The drive to control : how affect and motivation regulate cognitive control

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The Drive to Control:

How Affect and Motivation Regulate Cognitive Control

Henk van Steenbergen

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The Drive to Control:

How Affect and Motivation Regulate Cognitive Control

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1

Introduction

"The aim of our emotions, and the reason we have emotions in the first place, is to enhance our lives, to make them better, to help us get what we want out of life."

Robert C. Solomon (2007)

A life well-lived requires a careful balance between short-term and long-term reward, between a choice for convenience and expenditure of effort, and between letting go and taking control. By keeping higher goals in mind, people are able to resist an excess of leisure in favor of personal growth, for example, but also to give in to the pleasure of a well-earned vacation. That is, throughout life, people need to flexibly adapt their control. This thesis focuses on the question how emotion and motivation regulate this adaptation.

In this introductory chapter, an overview of the scientific basis for a link between emotion, motivation, and cognitive control is described. After introducing the concept of cognitive control, a theoretical framework is proposed that describes how affective valence and cognitive control may be related. This is followed by an elaborate discussion of psychological and neuropsychological theories. An outline of the empirical work presented in this thesis concludes this chapter.

Adaptive cognitive control

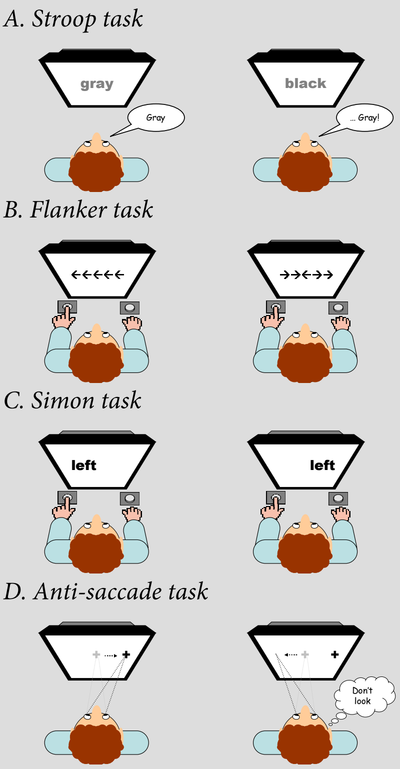
A fundamental issue that cognitive psychologists have been examining since the 1950s is how humans are able to focus their attention on relevant information and shield it against distraction from irrelevant information. This process, referred to as executive function or cognitive control, is thought to origin from a dedicated cognitive mechanism that orchestrates goal-driven behavior (Norman & Shallice, 1986; see also, Broadbent, 1958; Posner & Snyder, 1975; Shiffrin & Schneider, 1977). Cognitive control can be investigated with laboratory tasks assessing reaction times, such as the classical Stroop task (Stroop, 1992). This 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), reactions to name the color typically slow down and participants make more errors in comparison to conditions where the color of the ink matches the name of the color. This effect shows that controlled processing usually cannot completely overcome the automatic tendency to read the word (cf. Cattell, 1886; Macleod, 1991). Because the sharpness 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 mood or motivation. Similar measures can be obtained with other laboratory tasks, such as the flanker task, the Simon task, and the anti-saccade task (see Box 1 for a description of these tasks).

An important function of cognitive control is to adapt the cognitive system to situational demands (Kahneman, 1973). According to the ‘difficulty law of motivation’ (Ach, 1935), people automatically “try harder” when task demands call for it, an idea that has already been investigated by Hillgruber (1912). Since then, numerous studies have found support for this claim, showing that demanding situations trigger subsequent effort mobilization as measured by physiological measures, subjective evaluations, and behavioral adjustments in laboratory tasks (Gendolla, 2000). A similar adaptation can also be shown in the context of cognitive control tasks that use random presentation of confusing (incompatible) and nonconfusing (compatible) stimuli, such as the Stroop task. Here, the compatibility of the immediately preceding trial typically results in a dynamic trial-to-trial adjustment in performance (Egner, 2007; Gratton, Coles, & Donchin, 1992). Specifically, the Stroop effect is smaller on trials that follow incompatible trials than on trials that follow compatible ones. Figure 1C illustrates this sequential effect. This trial-to-trial effect has been referred to as conflict adaptation, and is thought to reflect a temporary improvement in cognitive control (Botvinick et al., 2001; for alternative views see Egner, 2007; Gratton et al., 1992; Hommel, Proctor, & Vu, 2004; Mayr, Awh, & Laurey, 2003). According to the conflict monitoring theory (Botvinick et al., 2001), this adaptation origins from the conflict in information processing induced by the preceding incompatible trial. This conflict is thought to trigger an adaptive increase in selective attention that helps to prevent a future occurrence of such interference (Botvinick et al., 2001; cf. Berlyne, 1960).

Affective valence and cognitive control

It has since long been recognized that cognitive control is not only needed in situations of cognitive interference and conflict, but that it should also be recruited when coming across dangerous situations (Baddeley, 1972; Norman & Shallice, 1986). This implies that cognitive control adaptations may be informed by affective signals in general, of which conflict could just be a special case. Some preliminary evidence for this possibility has been provided by neuroimaging studies on the function of the Anterior Cingulate Cortex (ACC) a brain region thought to register the need for extra cognitive control (Botvinick et al., 2001). It has been

Box 1: Cognitive control paradigms



Psychologists use a wide variety of laboratory tasks to measure conflict interference and cognitive control in humans. Nonetheless, all these tasks share an important feature: they induce information processing conflict between the processing of relevant and irrelevant information (cf. Botvinick, Braver, Barch, Carter, & Cohen, 2001). ***A.*** *For example, in the classical Stroop task (Stroop, 1992), the tendency to automatically read the word interferes with color naming.* ***B.*** *In the flanker task (Eriksen & Eriksen, 1974), distracting flankers interfere with the manual response to the central target.* ***C.*** *The automatic tendency to respond to the stimulus location interferes with a response to the relevant dimension in the Simon task (Simon & Rudell, 1967). In all these tasks, incompatible stimuli (right picture) make people slower and less accurate in comparison to compatible conditions (left picture). Moreover, sequential analyses have provided evidence for trial-to-trial adjustments, indicating conflict adaptation across these paradigms (for a review, see Egner, 2007).* ***D.*** *The anti-saccade task (Hallett, 1978) is another example of a conflict task. Subjects are instructed to either move their eyes to the target (pro-saccade instruction) or to look in the direction opposite to the target (anti-saccade instruction). This task usually involves a block-wise manipulation of instructions, which does not allow studying sequential effects. Because monkeys can also be trained to perform the anti-saccade task, they provide an important animal model to investigate neural processing related to inhibitory control (Munoz & Everling, 2004).*

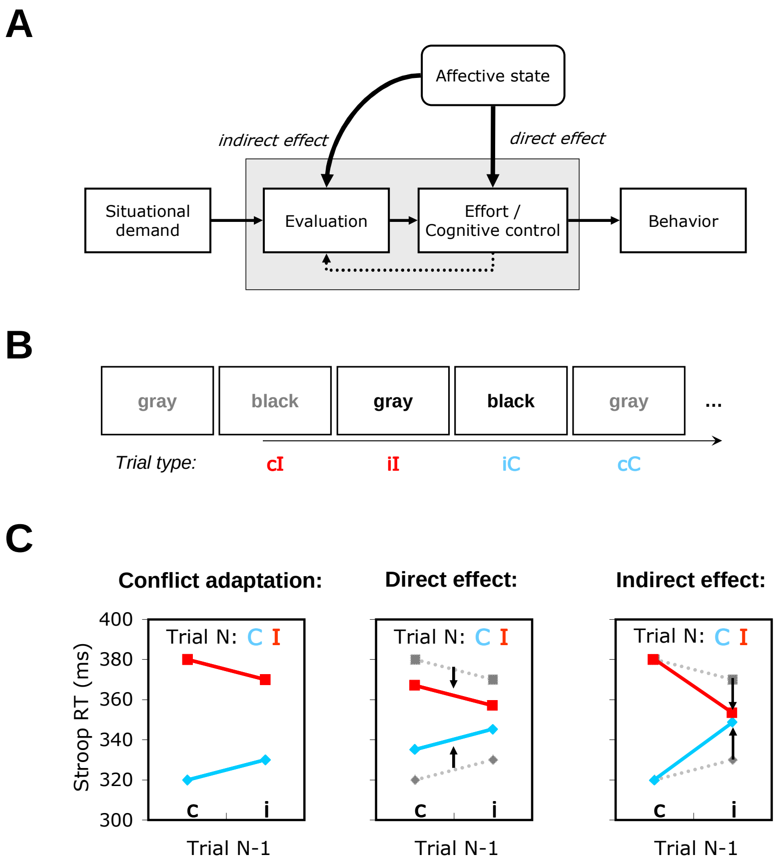


Figure 1. A. *Demands drive behavior via the mobilization of effort and cognitive control. Affective states may influence effort and cognitive control either directly or indirectly. Whereas direct effects can have immediate consequences for behavior, indirect effects are mediated via the evaluation or appraisal of situational demands.* ***B.*** *Example of a randomly selected sequence of Stroop trial being either compatible (C) or incompatible (I). Sequential-effect analyses compare Trial N compatibility effects (as indicated by upper-case letters C and I) on behavior as a function of the compatibility of the preceding trial (Trial N-1; indicated by lower-case letters c and i).* ***C.*** *Example of conflict adaptation: the Stroop interference effect is smaller on trials that follow incompatible trials than on trials that follow compatible ones. A hypothetical direct improvement of cognitive control will reduce the interference effect, whereas a hypothetical indirect improvement of cognitive control will increase conflict adaptation.*

shown that the ACC not only monitors information processing conflict, but that it also responds to situations involving negative emotions, such as monetary loss, pain, negative feedback, and social rejection (Botvinick, 2007; Bush, Luu, & Posner, 2000; Shackman et al., 2011). These data point to the interesting possibility of a common affective factor driving this neural activation. That is, demanding situations may trigger a negative state like aversive stimuli do. Historically, this idea comes close to Hull's (1943) 'law of least effort', which assumes that organisms tend to avoid demanding situations. More recent studies indeed have shown that situational demands become hedonically marked (Winkielman, Schwarz, Fazendeiro, & Reber, 2003) and usually are associated with negative valence (Botvinick, 2007; Lewin, 1935; Morsella, Feinberg, Cigarchi, Newton, & Williams, 2011). One of the functions of the resulting negative emotional state may be to guide future behavioral optimization, such as the tuning of cognitive control (cf. Cabanac, 1992).

