiently induced depressive symptoms reported here may differ from the chronic effects observed in depressed patients. As other studies have shown, depression has been associated with reduced control adaptation (Clawson et al., 2013; Meiran et al., 2011; Pizzagalli, 2011). It is possible that differences in task-difficulty appraisal account for these conflicting findings. As mentioned earlier, MBM theory (Gendolla, 2000) proposes that the association between mood and effort mobilization is linear only up to the point that success is possible and worthwhile for the participant. However, when demands become perceived as too high to actively cope with, negative mood may actually trigger demand-driven disengagement (cf. Brehm and Self, 1989; Kahneman, 1973; Kukla, 1972). Evidence for this effect has been reported in mood induction studies and can also be shown in dysphoric participants when they perform tasks with extremely high fixed demands (Brinkmann and Gendolla, 2008). Thus, it is possible that depressive patients show reduced control adaptation because they experience conflict as too difficult to adequately cope with.

More evidence for reduced control adaptation comes from stress research, which often exposes people to extreme demands that are difficult to cope with. For example, reduced control adaptation has been observed when participants are exposed to the Trier Social Stress Task in comparison to a control group (Plessow et al., 2011). Decreased control adaptation has also been observed when participants receive negative feedback concerning their task performance, an effect that is particularly strong in (subclinically) depressed participants (Holmes and Pizzagalli, 2007).

Collectively, these observations suggest an inverted-U relationship between negative affect and control adaptation (cf. Brehm and Self, 1989). It is an important aim for future studies to understand the generalizability of these findings and to disentangle the effects of increased negative affect and putative reduced availability of resources (e.g., due to

rumination) in depression (cf. Meiran et al., 2011) as well as in other mood and anxiety disorders (cf. Larson et al., 2013). MBM theory assumes that the interaction between both factors determines the actual appraisal of the demand, which in turn modulates effort mobilization. Future studies might test whether this also holds true for control adaptations.

2.5 Neural mechanisms

As described earlier in this chapter, indirect effects of affect on cognitive control may involve the PFC, in particular its medial parts including the ACC. To test this hypothesis, in one study we (van Steenbergen et al., 2012a) recorded EEG while participants responded to the flanker task with smileys presented during the inter-trial interval (cf. van Steenbergen et al., 2009). The EEG allowed us to analyze neural oscillations in the theta band, which are likely to originate from the ACC and the surrounding medial frontal wall (Cohen et al., 2008). In line with conflict monitoring theory (Botvinick et al., 2001) and previous findings, frontocentral theta power was increased by flanker conflict. More importantly, positive feedback following conflict inhibited this neural oscillation. Based on these findings, it might be argued that theta oscillation provides an index of ACC activity signaling the need for more cognitive control, and that the inhibition of this signal by reward prevented the subsequent control adaptation as observed in behavior.

Given that ACC modulation might originate from subcortical areas related to the processing of positive affect, such as the BG, fronto-striatal interactions were investigated in another study using fMRI. In this study, funny versus neutral cartoons were used to manipulate participants' hedonic state before they performed a flanker task (van Steenbergen et al., 2014). In line with predictions, humor was shown to decrease control adaptation. In addition, it increased neural activity in regions usually associated with hedonic states, particularly in the ventral striatum (VS) and ventral pallidum (VP), so-called "hedonic hotspots" that are responsible for pleasure causation in animals (Kringelbach and Berridge, 2009). We observed that activity in these areas, in turn, inhibited the neural response to conflict in a rostral ACC (rACC) region. Activation in this region also proved predictive of

adaptive control improvement in the neutral context. Thus, it is likely that the rACC is involved in the affective appraisal of task demands and/or online control improvements, driving performance adaptations as observed in the subsequent trial. Inhibition of this rACC response by positive affect might have prevented this control adaptation.

In the same study, we also showed that activity in the dorsal ACC was co-modulated with behavioral adaptation, suggesting that it is involved in monitoring the conflict at hand. Given the aversive quality of cognitive demands, it is likely that activity from the dACC acts as a general aversive (Botvinick, 2007) or error signal (Alexander and Brown, 2011; Dreisbach and Fischer, 2012a; Proulx et al., 2012) that inhibits hedonic processing in the VS (Leknes and Tracey, 2008).