The theoretical framework in this dissertation builds on the assumption that aversive states, irrespectively of being triggered by negative stimuli or demanding situations, help to mobilize cognitive effort. Thus, negative emotions may directly improve attentional focus, a hypothesis dating back to the work by Easterbrook (1959). Besides these direct effects, affect may also modulate the emotions triggered by the demand, thus regulating cognitive control indirectly (see Figure 1A for an illustration). For example, positive emotions may undo the negative state induced by the demand (Fredrickson, Mancuso, Branigan, & Tugade, 2000). In addition, indirect effects may also occur because the evaluation of the situational demands is changed by one's emotional state. For example, it has been shown that mood states have an informational function, making people more optimistic when in a positive mood than in a negative mood (Schwarz & Clore, 1983). Thus, congruence between mood and task demands modulates how demand is perceived and subsequently how the mind and body prepare for adaptation (Gendolla, 2000). To put it simple, positive affect may counteract and negative affect may facilitate the sensitivity to demands and subsequent control adaptation.

Using a classic Stroop task as an example, Figure 1 illustrates how direct and indirect effects on cognitive control impact behavior differently. For example, a direct effect that leads to a general improvement of cognitive control would reduce interference effects, that is, it speeds up responding to incompatible trials and slows down responding to compatible trials. On the other hand, an indirect effect via the negative appraisal of demands may cause a transient trial-to-trial adaptation increase in cognitive control. Thus, increased conflict adaptation should reduce interference effects in trials following incompatible (conflict) trials.

Beyond valence: core affect and cognitive control

The rationale presented in the previous section suggests that affective valence (i.e., whether affect is positive or negative) may be an important determinant of cognitive control regulation. However, emotional states are multifaceted phenomena and different aspects of emotions may have different effects on cognitive control. Therefore, it is important also to consider the impact of factors other than valence. Since the work of Wilhelm Wundt (cf. Reisenzein, 1992), emotion researchers have been using dimensional descriptions to account for the wide variety of emotional states. As a result, several different theoretical frameworks have emerged that describe emotional 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.

However, 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, Russell, & Barrett, 1999). The valence or hedonic axis defines where emotions are 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 (see Figure 2A). The combination of these two fundamental dimensions has been referred to as core affect (Russell, 2003). Core affect describes the affective experience manifest in both emotions and moods. Whereas moods are long-term affective states and usually not object-specific, emotions are short-lived and usually directed to a particular object that triggered it. Figure 2 shows that different states of emotions and moods can all be described in a framework that includes a valence and arousal dimension. An anxious mood for example, has a relatively high arousal level combined with a negative valence, whereas a calm mood has a positive value accompanied with a low activation level (Figure 2B). Similarly, emotions can also be characterized by these two dimensions (Figure 2C), as has been illustrated with ratings of affective states induced by emotional pictures from the IAPS set (International Affective Picture System; Lang et al., 2008).

Introducing core affect as a fundamental description of affect imposes a refinement of the framework introduced in the previous section. This need for a modification can be illustrated with the influential hypothesis raised by Easterbrook (1959). According to Easterbrook, noxious stimulation or threat enhances perceptual focus. However, Easterbrook's hypothesis does not specify where this narrowing of attention comes from. Given that the emotional state described involve both

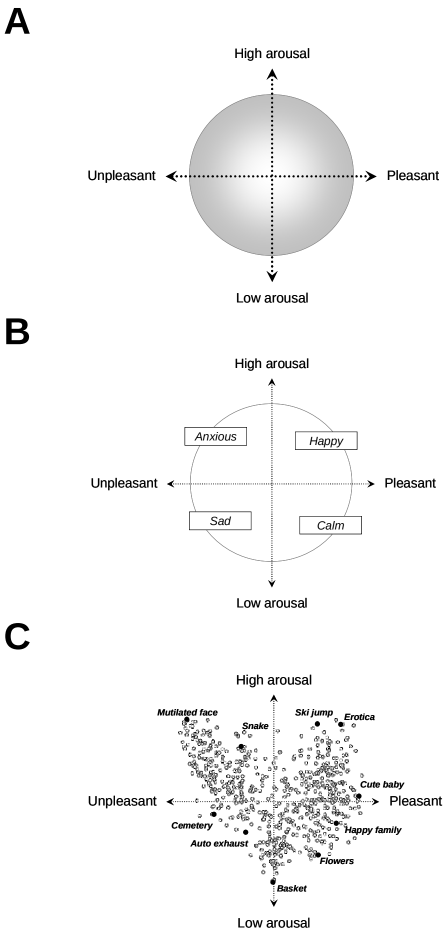


***Figure 2. A**. Core affect as defined by a Cartesian space that includes the dimensions valence and arousal. **B.** Core affect as reflected in possible mood states. **C.** Core affect as reflected in emotional states induced by pictures from the IAPS set*

a negative valence and a high level of arousal, narrowing effects may be driven by the negative valence alone, the high arousal alone, or a combination of both.

Interestingly, more recent theories on the role of affect on attentional focusing disagree on what factors are actually driving the narrowing effect. For example, Schwarz's (1990) cognitive tuning theory assumes that affective valence regulates the breadth of attention, but it does not refer to a possible role of arousal. One reason for this might be that the tuning theory extends Schwarz' former mood-as-information theory which was primarily concerned with the question how mood valence informs people's evaluative judgments: Whereas, positive affect may inform the person that everything is alright, negative affect may indicate that there are problems (Schwarz & Clore, 1983). Consequently, the tuning hypothesis proposed that negative mood not only induces systematic processing but that it also directly mobilizes effortful strategies. Similarly, positive mood is thought to induce heuristic processing and may directly mobilize effortless strategies. Thus, according to Schwarz (1990), mood is already associated with general motivational implications, irrespective of arousal effects. A similar perspective has been adopted by Fredickson, whose broaden-and-build theory suggests that positive emotional states broaden one's perception and action repertoire (Fredrickson, 2001). In contrast to these valence-based models, Derryberry and Tucker (1994) have hypothesized that only states combining negative valence and high arousal will increase selective attention. Conversely, high-arousal positive states will do the opposite, that is, broaden selective attention. According to their theory, narrowing and broadening effects are thought to include not only perceptual focus but also conceptual attention (e.g., semantic scope, cf. Isen et al., 1987).

However, alternative frameworks as proposed by Kuhl (Kuhl & Kazen, 1999; Kuhl, 2000) and Gable and Harmon-Jones (2008; 2010b) further qualify these theories. They suggest that some positive affective states, such as those associated with reward and approach motivation, increase rather than decrease selective attention. These motivational effects might be related to arousal increases (Gable & Harmon-Jones, 2010b). Furthermore, some theories have suggested that not all affective states have motivational implications. The Mood-Behavior-Model (Gendolla, 2000) states that moods usually are not related to an object and therefore lack the motivational function emotions have. According to this model, moods do not have direct effects on motivation, although they can have an indirect impact via informational effects on demand-related judgments. As explained in the previous section, such mood-congruency effects on the appraisal of demands may modulate the subsequent mobilization of cognitive control thus producing indirect effects (Gendolla, 2000).

It is also important to note that theorists have emphasized that emotion effects are subject to important boundary conditions. For example, Easterbrook (1959) already suggested that the increased perceptual focus driven by aversive situations will be beneficial to cognitive performance only up to the point that it shields irrelevant information; too high perceptual shrinking, however, may exclude relevant task information too, which impairs cognitive control performance. A parallel relation has been suggested between task demands and motivation. Increased task demands improve cognitive control, but only up to a certain point: When tasks become too difficult, people give up and effort decreases (Brehm & Self, 1989; Kahneman, 1973; Kukla, 1972). Two other important limitations have been suggested by Schwarz (1990). First, affect-inducing stimuli, though irrelevant to the task at hand, consume processing resources, and thus can effectively reduce task performance. Indeed, high-arousing emotional stimulation, such as fearful faces associated with an electrical shock, have been shown to impair executive functions (Pessoa, 2009). Secondly, the affective modulation of cognitive control may be reduced by the impact of other currently active goals. In line with this suggestion, numerous studies indeed show reduced emotional impact under conditions of increased control (Ochsner & Gross, 2005). Experimental work needs to consider these factors carefully when designing experiments and when interpreting the generalizablity of their results.

To summarize, several theories suggest that, under some circumstances, affective valence and arousal may have motivational and informational functions. The motivational function of affect is evident for some negative and positive emotions that directly trigger increased or decreased cognitive control. Theories tend to converge on the prediction that negative emotions improve selective attention, although the role of arousal in this modulation is not clear. On the other hand, conjectures about the role of positive affect and arousal are contradictive. Furthermore, theories do not agree whether the motivational function of affect is limited to emotions, or whether it can also be observed in mood states. That is, it has been argued that moods lack motivational implications for direct effects, although they still may have indirect effects on cognitive control through an informational effect on demand-related judgments. Which theoretical framework is best applicable to account for emotion effects on cognitive control is currently not known. This thesis aims to provide a substantial contribution in formulating an answer to this question.

Box 2: Affect induction methods

Several methods can be used to induce emotional states in humans. One well-known method to induce short-term emotional states is a feedback manipulation using ***reward*** *and* ***punishment*** *(e.g., Gehring & Willoughby, 2002). Studies in animals and humans have suggested that unexpected reward triggers a phasic increase of dopamine levels in the midbrain, which may regulate motivated behavior and learning (Schultz, 2006). Experiments with human subjects typically use secondary rewards, such as winning or losing points or money. Like natural rewards in animals, these feedback stimuli modulate the dopamine system and ACC activity in humans (Schott et al., 2008).*

Another way to induce transient emotional states is to present ***pictures****. A well-known stimulus set used for emotion induction is the International Affective Picture System (IAPS). This picture set includes photos of emotion-loaded daily-life scenes, people, and animals. Pictures induce emotional states that vary widely across valence and arousal dimensions (Lang, Bradley, & Cuthbert, 2008; cf. Figure 2C). Presenting funny cartoons is another example of how pictures can be used to induce emotions (e.g., Abel & Maxwell, 2002; Isen, Daubman, & Nowicki, 1987).*

Sustained affect can be manipulated using ***mood induction procedures****. These procedures usually include film fragments, imagination, emotional statements, and music, either alone or in combination, to induce positive or negative moods. The induction appears to be most successful when combined with an explicit instruction to come in a particular mood (Westermann, Spies, Stahl, & Hesse, 1996). It remains a matter of debate to what extent manipulation checks (usually involving self-reported affect) may reflect socially desirable responding (a.k.a. demand characteristics).*

Mood states can also indirectly be induced by ***pharmacological manipulations*** *that directly manipulate neurotransmission. For example, Acute Tryptophan Depletion (ATD) has been used to investigate the role of serotonin regulation in depression. ATD temporarily lowers the availability of L-Tryptophan (Trp), the precursor of serotonin. This leads to a transient increase in depressed mood in individuals who are vulnerable to depression, such as former patients and first-degree relatives of patients (Ruhe, Mason, & Schene, 2007).*

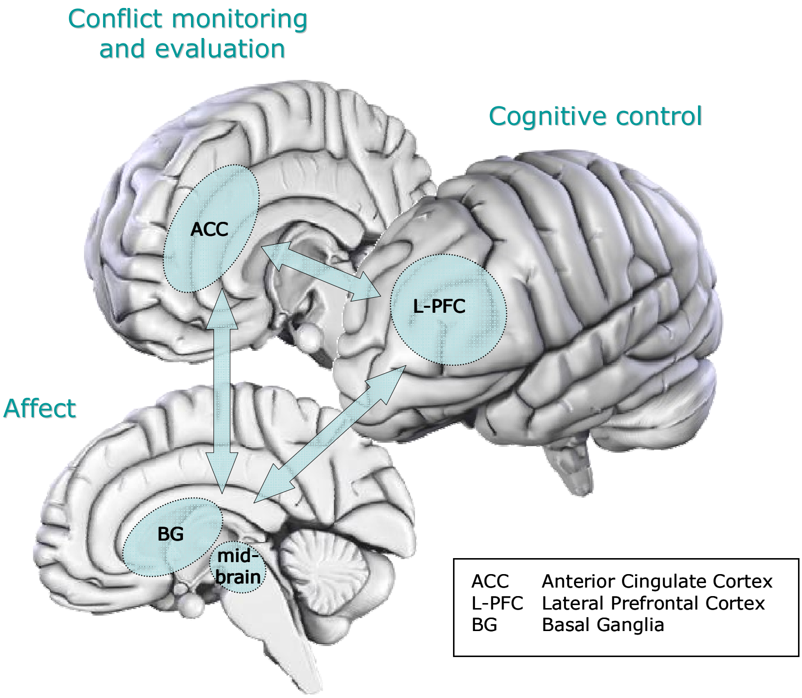


Figure 3. *Brain areas involved in the interactions between affect and cognitive control.*

Neuropsychological models

In addition to understanding the behavioral consequences of the modulation of cognitive control, the project described in this thesis also aims to investigate the neural mechanism supporting such regulation. Cognitive control regulation involves the prefrontal cortex (PFC). This brain region plays an important role when situations require cognitive control, that is when behavior must be guided by internal states or intentions (Miller & Cohen, 2001). Whereas the implementation of control may involve the lateral parts of the PFC, the need for the allocation of extra cognitive control is thought to be signaled by the more medial parts of the PFC, in particular the ACC (Botvinick et al., 2001), Although traditionally being envisaged as part of the affective ‘limbic system’ (Papez, 1937), neuroimaging studies have shown that the ACC is also involved in the processing of demanding situations (Botvinick, 2007; Bush et al., 2000; Shackman et al., 2011). According to the conflict monitoring hypothesis, demanding situations induce conflict in information processing which acts as a signal that indicates the need for additional control. The ACC may drive control improvements by amplifying goal-related processing in the more lateral part of the PFC (Botvinick et al., 2001). The ACC has also been conceived of as an important region for affective modulation, given that the processing of affective valence and processing demands converges and becomes integrated in this area (Bush et al., 2000; Luu, Collins, & Tucker, 2000; cf. Pessoa, 2008). There is some evidence suggesting that negative affect amplifies conflict-related ACC activity (e.g., Luu et al., 2000) whereas positive affect inhibits this activity (van Wouwe, Band, & Ridderinkhof, 2011). This modulation may be central to indirect effects of emotion on cognitive control.

Motivational effects on cognitive control may also modulate the lateral PFC directly. For example, according to the model by Tucker and Williamson (1984), affect may cause asymmetric involvement of the hemispheres via sub-cortical limbic processing. These authors have speculated that negative affect facilitates analytic processing via a bias of left hemispheric activity, whereas positive affect biases heuristic processing via the right hemisphere. In contrast, more recent theories have suggested that affect is lateralized in exactly the opposite order, that is, withdrawal- and avoidance-related emotions are related to right-hemisphere dominance, whereas approach-related emotions are represented by left-hemisphere dominance (e.g., Davidson, 1993; Davidson, 2004; Gray, 2004). However, empirical evidence for a lateralization of emotions is mixed (e.g., Wager, Phan, Liberzon, & Taylor, 2003), and effects observed may reflect the direction of the action (approach versus avoid) rather than the actual valence of the emotional state (Berkman & Lieberman, 2010).

Affective modulation of medial and lateral parts of the PFC may also be supported by projections from neuromodulator systems. Neurotransmitters such as dopamine (DA), norepinephrine, serotonin, and endogenous opioids may regulate attention by adjusting neural signal-to-noise ratios (Briand, Gritton, Howe, Young, & Sarter, 2007; Robbins & Arnsten, 2009; Leknes & Tracey, 2008). For example, DA projections from the midbrain to the prefrontal cortex have been thought to regulate working memory, cognitive control, and behavioral flexibility (Ashby, Isen, & Turken, 1999; Braver & Cohen, 2000; Dreisbach & Goschke, 2004). Given that DA is involved in the neural representation of monetary reward and positive affect (Ashby et al., 1999; Phillips, 1984; Schultz, 2007), it has been proposed that effects of incentive motivation on cognitive control (e.g., Savine & Braver, 2010) and positive affect (Ashby et al., 1999) may be mediated by this system. Conversely, projections from the prefrontal cortex (including the ACC) back to the midbrain via the basal ganglia, have been proposed to induce phasic inhibition of DA levels during aversive events. This feedback system may provide important learning signals needed for behavioral optimization (Frank, 2005). Reward and conflict processing may thus have opposing influences on DA levels, possibly reflecting positive and negative emotional valence (cf. Holroyd & Coles, 2002; Jocham & Ullsperger, 2009). Evaluative feedback signals from the ACC may also drive the locus coeruleus-norepinephrine system. This arousal-mediated response may augment a phasic release of NE that enhances task-specific control representations in prefrontal cortex (Aston-Jones & Cohen, 2005; Aston-Jones, Rajkowski, Kubiak, Valentino, & Shipley, 1996; Verguts & Notebaert, 2009). Serotonin is another neurotransmitter that might be involved in the neuromodulation of signals related to punishment and aversion, and which is also involved in negative and depressed mood (e.g., Cools, Roberts, & Robbins, 2008; Ruhe et al., 2007). Finally, recent evidence suggests that opioid-driven modulation may underly the hedonic dimensions of affect (Kringelbach & Berridge, 2009; Leknes & Tracey, 2008). Unlike DA which is primarily associated with the motivational aspects of reward, the opioid system is thought to be involved in the hedonic liking aspects of reward (Barbano & Cador, 2007; Berridge, 2007). Increased opioid function has been linked to positive emotional states such as relief of pain and feelings of euphoria, wellbeing, and relaxation. 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. Consistent with this possibility, opioid receptors have been found to be most densely distributed in the ACC (cf. Luu et al., 2000). This modulation may support the informational function affect has in producing indirect effects on cognitive control.

In sum, direct and indirect emotional effects may modulate prefrontal cortex via subcortical regulation (see Figure 3). Whereas the medial part of the prefrontal cortex may be involved in the detection and evaluation of cognitive demands, the more lateral parts of the prefrontal cortex may actually implement the cognitive control needed. Subcortical reward systems including the dopamine and opioid systems may play an important neuromodulating function via which direct and indirect affective regulation of cognitive control may occur. The research described in this thesis aims to investigate the role of these neural circuitry in this regulation.

Box 3: Beyond behavior: psycho-physiological methods

Emotion and cognitive control direct behavior via a biological substrate, that is, the brain and the body. One way to measure bodily responses to environmental changes is ***pupillometry****. This method tracks the size of the pupil using an eye tracking device or a camera. Task-related pupil dilation has been used as an index of autonomic nervous system activation. The pupil contains two antagonistic smooth muscle groups, the sphincter and dilator muscles, that are differentially influenced by activity in the sympathetic and parasympathetic branches of the nervous system. Sympathetic activity drives the dilator muscle evoking dilation, whereas inhibition of parasympathetic activity reduces constriction of the sphincter muscle, which also results in dilation (Beatty & Lucero-Wagoner, 2000). There are many determinants of pupil dilation (cf. Kahneman, 1973). For example, high-arousal states such as anxiety, fear, and anger increase arousal and pupil dilation (Bradley, Miccoli, Escrig, & Lang, 2008). On the other hand, task difficulty manipulations also increase pupil dilation, an effect probably reflecting mental effort (e.g., Beatty, 1982). Recent studies have suggested that these effects origin from different sources: emotional arousal is most likely associated with sympathetic nervous system stimulation, whereas effort primarily origins from parasympathetic inhibition (Bradley et al., 2008; Steinhauer, Siegle, Condray, & Pless, 2004).*

Neural activity during task performance can be measured with neuroimaging techniques. ***Electroencophalography (EEG)*** *provides a noninvasive, inexpensive, and instantaneous measure of neural activity using recordings from the scalp. In contrast to its excellent temporal resolution, the spatial resolution of the EEG is low because of resistive properties of the scalp. Moreover, a particular distribution of scalp potentials can be generated by many different combinations of intra-cerebral sources. The inability to mathematically trace this compound EEG signal back to its neural sources has been referred to as the 'inverse problem'. EEG recordings during task performance can be used to index different neural processes. For example the ERP (Event Related Potential) technique averages EEG activity across trials, which makes it possible to identify components defined by specific characteristics such as scalp distribution and time range. ERP components measure neural oscillations that are phase-locked to the event of interest. Time-frequency decomposition analyses such as the Continuous Wavelet Transformation overcome this limitation. These methods allow to trace induced neural oscillatory activity which is not phase-locked to the event (cf. Cohen, 2011; Luck, 2005).*

Functional Magnetic Resonance Imaging (fMRI) *is a neuroimaging technique that complements the limitations of EEG. Although this method lacks fine temporal resolution, it provides a better spatial resolution of neural activity. fMRI makes use of the magnetic properties of oxygenated blood in the brain using the BOLD (blood-oxygen-level dependence) response. This indirect measure of local neural activity can be obtained in a high magnetic field using an MRI scanner. Neural activation maps can be derived from analyses that model conditional differences in neural activity. Because fMRI can measure the activation and interactions of both cortical and subcortical neural structures, it is an important tool to identify the neural networks involved in the interaction between emotion and cognition (cf. e.g., Pessoa, 2008).*

Outline of this thesis

The research presented in this thesis focuses on the question how affect and motivation regulate cognitive control. The following eight chapters describe empirical studies that explore this link across different cognitive control paradigms (see Box 1) and affect-inductions methods (see Box 2). Apart from behavioral measures that index the efficiency of cognitive control, several physiological and neuroimaging methods are applied to investigate bodily and neural correlates (see Box 3). Table 1 provides an overview of the empirical chapters, the paradigm and measures used, and the main findings. Part I and II include chapters investigating the effects of affective states with a short time course (emotions) and those with a longer time course (including mood), respectively. Part III describes empirical evidence for the modulation of cognitive control by motivational factors. The General Discussion in Chapter 10 summarizes and integrates the findings.