Functional connectivity analyses further confirmed the interactions between conflict and hedonic areas. Results showed that neural signals in the VS were negatively coupled (anti-correlated) with dACC, whereas the VP was negatively coupled with rACC. Given these findings, it is most likely that the VP modulates rostral ACC activation, which in turn drives conflict-driven control. The resulting adaptation might subsequently be registered in the dorsal ACC, which then sends feedback signals back to the VS. Affective state are likely to modulate these interactions via the BG (van Steenbergen et al., 2014).. Figure 2 illustrates these interactions.

Taken together, our neuroimaging findings are in line with predictions from conflict-monitoring theory suggesting that the ACC plays an important role in the online evaluation of demands, which may subsequently drive extra cognitive control. Indirect affective modulation of cognitive control probably involves the modulation of rACC and dACC activity via reward-related processing in the VS and the VP (van Steenbergen et al., 2014). The exact temporal dynamics and neurochemical basis of this neural circuitry have not been investigated yet.

3 Future Directions

3.1 Different affects, different effects

Although many studies reviewed in this chapter found evidence for emotion and mood effects on adaptive control, some studies have shown that it is not likely that positive affect *sui generis* reduces adaptation effects, in particular not when short-term affect is induced. For example, depending on the way the reward manipulation was implemented, decreased (van Steenbergen et al., 2009; van Steenbergen et al., 2012a) versus increased (Braem et al., 2012; Sturmer et al., 2011) control adaptation was observed (see also Braem et al., 2013b).

One critical issue for future research is to investigate which underlying dimensions or aspects of reward drive increases versus decreases in adaptive control. For example, research by Berridge and colleagues (e.g. Berridge and Robinson, 2003) has shown that reward involves different components, including learning, affect (liking), and motivation (wanting). As has recently been argued by Chiew & Braver (2011), it is likely that those components have different effects on cognitive control. We have proposed that affective liking might be associated with reductions in adaptive control, whereas motivational states (wanting) increases adaptive control (van Steenbergen et al., 2012a; cf. Gable and Harmon-Jones, 2011).

Considering the diverging findings from studies on negative mood, depression and stress, the influence of negative affect also needs further study. Building on the assumed non-linearity between task demands and effort mobilization (Brehm and Self, 1989; Kahneman, 1973; Kukla, 1972), we have postulated that the relationship between negative affect and control adaptation is inverted U-shaped (van Steenbergen et al., 2012b). Studies investigating control adaptation may investigate this possibility by manipulating multiple levels of conflict/task difficulty (cf. Forster et al., 2011) and affective valence.

3.2 Neurochemistry

Although BG-ACC interactions are likely to drive affective modulation of control adaptation, the neurotransmitter systems supporting this modulation are currently not known. Although many neurotransmitters have been proposed to modulate cognitive processing by adjusting neural signal-to-noise ratios, it is likely that dopamine and opioids are

among the central ones involved in the affective and motivational modulation of cognitive control (Aarts et al., 2012; Chiew and Braver, 2011).

It is possible that the BG-ACC interactions identified by our research, in particular those between dACC and ventral striatum, critically depend on dopamine. Dopaminergic signaling might support control adaptations (cf. Duthoo et al., 2013; van Bochove et al., 2013), especially their motivational aspects (Barbano and Cador, 2007; Berridge, 2007; Kringelbach and Berridge, 2009; Leknes and Tracey, 2008). On the other hand, recent evidence suggests that the hedonic dimensions (liking) of affect are under control of opioid transmission (Barbano and Cador, 2007; Berridge, 2007; Kringelbach and Berridge, 2009; Leknes and Tracey, 2008). Because opiates can reduce or eliminate the negative emotional state induced by painful stimuli, they may also mediate the modulating role affect has on evaluating and monitoring behavioral demands (Shackman et al., 2011). Interestingly, opioid receptors have been found to be most densely distributed in the ACC, particularly in its rostral parts (Luu et al., 2000; Zubieta et al., 2003). Opioids may therefore support the informational function affect has in producing indirect effects on cognitive control, possibly via interactions between VP and the rACC. One essential topic for future research is to investigate the shared neural mechanisms of demand and pain processing (Shackman et al., 2011) and to study whether opioid signaling also mediates the hedonic impact on control adaptation.

3.3 Other types of adaptive control

A final issue for future research to be mentioned here concerns the question how affective modulation of control adaptation is related to other measures of adaptation in experimental paradigms. For example, according to conflict monitoring theory, adaptation to demanding events has much in common with another type of adaptation, usually referred to as post-error adaptation (Botvinick et al., 2001): Reactions after an error are usually slower than after correct trials. Because post-error slowing may reflect cautious processing in response to the error, it has been taken as an index of cognitive control. Given that both errors

and demands are generally thought to be registered in the brain as aversive events, affective modulation may involve a similar mechanism, probably involving the ACC (Botvinick, 2007).

Indeed, several studies have shown that negative affect amplifies the neural processing of errors, although this increased neural activation does not always modulate post-error slowing (e.g. Hajcak et al., 2004; Luu et al., 2000; Lindstrom et al., 2013). However, whether effects on post-error slowing reflect an adaptive increase of cognitive control is subject to debate. It is also possible that post-error slowing reflects attentional capture which hinders subsequent performance (Notebaert et al., 2009). Post-error slowing has also been associated with steeper increases in negative affect and reduced task-focused coping in response to stressors in daily life, suggesting that it might be an index of maladaptive strategies (Compton et al., 2011).

Adaptations of control have also been observed in task-switching tasks. Here conflict has been shown to impair the efficiency to subsequently switch to other tasks (Goschke, 2000). Moreover, adaptation effects have been observed to reverse after task switches. This suggests that interference control also tends to reduce following conflict introduced by another task (e.g. Notebaert and Verguts, 2008). Thus, conflict-driven adaptations seem to improve performance of the (local) task at hand, which is maladaptive when a switch to another task is necessary. Reward (motivation) has already been shown to increase conflict-driven task switch costs (Braem et al., 2012) and future studies should investigate whether positive affect reduces it. Such a finding would be in line with other studies linking positive affect to cognitive flexibility (Dreisbach and Goschke, 2004).

Finally, it has been argued that sequential congruency effects do not only reflect control adaptation, but also other processes (see for reviews Egner, 2007; Schmidt, 2013). For example, stimulus/response repetitions and contingency learning are likely to contribute to the sequential adaptations observed (Hommel et al., 2004; Mayr et al., 2003; Schmidt & De Houwer, 2011), although it is challenging to experimentally control for these effects without introducing new confounding factors (Duthoo and Notebaert, 2012; Schmidt and De

Houwer, 2011). Nonetheless, it is not unlikely that behavioral adaptations reflects not only conflict-driven control processes , but also feature binding and contingency learning (Botvinick et al., 2001; Hommel et al., 2004; Schmidt and De Houwer, 2011), and/or a combination of control and learning (Verguts and Notebaert, 2009). Future studies should investigate whether the influence of affect and motivation as reviewed here are affecting control adaptation specifically, or whether (a combination of) other processes are also modulated (cf. Trübutschek and Egner, 2012).

4 Conclusions

As many studies reviewed in this chapter have shown, positive affect helps to reduce control adaptations to cognitive demands, likely by reducing the aversive state induced by these demands. Negative affect, on the other hand intensifies such adaptation – at least as long as success is possible and worthwhile. This affective modulation of control control was found to be driven by neural processing in subcortical "hedonic hotspots" which attenuated demand-related processing in the ACC and behavioral adaptation.

Viewed from a broader perspective, the findings I have reviewed here demonstrate the importance of the temporal dynamics that underlie self-regulation processes; they show that cognitive control can quickly increase in response to stimuli that conflict with our current goals. The ability to quickly allocate more cognitive control in challenging situations might prove critical in many situations requiring self-regulation. Particularly, quick increases in self-control might be adaptive when the stimulus that conflict with one's primary goal is only available for a short period of time. Those situations occur rather often in daily life, for example when one passes a McDonald's while driving on a highway or when a waitress offers a delicious but unhealthy snack during a cocktail party. Transient increases in cognitive control in such situations might be sufficient to behave in according with long-term goals (e.g. staying healthy). In other situations, quick increases in self-control might be sufficient to drive behavioral strategies such as moving unhealthy food out of sight or reach, making the need for

intensive sustained self-control superfluous. Such flexibility in the short-term implementation and adjustment of goals has been seen as characteristic of good self-management and self-regulation skills (Baumeister et al., 1994).