The central assumption that aversive states enhance cognitive control is tested in Part I (Chapters 2 – 4). The research presented in Chapter 2 shows that task-irrelevant monetary reward can counteract the adaptations driven by conflict trials in a flanker task. These data are consistent with the assumption that cognitive demands evoke negative emotions, which may function to adapt cognitive control; stimuli with opposed valence may counteract such a state, thus indirectly regulating cognitive control. In Chapter 3, we show that this behavioral finding is replicated in a setup that allows for measuring brain activity online using EEG. Behavioral modulation is shown to be accompanied with neuromodulation in the ACC, implying that conflict and affective states may become integrated in this brain area. The effects of top-down control adaptations are also reflected in a narrowing of visual processing in posterior brain areas. Chapter 4 describes a study in which aversive states induced by negative IAPS pictures are shown to increase cognitive control directly. Positive pictures do not have this effect. Thus, only negative affect is shown to have a direct effect on cognitive control. Pupil dilation data indicate that the arousal state induced by these pictures seems not to mediate these effects.

Part II (Chapters 5 – 7) provides evidence for an informational function of affect, producing indirect effects, but not direct effects, on cognitive control adaptations. Chapter 5 describes a standard mood induction procedure that simultaneously manipulated valence and arousal levels. Affective valence only was shown to modulate conflict adaptation in a flanker task: moods with a negative valence increase conflict adaptation in comparison to positive moods. Chapter 6 describes a similar effect of hedonic value on conflict adaptation after the presentation of funny cartoons. Moreover, the fMRI results obtained in this study reveal a neural mechanism that may be responsible for this effect. Humor is shown to activate the basal ganglia (ventral striatum and ventral pallidum), which inhibits ACC responses to conflict. Functional connectivity analyses suggest that the ACC and the basal ganglia may interact through reciprocal loops. The study in Chapter 7 provide evidence for the idea that affective modulation of conflict adaptation is not limited to mood swings in healthy samples, but can also be observed in depression-vulnerable subjects who report increased depressed symptoms after a pharmacological manipulation that lowers their central serotonin levels via tryptophan depletion.

The final two empirical chapters in Part III illustrate that cognitive control can also be modulated by motivational factors not directly related to emotion. As described in Chapter 8, demanding situations enhance cognitive control, but only if overall task difficulty is not too high. Behavioral adaptation is found to drop if situational demands became too difficult, illustrating that the relationship between task difficulty and motivation is not linear. Finally, in Chapter 9 it is shown that passionate love, an affective state accompanied with strong motivational implications, does not necessarily improve cognitive control. Passionate lovers who have a nearly-obsessive attention for their beloved actually show decreased cognitive control, although their mood ratings are not related to this impairment. This finding illustrates a situation where motivation actually consumes resources needed to perform well on cognitive tasks.

Table 1. *Overview of the empirical chapters*

Part / Chapter	Conflict paradigm	Manipulation / Instrument	Measurement	Effect	Main finding
Part I. Emotions and cognitive control:					
2. Reward and conflict adaptation	Flanker task	Monetary gains and losses	Manual RT	indirect	Gain (vs. loss) reduces conflict adaptation
3. Electrophysiology of reward and conflict adaptation	Flanker task	Monetary gains and losses	Manual RT + EEG	indirect	Gain (vs. loss) reduces conflict adaptation
4. Emotion, arousal, and focused attention	Anti-saccade task	IAPS pictures	Eye saccades + Pupil dilation	direct	Negative (vs. neutral) emotion increases cognitive control
Part II. Sustained affect and cognitive control:					
5. Mood and conflict adaptation	Flanker and Stroop task	Mood induction	Manual RT	indirect	Positive (vs. negative) mood reduces conflict adaptation
6. Humor and conflict adaptation: a neural mechanism	Flanker task	Funny cartoons	Manual RT + fMRI	indirect	Positive (vs. neutral) affect reduces conflict adaptation
7. Depression and conflict adaptation	Simon task	Acute Tryptophan Depletion	Manual RT + Pharmacology	indirect	Depressive mood / symptoms is associated with increased conflict adaptation
Part III. Motivation and cognitive control:					
8. Task difficulty and conflict adaptation	Flanker and Stroop task	Task difficulty	Manual RT + Pupil dilation	indirect	Increased task difficulty reduces conflict adaptation
9. Romantic love and attentional focus	Flanker and Stroop task	Passionate Love Scale	Manual RT	direct	Intensity of passionate love is associated with reduced cognitive control

2

Reward and Conflict Adaptation

> "Pleasure drives out pain; and excessive pain leads men to seek excessive pleasure, and bodily pleasure generally, as a restorative. And these restorative pleasures are intense, and therefore sought for, because they are seen in contrast with their opposite."
>
> Aristotle

This chapter is based on:

van Steenbergen, H., Band, G.P.H., & Hommel, B. (2009). Reward counteracts conflict adaptation: Evidence for a role of affect in executive control. *Psychological Science, 20*, 1473-1477.

Abstract

The conflict-adaptation effect has been observed in several executive-control tasks and is thought to reflect an increase in control, driven by experienced conflict. We hypothesized that if this adaptation originates from the aversive quality of conflict, it would be canceled out by a positive, rewarding event. Subjects performed an arrow flanker task with monetary gain or loss as arbitrary feedback between trials. As predicted, we found a reduction in conflict adaptation for trials in which conflict was followed by monetary gain. The strength of this gain-induced modulation was found to depend on subjects' motivation to pursue reward, as measured by the Behavioral Activation System Drive scale. Our findings demonstrate for the first time that the conflict-adaptation effect can be strongly reduced by reward contexts, suggesting that reward and conflict can compensate for each other's effects, probably via changes in dopamine levels.

Introduction

In decision making, the heart is the adversary of the mind—at least according to folk wisdom. Emotions are commonly believed to create irrational behavior and to lead to wrong judgments. However, there is increasing evidence that emotion and cognition often cooperate in shaping adaptive behavior and that a dysfunction of emotional processing impairs rational reasoning and action control (e.g., Damasio, 1994). Considerable research effort has focused on the impact of longer term emotional states (i.e., mood) on cognitive functioning, and there is evidence that, for instance, positive mood improves performance in various cognitive tasks (Ashby et al., 1999) and affects cognitive-control operations in systematic ways (Dreisbach & Goschke, 2004). However, recent observations suggest that even very brief affective states are associated with adaptations in cognitive control and may thus be involved in tailoring control strategies to the situation at hand. This seems particularly true for states induced by aversive and rewarding events, presumably because such events directly affect the current level of dopamine (Schultz, 2007), a neurotransmitter that plays an important role in regulating the (frontal) brain areas underlying cognitive control (Miller & Cohen, 2001).

One important function of cognitive control is to adapt control parameters to current task requirements. It is assumed that the adaptation of such parameters is, or at least can be, driven by the registration of conflict (e.g., between competing responses; Botvinick et al., 2001). Evidence supporting this view comes from tasks in which participants need to focus on a relevant target while ignoring distracting information (cf. Egner, 2007, for a review). For example, in the flanker task (Eriksen & Eriksen, 1974), congruent (C) flankers are known to facilitate, and incongruent (I) flankers to interfere with, speeded responses to the central target. This congruency effect is modulated by the amount of conflict perceived on the preceding trial. Gratton et al. (1992), who reported this effect originally, argued that participants focus their attention more on the target after an incongruent trial (i), which reduces the congruency effect (I – C) in the next trial (iI – iC), as compared with trials following a congruent trial (cI – cC). This effect has been called the “conflict-adaptation effect” because it is believed to reflect adjustments in cognitive control that are driven by conflict information (Botvinick et al., 2001). Although episodic memory retrieval of stimulus and response associations may account for some of the published findings (Hommel et al., 2004), more recent studies suggest that control-related portions of the effect remain, even if episodic effects are controlled for (Egner, 2007).

Botvinick (2007) has recently suggested that conflict may be experienced as an aversive, or negatively reinforcing, event. It may thus be the aversive quality of a conflict that signals the need for adjustment to cognitive-control systems, which then respond by refreshing or strengthening the representation of the current intention or goal. If the need for control is indeed signaled by an aversive (negative) event—so we reasoned in the present study—it should be possible to counteract control operations by presenting a rewarding, positive event at about the same time. This is what we tried to do by signaling an unexpected monetary gain. The idea was that this reward cue might outweigh the conflict-induced control signal and prevent behavioral adaptation.

Applying this reasoning to the conflict-adaptation effect, we predicted that the presentation of a rewarding stimulus immediately after an incongruent trial would reduce conflict-driven adaptation in the next trial. This was tested in an otherwise standard flanker task by providing unpredictable monetary gains or losses during the response-stimulus interval. According to our prediction, the conflict-adaptation effect would be diminished in the gain condition as compared with the loss condition. We also included neutral trials, without gain or loss, to demonstrate normal conflict-adaptation effects in a standard, emotionally neutral context.*

Our second prediction considered that the effect of the gain manipulation may depend on individual sensitivity to reward. Gray (1989) suggested that a Behavioral Activation System (BAS) may guide behavior in response to reward signals via the dopamine system. Based on his work, self-report BAS scales have been developed to describe BAS activation as a personality dimension (Carver & White, 1994). Previous research has shown that the BAS Drive and BAS Reward Responsiveness scales predict hedonic responses and behavioral regulation in response to reward and can be used as a reliable index of trait reward sensitivity (e.g., Carver & White, 1994; Franken & Muris, 2006). If our gain condition reduces conflict adaptation in general, individuals who score high on these scales would thus be

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* One may speculate that loss might increase the conflict-adaptation effect beyond what can be observed with neutral trials: Loss may increase the aversiveness of the situation and therefore support or strengthen the conflict signal. However, it is not clear whether aversiveness can be further increased by our manipulation or whether conflict in the neutral condition leads to some maximum aversion limit already—so we hesitated to predict differences between the loss and the neutral condition.

more likely than individuals who scored low to show particularly strong reductions.

Methods

Participants

Thirty-three university students participated (18–30 years of age; 8 men and 25 women). They were informed about the duration of the experiment (15 min) and that they would earn €2.00, plus a bonus that could increase to a few euros if they were lucky. One subject was excluded from analyses because of response omissions on more than 10% of the trials.

Procedure

Instructions were given on a computer screen. Subjects were informed about the task and that smiley, sad, and neutral faces would appear between trials independently of their responses. The computer would add €0.20 to their bonus if a smiley face appeared and would subtract €0.20 if a sad face appeared. Neutral faces were not associated with any gain or loss. Subjects were encouraged to make quick and accurate responses with their index fingers on the keyboard, to the central target of an arrow flanker stimulus. After giving consent, participants performed 24 practice trials and were given accuracy feedback for 600 ms at the end of each trial. Then they were given the opportunity to read the instructions again, and they were informed about the three test blocks in which they would earn money, each lasting about 4 min. Self-paced break screens with a maximum duration of 40 s were shown in between. We did not tell the subjects that the last test block annexed a filler block of 24 trials, where gain trials were overrepresented. This resulted in a random bonus payoff of between €0.40 and €2.00 for each person.

The stimuli were presented on a white background on a 15-in. monitor, and participants viewed the monitor from a distance of about 60 cm. Each of the 612 test trials started with a fixation cross (for varying intervals of 200, 300, and 400 ms), followed by the flanker stimulus. Immediately after a response to the flanker stimulus or, in the case of omission, after 1,000 ms, a line-drawn face was presented for 500 ms, after which the next trial started. Flanker stimuli comprised a row of five black arrows pointing either left or right. We used the same number of congruent (flankers in the same direction as the target) and incongruent (flankers opposite to the target) trials. Smiley, sad, and neutral faces were distributed uniformly and served as cues for monetary gain or loss.

Scales

A subset of 22 participants had filled out questionnaires in an earlier unrelated experiment. To explore associations with reward-related traits (measured with the BAS scales) and reward-unrelated traits (measured with other scales), individual scale scores were correlated with conflict-adaptation latency effects for the gain condition. We used the following trait scales translated into Dutch: the Behavioral Inhibition System/Behavioral Activation System (BIS/BAS) Scales (Franken, Muris, & Rassin, 2005), the Positive and Negative Affect Schedule (Hill, van Boxtel, Ponds, Houx, & Jolles, 2005), the Eysenck Personality Questionnaire (Sanderman, Arrindell, Ranchor, Eysenck, & Eysenck, 1995), and the Action Control Scale (Koole & Jostmann, 2004). To provide a safeguard against multiple testing, we used a conservative criterion ($\alpha = .01$) for significant correlations. Because only one subscale from the BIS/BAS Scales was significantly correlated with performance, scores from the other reward-unrelated scales are not further considered here.

Data Analysis

We used repeated measures analyses of variance and t tests to analyze correct reaction time (RT) and error rates for test trials, as a function of the congruency of the current trial (I vs. C); the congruency of the previous trial (i vs. c); and the reward signal (gain, neutral, or loss), shown as feedback in the previous trial. The first trial of each block (0.5%), trials following an error (5.9%), and trials with RTs not fitting the outlier criterion (2.5 SD; 2.6%) were excluded from analysis.

Results

As usually found, performance on the flanker task was faster (415 ms vs. 458 ms), F(1, 31) = 316.23, prep = .99, d = 4.52, and more accurate (2.3% vs. 8.2% errors), F(1, 31) = 84.54, prep = .99, d = 2.34, on congruent than on incongruent trials. Moreover, as predicted, normal conflict-adaptation latency effects were found for the neutral and loss conditions, respectively, F(1, 31) = 7.83, p < .01, prep = .95, d = 0.71; F(1, 31) = 13.96, p < .001, prep = .99, d = 0.95, whereas no evidence for this effect was found for the gain condition, F(1, 31) = 0.03, p > .05, prep = .21, d = 0.04 (see Table 1). A direct comparison of conflict-adaptation effects, (RTcI – RTcC) – (RTiI – RTiC), for the gain and the loss conditions confirmed the predicted effect, t(31) = 1.844, p < .05, prep = .85, d = 0.49. Analyses on high-conflict (iI) versus low-conflict (cI) trials also illustrate this influence of gain context, F(2, 62) = 3.59, p < .05, prep = .90, d = 0.48 (see Table 1 for details): Normal conflict-driven speedup was found for the loss (6 ms) and neutral (5 ms) conditions, whereas in the gain condition, this effect disappeared (–3 ms). Explanations suggesting an influence of gain that is independent of previous-trial conflict could be ruled out, given that gain on the previous trial was not associated with overall response slowing, F(2, 62) = 0.72, p > .05, prep = .51, d = 0.22, or increases in congruency effects on the next trial, F(2, 62) = 0.57, p > .05, prep = .45, d = 0.19. Comparable results were obtained for the error-rate data (see Table 1).

To test our second prediction, BIS/BAS subscale scores were correlated with the conflict-adaptation latency effect in the gain condition. Individual BAS Drive

Table 1. *Congruency and conflict-adaptation effects as a function of condition*

Condition	Trial type	Latency			Errors		
		RT (ms)	CE (ms)	CAE (ms)	Error rate (%)	CE (%)	CAE (%)
Gain	cC	413	44**	1	2.3	6.6**	0.3
	iC	457			9.1		
	cI	416			1.9		
	iI	460			8.3		
Neutral	cC	413	43**	9 **	2.1	5.6**	2.2*
	iC	461			8.8		
	cI	418			2.9		
	iI	456			7.4		
Loss	cC	412	42**	10**	2.1	5.6**	2.0†
	iC	459			8.7		
	cI	417			2.5		
	iI	453			7.1		

Note: CE = Congruency effect (= I–C), CAE = Conflict-adaptation effect (= (cI-cC) – (iI-iC)), t-tested against zero: †p < .10; * p < .05; ** p < .01

scores (possible range from 4 to 16) strongly predicted a gain-induced increase in conflict adaptation (r = −.576, p < .005, prep = .97). The other subscales (BIS, BAS Reward Responsiveness, and BAS Fun Seeking) were not associated with this measure (ps > .05), nor were any correlations found for the neutral and loss conditions (ps > .10).

Discussion

Our results demonstrate for the first time that unexpected monetary gain leads to a strong reduction of conflict-driven adaptation. This observation is in keeping with the assumption that (a) response conflict may be experienced as an aversive event that signals the need for adaptive control (Botvinick, 2007); (b) unexpected monetary gain represents a positive, rewarding event; and (c) the effects of these two events can cancel each other out. The observation that the effects of rewarding and aversive events can compensate for each other suggests some common currency, some shared dimension on which positivity and negativity can be directly compared. We suggest that the dopamine system may provide this common currency, which is consistent with earlier findings showing that rewarding events involve phasic increases in dopamine level (Schott et al., 2008; Schultz, 2007), whereas decreases are associated with aversive events, including conflicts (Jocham & Ullsperger, 2009; Schultz, 2007). A dopaminergic modulation is also suggested by our observation that individual differences in reward sensitivity predict the influence of gain on conflict-driven adaptation. Interestingly, only the individual goal-directed drive to pursue reward (as measured by BAS Drive) was involved in this modulation, whereas differences in hedonic responsiveness to reward (as measured by BAS Reward Responsiveness) were not. A similar pattern has been observed for dopamine responses to rewarding stimuli (Beaver et al., 2006). These findings suggest a dominant modulating role for the motivational rather than the hedonic aspect of reward, which presumably involves dopamine (Berridge & Robinson, 2003). However, because the direction of this motivation modulation was opposite to the main compensatory effect of reward on conflict-driven control, the presumed role of dopamine in this modulation needs further study

Future work, including brain imaging, may reveal the underlying mechanisms of conflict adaptation, reward processing, and their interactions. It would be interesting to study the performance of clinical samples as well. People with depression, for instance, may show smaller reductions in the gain condition because of their lower responsiveness to reward (Nestler & Carlezon, 2006), an effect that may interact with general changes in conflict adaptation as well (cf. Mansouri, Tanaka, & Buckley, 2009; Holmes & Pizzagalli, 2007).

Taken all together, our observations support the idea that emotion and cognition need to cooperate to generate adaptive behavior. That is, the affective quality of an event provides important information about the amount and type of executive control needed to make sure that goals are reached as planned. Conflict-adaptation studies from the past have shown that increased control is a natural response to conflicts. However, people have a desire for rewards and—as demonstrated in this article—once they get them, their control system relaxes immediately.

Acknowledgments

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3

Electrophysiology of Reward and Conflict Adaptation

"The gyrus cinguli is the seat of dynamic vigilance by which environmental experiences are endowed with an emotional consciousness."

James W. Papez

This chapter is based on:

van Steenbergen, H., Band, G.P.H., & Hommel, B. (submitted for publication). Reward counteracts conflict-driven attentional adaptation: Electrophysiological evidence.

Abstract

Recent findings suggest that positive feedback counteracts the attentional adaptation to conflict triggered by incompatible distracting information. Here we hypothesize that these compensatory effects of reward on conflict processing may regulate subsequent behavioral optimization and perceptual focusing via the Anterior Cingulate Cortex (ACC). We recorded EEG while participants performed an arrow flanker task with monetary gain or loss as arbitrary feedback between trials. As predicted, we found a reduction in conflict adaptation for trials in which conflict was followed by monetary gain, a behavioral effect accompanied by a modulation in early visual processing related to the processing of the distracters. Moreover, time-frequency analyses showed that reward inhibits ongoing fronto-central theta oscillations induced by previous conflict, an interaction presumably reflecting ACC modulation. These data provide a first important step towards understanding the neural mechanism underlying the affective regulation of conflict-driven behavior.

Introduction

When people face adverse events, they typically adapt their attentional resources to deal with this demand. This adaptation of cognitive effort and attentional control has been reported for numerous changes in situational demands varying from increases in task difficulty (Botvinick et al., 2001; Dreisbach & Fischer, 2011; Gratton et al., 1992; Hillgruber, 1912), the experience of stressful and aversive stimulation (Easterbrook, 1959; Finkelmeyer et al., 2010) to the registration of performance errors (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). More recent work shows that positive affective states may undo or neutralize the impact of these adverse events, as measured by self-report, behavioral, physiological, and neural measures (Cabanac, 1971; Fredrickson et al., 2000; Leknes & Tracey, 2008; van Steenbergen, Band, & Hommel, 2009). Thus, aversive and rewarding events may compensate for each other's effects, possibly via a common mechanism that aims at behavioral optimization (Cabanac, 1992; Botvinick, 2007).

The anterior cingulate cortex (ACC) is thought to play an important role in this optimization process (Botvinick et al., 2001; Gehring & Willoughby, 2002; Holroyd, Pakzad-Vaezi, & Krigolson, 2008). Event-related brain potential (ERP) studies have shown that the ACC generates a mediofrontal negativity wave, called the N2 component, which can be elicited by conflict, as triggered by competing responses in tasks where participants need to focus on a relevant target while ignoring distracting information (Forster, Carter, Cohen, & Cho, 2011; Yeung, Botvinick, & Cohen, 2004). It has been suggested that feedback stimuli signaling positive events and reward may inhibit this neural conflict signal, as evidenced by an opposite, positive-going, deflection in the ERP with a similar temporal and spatial distribution as the N2 component (Holroyd et al., 2008; Holroyd & Coles, 2002). These and other data suggest that unexpected monetary rewards may have a neutralizing effect on conflict monitoring activity in the ACC, presumably via phasic dopamine signaling from the midbrain (Jocham & Ullsperger, 2009; Munte et al., 2008; Schultz, 2007).