The evidence for a role of affect in and on the dynamic adjustments in cognitive control, as reviewed in this chapter, emphasize the important role that affect plays in the mobilization of effort and self-control processes. Whereas positive affect might help to prevent a too strong impact of cognitive demands on self-control (Garland et al., 2010), a little bit of negative affect on the other hand might help us to stay focused when dealing with a difficult situation. In other words, positive and negative affect might help to regulate the balance between task perseveration and flexibility (Dreisbach and Goschke, 2004; cf. Carver and Scheier, 1990; Carver, 2003; Kuhl and Kazen, 1999) In this respect, both positive and negative affective states can have adaptive value for self-control when experienced in the right context (Gruber et al., 2011).

By showing how neural interactions drive adjustments in cognitive control, we have started to develop a more mechanistic understanding of self-control processes and the role that affect plays in its modulation. In particular, we have suggested that mutual interactions between hedonic hotspots in the basal ganglia on the one hand, and dorsal and rostral parts of the ACC on the other hand, drive the hedonic regulation of adjustments in cognitive control (van Steenbergen et al., 2014). Examining these mechanisms further may provide new insights in the biobehavioral basis of a wide range of other phenomena where affect plays a critical role in adaptive behavior and self-regulation (cf. Proulx et al., 2012).

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Figures

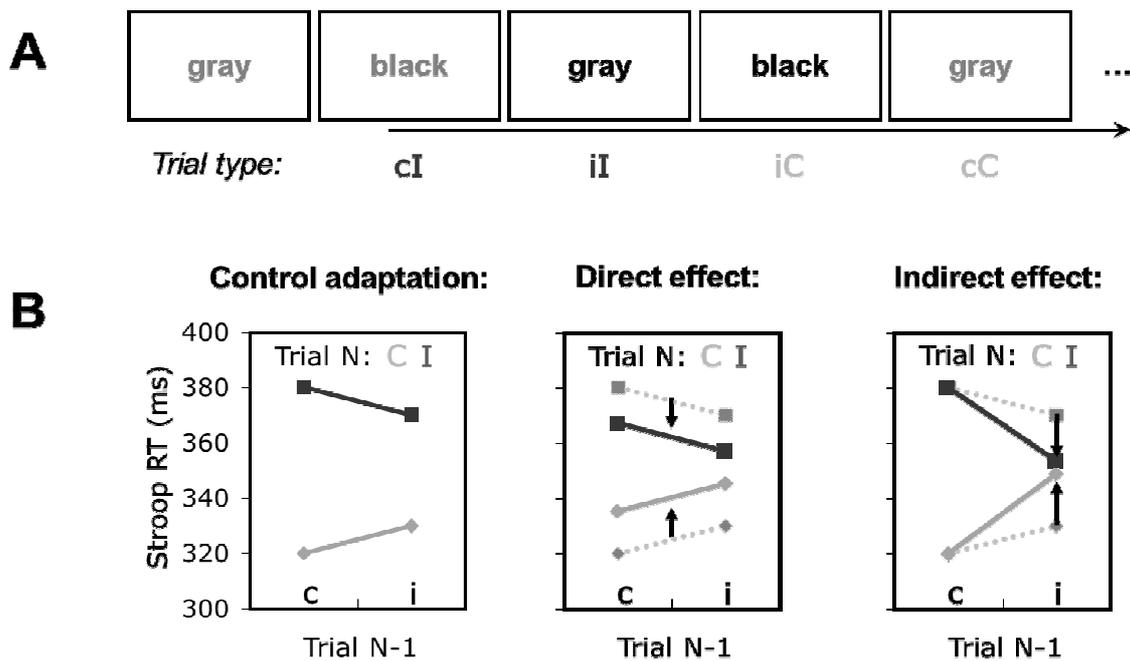


Figure 1. A. Example of a randomly selected sequence of Stroop trials being either compatible (C) or incompatible (I). Sequential-effect analyses compare current-trial compatibility effects (as indicated by upper-case letters C and I, trial N) on behavior as a function of the compatibility of the preceding trial (indicated by lower-case letters c and I, trial N-1). **B.** Left panel: A typical example of control adaptation: the Stroop interference effect is smaller on trials that follow incompatible trials than on trials that follow compatible ones. Middle panel: A possible direct improvement of sustained cognitive control will reduce the interference effect. In other words, a main effect on current compatibility. Right panel: A possible indirect improvement of cognitive control will increase conflict adaptation: the interference effect following a conflict trials is reduced in these cases.

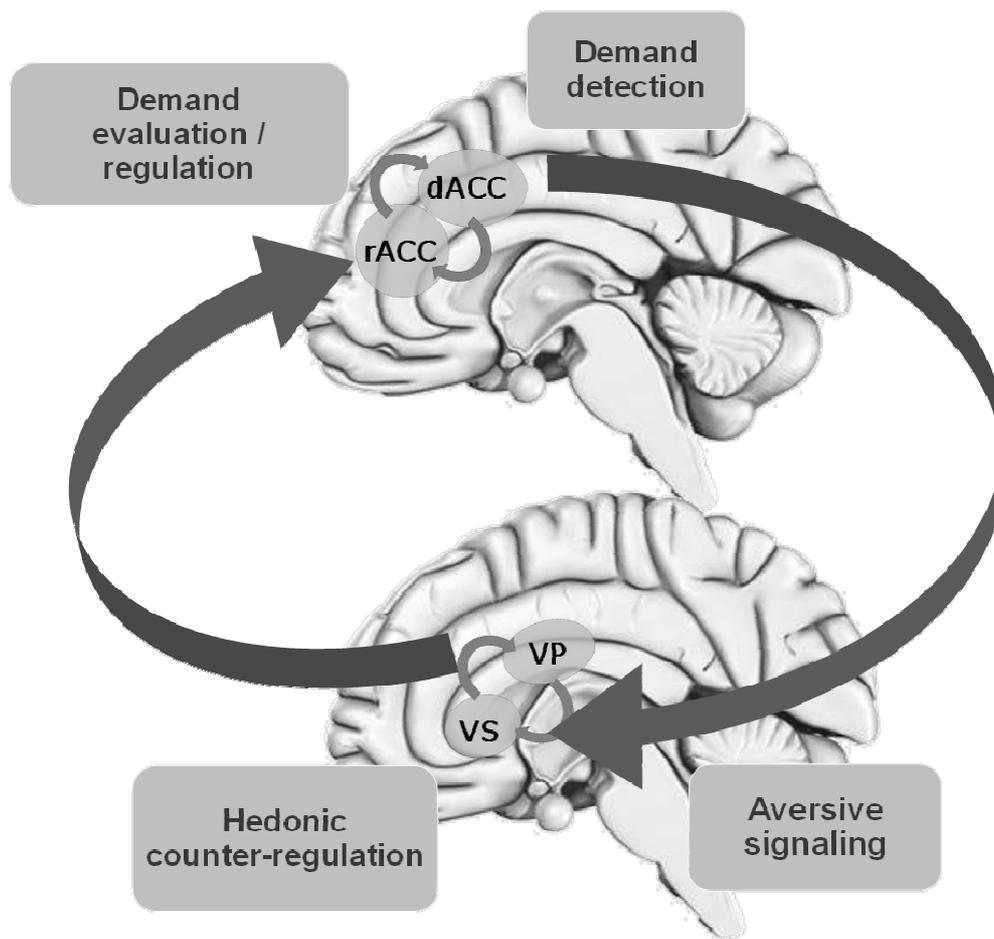


Figure 2. Interactions between basal ganglia and ACC that are likely to support the affective modulation of control adaptation. Labels indicate the proposed function of the respective areas. rACC: rostral Anterior Cingulate Cortex; dACC: dorsal Anterior Cingulate Cortex; VS: Ventral Striatum; VP: Ventral Pallidum. Reprinted by permission from Oxford University Press: *Cerebral Cortex*, van Steenbergen et al. (2014), copyright (2014).