The present study was designed to investigate whether these neutralizing effects of reward on neural conflict monitoring may account for the recent observation that unexpected reward prevents the adaptive upregulation of attentional control in conflict-inducing flanker tasks (van Steenbergen et al., 2009). In flanker tasks, participants respond to centrally presented visual targets while ignoring surrounding non-targets that may signal the same or a different response as the target (Eriksen & Eriksen, 1974). The degree to which performance is worse in response-incompatible as compared to response-compatible trials can be taken to reflect the participant's ability to focus on relevant information in the face of distraction. Interestingly, the size of this compatibility effect is typically reduced in trials following incompatible trials (the so-called conflict-adaptation effect; Gratton et al., 1992), which has been taken to reflect a conflict-induced sharpening of the attentional focus (e.g., Botvinick et al., 2001; Egner, 2007). However, we have recently shown that unexpected positive feedback presented immediately after a response in an incompatible trial (cf. Figure 1A) eliminates the conflict-adaptation effect, presumably by counteracting attentional adaptation to conflict (van Steenbergen et al., 2009). Given the well-known role of the ACC in producing adaptive behavior, this effect of reward on subsequent adaptation might be driven by a modulation of ongoing oscillatory neural activity produced by previous response conflict (Botvinick et al., 2001; Cohen, Ridderinkhof, Haupt, Elger, & Fell, 2008; Kerns et al., 2004).

Traditional ERP techniques are not suitable to address this hypothesis because averaging single-trial EEG traces will reveal only neural activity that is phase-locked to the onset of the stimulus (cf. Luu, Tucker, & Makeig, 2004; Yeung et al., 2004). In contrast, time-frequency decomposition analyses such as complex wavelet convolutions can assess sustained conflict-related processing in flanker, Stroop, and Simon tasks (Cavanagh, Cohen, & Allen, 2009; Cohen et al., 2008; Hanslmayr et al., 2008). Wavelet analyses are sensitive to oscillatory activity that varies in phase from trial to trial and can provide measures of instantaneous power (i.e., energy at different frequencies, a.k.a. induced activity) and inter-trial phase coherence (i.e., consistency of oscillation onset across trials, a.k.a. evoked activity). Cumulating evidence suggest that ongoing fronto-central midline theta (4-8 Hz) power measured at the scalp can be modulated by conflict (Cohen et al., 2008; Hanslmayr et al., 2008) and feedback processing (Cohen, Elger, & Ranganath, 2007; Cohen, Elger, & Fell, 2009). As implied by intracranial recordings, this theta effect may originate from the ACC and the surrounding medial frontal wall (Cohen et al., 2008). Based on these observations, we hypothesized that oscillations in the theta band may reflect the actual conflict parameter and the compensatory effects of reward on the conflict state, and thus show a conflict-induced increase that is attenuated by subsequent unexpected positive feedback.

A second aim of the present study was to test the idea that conflict and reward do not only co-modulate subsequent selective attention and the resulting behavioral adaptation (cf. van Steenbergen et al., 2009), but also alter early distracter processing in the visual cortex. Thus, if conflict on a previous trial intensifies the attentional focus on the target on the subsequent trial, this should lead to a shallower processing of the surrounding flankers (cf. Treue, 2001). Reward may counteract this effect. Evidence for distracter-related modulation in the visual cortex in humans has mainly been provided by fMRI studies on the effect of perceptual and working memory load on attentional focus (for a review, see Lavie, 2005). Reduced distracter activation in visual cortex has also been reported during post-error adaptation (Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011). However, there is no evidence yet that conflict in correct responses triggers a similar adaptation (Egner & Hirsch, 2005). In order to test this possibility, our task used vertically moving flankers that elicit a motion-sensitive ERP component in the visual cortex known as the motion visual evoked potential (motion VEP; for a review, see Heinrich, 2007). Using the motion VEP as an index of distracter-related processing, we hypothesized it to be sensitive to the modulation of attentional focus triggered by the interaction between reward and conflict on the preceding trial.

To summarize, we predicted that 1) conflict induced by incompatible flankers increases fronto-central midline theta oscillations and sharpens the attentional focus, thus decreasing distracter-related visual processing and behavioral compatibility effects in the subsequent trial; and 2) the presentation of a rewarding stimulus immediately after an incompatible trial counteracts these neural and behavioral effects. This was tested in a flanker task by providing unpredictable monetary gains or losses during the response-stimulus interval (see Figure 1A). Neutral trials, without gain or loss, were also included to provide a baseline condition.

Methods

Participants

Thirty-three right-handed university students participated (18–27 years of age; 6 men and 27 women). They were informed about the duration of the experiment (2 hours, including EEG preparation) and that they would earn € 13 (or course credits), plus a bonus that could increase to a few euros if they were lucky. Three participants were excluded from analyses because of technical problems during the acquisition of the physiological data. The experiment was conducted in accordance with relevant regulations and institutional guidelines and was approved by the local ethics committee from the Faculty of Social and Behavioral Sciences. All students read and signed informed consent.

Experiment

Subjects were informed about the task and that positive, negative, and neutral cartoon faces (smilies, grumpies, and neutral faces) would appear between trials independent of their responses. The computer would add € 0.20 to their bonus if a smiley appeared and would subtract € 0.20 if a grumpy appeared. Neutral cartoon faces were not associated with any gain or loss. Subjects were encouraged to make quick and accurate responses with their index fingers, to the central target of an arrow stimulus array. After informed consent, EEG preparation and a 6-min resting state EEG measurement, participants performed 24 practice trials in which they were given accuracy feedback for 600 ms at the end of each trial. Following this practice block, subjects performed a motion localizer block with 168 flanker trials using moving and still flankers (not followed by any faces or feedback). These trials started with a fixation cross (800 – 1000 ms, jittered), after which the stimulus array was presented until a response was given (maximum duration of 1,000 ms).

Task instructions were repeated before the test trials started. Participants were informed about the seven blocks in which they would earn money, each lasting about 5 min. Self-paced break screens were shown in between. We did not tell the subjects that the last test block annexed a filler block of 36 trials, where gain trials were overrepresented. This resulted in a random bonus payoff of between € 1.60 and € 4.00 for each person. The stimuli were presented on a white background on a 17-in. CRT monitor (1025 x 768 pix), and participants viewed the monitor from a distance of about 60 cm. Each of the 840 test trials started with a fixation cross (900 - 1100 ms, jittered), followed by the stimulus array (99 x 7 pix) that always comprised a target without motion and four vertically moving flankers (using a triangle wave function, amplitude = 10 pixels, period = 200 ms). Targets and flankers were black arrows pointing either left or right. We used the same number of compatible (flankers in the same direction as the target) and incompatible (flankers opposite to the target) trials. Almost immediately (30 ms) after a response to the stimulus array or, in the case of omission, after 1,000 ms, a yellow line-drawn face (200 x 200 pix) was presented for 750 ms, after which the next trial started. The three types of cartoon faces appeared with equal probability and served to indicate monetary gain or loss.

EEG recording

Electroencephalographic (EEG) activity was recorded over positions AFz, F5, Fz, F6, FC3, FCz, FC4, C5, C3, C1, Cz, C2, C4, C6, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, POz, PO8, O1, Oz, and O2 of the 10/10 standard. Horizontal eye movements were calculated by bipolar derivations of electro-oculogram (EOG) signals over the left and right outer canthus. Vertical eye movements were calculated by bipolar derivations of signals above and below the left eye. Monopolar recordings were referenced to the common mode sensor (CMS) and drift was corrected with a driven right leg (DRL) electrode (for details see http://www.biosemi.com/faq/cms&drl.htm). In order to re-reference the data off-line, two electrodes were placed at the left and right mastoid. Signals were DC amplified and digitized with a BioSemi ActiveTwo system at a sampling rate of 512 Hz.

Data analysis

Behavioral data

Repeated measures analysis of variance (ANOVA) and t-tests were used to analyze correct reaction time (RT) and error rates for test trials at Trial N+1, as a function of the compatibility of Trial N+1 (I vs. C); the compatibility of Trial N (incompatible / conflict vs. compatible / no conflict); and the reward signal (gain, neutral, or loss), shown as arbitrary feedback after Trial N, see Figure 1A. To provide a stable baseline for conflict and reward at the trial N, we only included those trial sequences that followed correct responses and neutral feedback. In addition, the first two trials of each block, trials following an error, and trials with RTs not fitting the outlier criterion (2 SDs from the individual condition-specific mean) were excluded from the analysis.

EEG analyses

Off-line analyses were performed with Brain Vision Analyzer. After rereferencing the channels to the average mastoid, data were high-pass filtered 0.01 Hz (24 dB/oct), and ocular artifacts were corrected using the standard Gratton, Coles, & Donchin (1983) method. EEG artifacts were automatically identified using four criteria: 1) bad gradient (> 50 μV / sample), 2) bad max-min difference (> 200 μV / 200 ms), 3) bad amplitude (absolute value > 1000 μV), 4) low activity (< 0.50 μV / 100 ms). Before this procedure was applied, artifacts caused by high scalp impedance of a particular electrode were corrected on an individual basis (2 participants), using a linear derivation of surrounding electrodes. Artifacts elicited by power line noise were also corrected on an individual basis (15 participants) using a low-pass 50 Hz filter (24 dB/oct). Stimulus-locked artifact-free segments were created for EEG activity during the motion localizer block and during the test trials. For the test trials we used exactly the same trials as those used for behavioral RT analyses, provided they were artifact free (see above).

Fronto-central theta oscillations as a function of compatibility and reward at Trial N segments were analyzed using a Continuous Wavelet Transformation as implemented in Brain Vision Analyzer (Morlet Complex waveform, frequency range from 2.5 to 50 Hz in 30 logarithmic steps, Morlet parameter c = 4.5). Induced power was calculated by averaging across trials after a percent change baseline correction from -300 to -100 ms. The amount of phase coherence was estimated using the Phase Locking Factor solution (version 1.1; 103), and was baselined from -300 to -100 ms for statistical analyses. After visual inspection, statistical analyses were conducted by entering average theta band (4-8 Hz) power and phase coherence values from 200 to 500, 500 to 800, and 600 to 700 ms windows for each condition into repeated measures ANOVAs and paired t-tests. For these analyses, we focused on data from electrode Cz because it showed the maximum modulation of reward on conflict-induced theta oscillation. One subject was excluded from these analyses because of an insufficient number of trials available (20 trials per condition on average) to perform reliable wavelet analysis.

Motion VEPs were identified in the motion localizer block by comparing ERPs elicited by moving flankers and still flankers. The Motion VEP was measured as the average ERP values from a window of 160 to 220 ms in occipital and occipito-temporal electrodes, using a 200-ms pre-stimulus baseline (cf. Heinrich, 2007). Statistical analyses (repeated-measures ANOVAs) of motion-related ERPs in the test trials at Trial N+1 segments were focused on electrode sites that showed a motion VEP maximum in the localizer block. Similar to earlier described methods (Heinrich, Schilling, & Bach, 2006), subjects with motion VEP amplitudes not exceeding a 2 uV threshold in both hemispheres during the motion localizer block were excluded from analyses in order to keep a sufficient signal-to-noise ratio (16 participants). Greenhouse-Geisser correction was applied whenever appropriate. For illustrative purposes, a 50-Hz low-pass filter was applied to all grand averages shown in Figure 3.

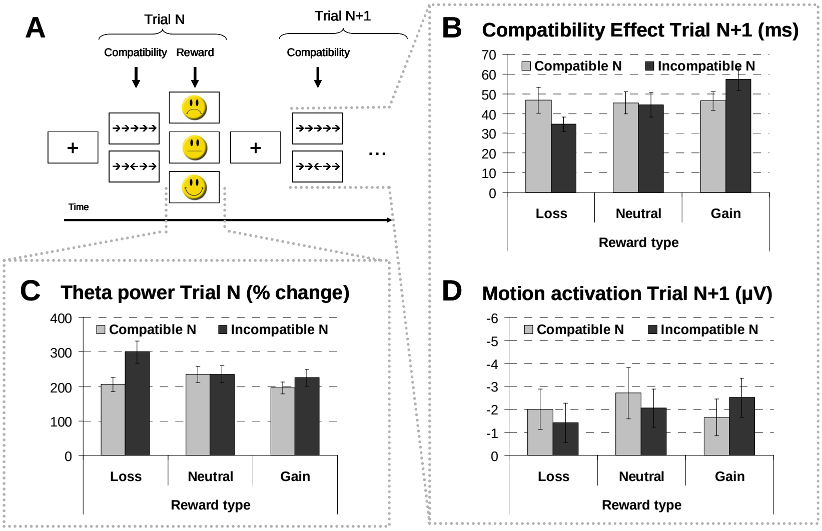

Figure 1. A. *Illustration of the experimental design. It was hypothesized that conflict induced by incompatible trials at Trial N is counteracted by subsequent gain feedback; this would reduce conflict-driven attentional focusing at Trial N+1.* ***B-D.*** *Summary of the main findings: In comparison to the loss condition, gain reduced conflict-induced fronto-central theta power measured at the 600 – 700 ms interval at Trial N (**C**), and reduced conflict-driven focusing at Trial N+1 both as measured in behavioral compatibility effects (**B**) and distracter-related visual processing as indexed by the Motion VEP in a 160 – 220 ms interval (**D**).*

Results

Behavioral data

As shown in Table 1, the flanker task produced standard RT compatibility effects indicating faster performance on compatible than on incompatible trials. Moreover, as Figure 1B shows, a standard conflict-adaptation effect (i.e., reduction of the flanker-compatibility effect after incompatible as compared to compatible flankers in the previous trial) was obtained in the loss condition, t(29) = 1.88, $p_{1\text{-sided}} < .05$, although not in the neutral condition, t(29) = 0.12, p = .90). Replicating our earlier observation (van Steenbergen et al., 2009), a direct comparison of the gain and the loss conditions confirmed the predicted effect of reduced conflict adaptation in the gain versus the loss condition for RT, as shown by a significant

CompatibilityN (2) x Reward (2) x CompatibilityN+1 (2) interaction, F(1,29) = 6.04, p = .02, MSE = 333.73 (see Table 1 for details). The Reward (2) x CompatibilityN+1 (2) interaction was also significant, F(1,29) = 5.46, p = .03, MSE = 345.21.

An ANOVA including all three levels of reward suggested a trend for a 3-way interaction effect, F(1,58) = 2.54, p = .087, MSE = 396.48. Subordinate ANOVAs showed that the effect of reward on conflict-adaptation modulated the compatibility effect adjustment following conflict (incompatible) trials, F(2,58) = 6.60, p = .003, MSE = 594.49, but did not affect the compatibility effect adjustments after

Table 1. *Behavioral data for each condition*

Condition	RT (ms)	Error rate (%)
Loss feedback		
Compatible trial following a compatible trial (cC)	387	1.0%
Compatible trial following an incompatible trial (iC)	391	0.4%
Incompatible trial following a compatible trial (cI)	433	6.4%
Incompatible trial following an incompatible trial (iI)	426	2.5%
Compatibility effect	41	3.8%
Conflict-adaptation effect	12	3.3%
Neutral feedback		
Compatible trial following a compatible trial (cC)	385	1.6%
Compatible trial following an incompatible trial (iC)	388	0.4%
Incompatible trial following a compatible trial (cI)	430	6.7%
Incompatible trial following an incompatible trial (iI)	432	4.2%
Compatibility effect	45	4.4%
Conflict-adaptation effect	1	1.2%
Gain feedback		
Compatible trial following a compatible trial (cC)	388	1.0%
Compatible trial following an incompatible trial (iC)	383	0.0%
Incompatible trial following a compatible trial (cI)	434	6.8%
Incompatible trial following an incompatible trial (iI)	441	2.6%
Compatibility effect	52	4.1%
Conflict-adaptation effect	-11	3.2%

Note. The compatibility effect was calculated from reaction times or error rates according to the following formula: (cI + iI)/2 - (cC + iC) / 2. The conflict-adaptation effect was calculated as follows: (cI - cC) - (iI - iC).

no-conflict (compatible) trials, F(2,59) = 0.02, p = .98, MSE = 843.52. A planned t-test focusing on trials following incompatible trials indicated a smaller compatibility effect for gain in comparison to the neutral, t(29) = 2.09, p = .045, and the loss condition, t(29) = 3.81, p = .001, which resulted in a reversed conflict-adaptation effect for the gain condition, t(29) = 2.04, p = .05. Error rate data showed significant main effects for CompatibilyN+1 (indicating more errors for incompatible trials) and CompatibilyN (indicating less errors after incompatible trials), but no (higher-order) interactions (see Table 1 for details). Thus, the modulation of conflict-adaptation in RT was not accompanied by a speed-accuracy trade off.

Theta frequency dynamics

Figure 2 shows the power and phase coherence measures of theta oscillations as induced by flanker compatibility at trial N and subsequently modulated by the feedback immediately following a key press to the stimulus array. An initial phase-locked theta response to the stimulus array was observed to be greater for incompatible than compatible trials, F(1,28) = 4.67, p = .039, MSE = .029, as was also visible in the power measure, F(1,28) = 15.66, p < .001, MSE = 46952.06. Moreover, as predicted, induced theta power sustained longer for incompatible versus compatible flankers during a subsequent 500 – 800 ms interval after loss feedback, t(18) = 3.02, p = .005 but not after gain feedback, t(18) = 1.15, p = .59, or neutral feedback, t(18) = .37, p = .71. As shown in Figure 2 (see also summary in Figure 1C), this modulation of reward on ongoing theta activity was maximal at the 600 – 700 ms interval, yielding a CompatibilityN (2) x Reward (3) interaction effect, F(2,56) = 3.26, p = .046, MSE = 10013.82. No interaction was observed in phase coherence (F < .5).

Distracter-related visual processing

As Figure 3A shows, moving flankers in comparison to still flankers elicited a standard motion VEP dominated by an occipito-temporal negativity that peaked around 200 ms and reached its maximum value in both hemispheres at electrode-pair P3/4. A direct comparison of the loss and gain conditions revealed a CompatibilityN (2) x Reward (2) interaction in the motion VEP elicited by the Trial N+1 for electrode P4, F(1,13) = 5.29, p = .039, MSE = 1.41, but not for electrode P3, F(1,13) = 1.62, p = .226, MSE = 1.48. Figure 3B and Figure 1D illustrate this interaction. A planned t-test indicated increased distracter-related motion activation following incompatible trials after gain in comparison to loss, t(13) = -2.54, p = .024, which mirrors the behavioral effect. However, when ANOVAs included the

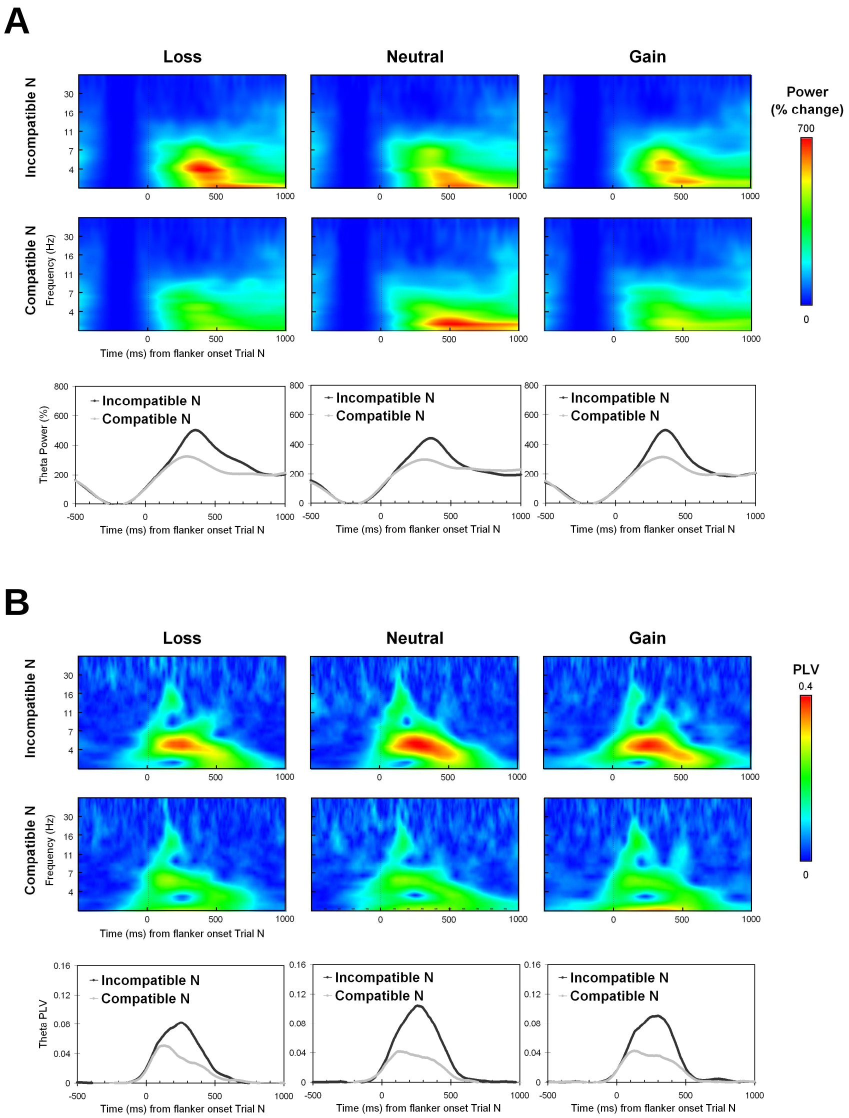

*Figure 2. Effect of conflict and reward at Trial N on frequency power (**A**) and phase coherence as indicated by Phase Locking Value (**B**) at electrode Cz. In comparison to gain feedback, induced theta (8-12 Hz) power sustained longer for incompatible versus compatible flankers after loss feedback.*

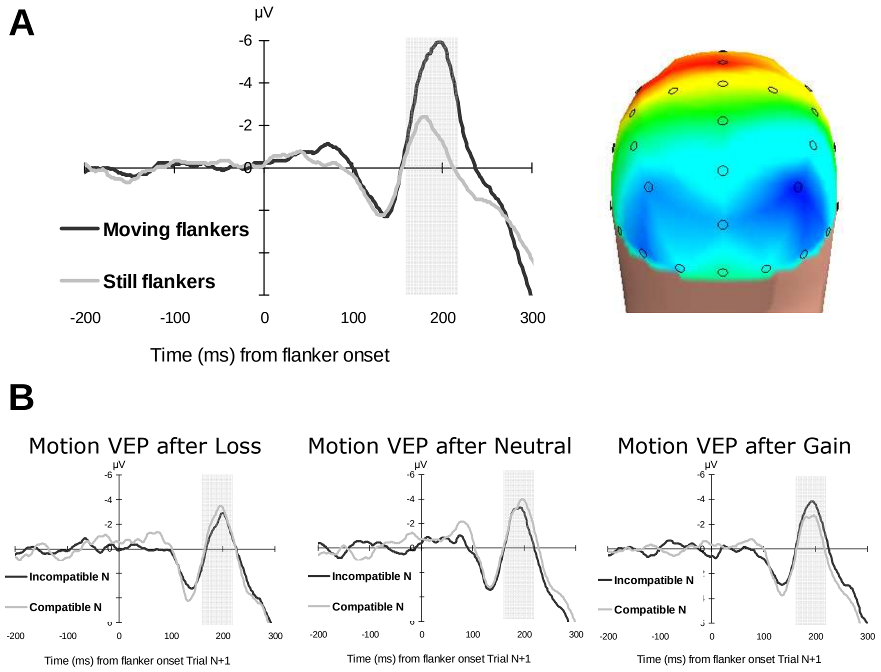

Figure 3. A. *In the motion localizer block, moving flankers in comparison to still flankers elicited a standard motion VEP with an occipito-temporal scalp distribution.* ***B.*** *During test trials, conflict and reward at Trial N modulated the motion VEP elicited at Trial N+1. All data are taken from electrode P4.*

neutral condition, no significant interactions emerged ($p > .15$), probably because the increased noise observed in the neutral condition reduced statistical power.

Discussion

The goal of the present study was to investigate the impact of interactions between conflict and reward processing on behavioral and neural adaptation. The behavioral effects replicated our earlier study (van Steenbergen et al., 2009) in showing reduced conflict-driven attentional adaptation in the gain condition. However, while in the previous study conflict adaptation was present in the neutral condition, this was not the case in the current study. This general reduction of adaptation might have been due to the fact that our study took about 2 hours to finish. As compared to the 15 minutes of our earlier study, this was likely to influence motivation and deplete attentional resources—conditions that are known to work against conflict adaptation (Fischer, Dreisbach, & Goschke, 2008).

Our study yielded two novel findings. First, as predicted, fronto-central theta power appears to reflect the compensatory effects of reward on conflict-related neural activity, as was shown by a sustained theta response during monetary loss, which was absent in the gain condition. This theta oscillation response may originate from the ACC and may represent a signal that indicates the need for more cognitive control, thus driving the sharpening of the attentional focus observed on the subsequent trial (Cohen et al., 2008). Such modulation may involve dopamine signaling from the midbrain. According to the theory by Holroyd and co-workers (Holroyd et al., 2008; Holroyd & Coles, 2002), negative and positive events interact via dopamine modulation, which drives ACC activity. More recent evidence suggests that the ACC may also provide feedback signals conveyed down to the midbrain, where it can inhibit dopamine neurons (Frank, 2005). It has been hypothesized that such fronto-striatial interactions may lower prefrontal dopamine concentrations, which shifts the balance of receptor activation towards D1 receptors, thus reducing distraction and improving attentional focusing (Jocham & Ullsperger, 2009). Our data suggest that theta oscillations may play an important role in this modulation. However, note that we can not claim that theta oscillations provide a unique neural signature of conflict- and reward-related processing, given that fronto-central oscillations have also been observed for other processes, such as attention and memory (e.g., Basar-Eroglu & Demiralp, 2001; Onton, Delorme, & Makeig, 2005; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005). Altogether, our data leave open the possibility that theta oscillations that originate from the same ACC region serve different functions in different tasks and circumstances. Further research is needed to understand the functional role of theta oscillations in the presumed interactions with dopamine neurons and other brain areas involved in the regulation of cognitive control.

The second novel finding concerns the modulation of distracter-related motion activation in the visual cortex as assessed by means of the motion VEP in the right hemisphere. Behavioral adaptation in the subsequent trial was accompanied by a corresponding adaptation in attentional focus as measured by an early modulation in distracter activation in the visual cortex (cf. Figure 1B and D). Note that an earlier study by Egner and Hirsch (2005) using fMRI did not find a distracter-related attenuation after conflict in a Stroop task. Our study points to the interesting possibility that ERP studies may actually be more sensitive to this modulation than BOLD responses are. Alternatively, it is possible that Stroop performance relies on different strategies than flanker task performance (cf. Lavie, 2005).

Two limitations of the present study need to be mentioned. First, as in the previous report, the reward manipulation affected behavioral and neural adaptation rather mildly, even though our sample was relatively large (N = 30). Second, when the neutral condition was included in the comparisons, statistical power to detect reward-related differences dropped, especially for the motion VEP analyses. One possible explanation of the larger inter-individual differences in the neutral condition might be that participants showed more variation in their appraisal of the situation of neither losing, nor winning any money. In other words, participants may have experienced the neutral condition as either a positive or negative situation, depending on subjective expectancies and affective state context (cf. e.g., Larsen & Norris, 2009).

To conclude, this study demonstrates that conflict triggered by incompatible trials in a flanker task increases fronto-central midline theta oscillations and sharpens the attentional focus, thus decreasing distracter-related visual processing and behavioral interference in the subsequent trial. We showed that adaptation effects in behavior and visual cortex are counteracted by unexpected monetary reward, which also involved the inhibition of ongoing theta oscillations. These data provide a first important step towards understanding the neural mechanism underlying the affective regulation of conflict-driven behavior.

Acknowledgments

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4

Emotion, Arousal, and Focused Attention

"To desire something and to recognize what must be done to attain it, as well as to recognize when its attainment has succeeded or failed, is to be inevitably emotional. In this way, emotions and reason are inextricably linked in an inescapable logic."

Richard S. Lazarus (1991)

This chapter is based on:

van Steenbergen, H., Band, G.P.H., & Hommel, B. (2011). Threat but not arousal narrows attention: evidence from pupil dilation and saccade control. *Frontiers in Psychology, 2*: 281.

Abstract

It has been shown that negative affect causes attentional narrowing. According to Easterbrook's (1959) influential hypothesis this effect is driven by the withdrawal motivation inherent to negative emotions and might be related to increases in arousal. We investigated whether valence-unspecific increases in physiological arousal, as measured by pupil dilation, could account for attentional narrowing effects in a cognitive control task. Following the presentation of a negative, positive, or neutral picture, participants performed a saccade task with a prosaccade versus an antisaccade instruction. The reaction time difference between pro- and antisaccades was used to index attentional selectivity, and while pupil diameter was used as an index of physiological arousal. Pupil dilation was observed for both negative and positive pictures, which indicates increased physiological arousal. However, increased attentional selectivity was only observed following negative pictures. Our data show that motivational intensity effects on attentional narrowing can occur independently of physiological arousal effects.

Introduction

In order to cope with threatening events, organisms often recruit extra resources. Regarding cognitive resources, there is evidence that affectively negative stimuli immediately prioritize the perceptual processing (Öhman, Flykt, & Esteves, 2001) and recall (Christianson, 1992) of related information at the cost of other processes (Bocanegra & Zeelenberg, 2009; Pessoa, 2009), and it has been argued that these effects are mediated by the organism's current state of arousal (Schimmack, 2005). According to Easterbrook's (1959) influential hypothesis, increased arousal may lead to the narrowing and focusing of attention, thus facilitating appropriate subsequent responding and coping behavior.

Although threatening events and stress have been demonstrated to narrow attention (Cohen, 1980; Chajut & Algom, 2003; Gable & Harmon-Jones, 2010a; for a discussion of opposite effects in trait anxiety, see Pacheco-Unguetti, Acosta, Callejas, & Lupianez, 2010), it is not clear whether these observations are due to nonspecific arousal or the activation of affect-specific emotional/motivational systems (Bradley, 2000). Even though Easterbrook's original hypothesis relates to unpleasant situations only, several authors have suggested that any increase of arousal—e.g., whether induced by caffeine ingestion or impulsivity traits—may modulate attentional selectivity (e.g., Anderson, 1990). Along similar lines, increasing motivational intensity has been reported to increase focused attention irrespective of the motivational system (approach versus avoidance) involved (Gable & Harmon-Jones Gable & Harmon-Jones, 2008; 2010a; Gable & Harmon-Jones, 2010b; Harmon-Jones & Gable, 2009). However, whether arousal can be conceived of as a unitary construct has been questioned (Lacey, 1967; Neiss, 1988; 1990) and it is not entirely clear how motivational intensity and arousal are conceptually related (cf. Gable & Harmon-Jones, 2010b). Accordingly, it remains to be shown whether the emotional modulation of the selective attention reflects nonspecific arousal that can vary orthogonally to the valence of the present affective state or whether it is specific to negative, potentially threatening events.

To index a possible narrowing of the attentional focus we used a visual antisaccade task (for a review, see Hutton & Ettinger, 2006). This task is typically used as a measure of cognitive control, which is closely related to attentional selectivity. That is, the amount of information that is entering the focus of attention may be limited by cognitive control exerted at a perceptual or more central processing level (Desimone & Duncan, 1995; Pessoa, Kastner, & Ungerleider, 2003; Miller & Cohen, 2001). Moreover, given that the neural mechanisms underlying the antisaccade task are well known and can easily be studied in monkeys as well (cf. Munoz & Everling, 2004), we considered this task to be particularly well suited for studying the neuro-cognitive effects of emotion on attentional selectivity. As a first step, our study aimed at disentangling the relative contributions of arousal and affective valence on attentional control using physiological and behavioral measures of arousal and focused attention, respectively.

In the antisaccade task, participants are presented with a peripheral, emotionally neutral target stimulus that appears with an abrupt onset on the left or right of the central fixation. Depending on the instruction, they are to move their eyes either to this target (prosaccade condition) or to the opposite side of the display (antisaccade condition). The common finding is that saccades are initiated more slowly and less reliably in the antisaccade than in the prosaccade condition. This cost is commonly attributed to the automatic tendency to look at novel events, which requires active inhibition in the antisaccade condition (Olk & Kingstone, 2003). Because improved attentional control decreases automatic capture by the target stimulus (Yantis & Jonides, 1990), reflexive saccades toward the stimulus become suppressed. Thus, we expected that manipulations improving focused attention reduce the size of the latency costs, with antisaccades becoming faster and prosaccades becoming slower (cf., Kristjansson, 2007).

Affective states were induced prior to each saccade-task trial using positive, negative, or neutral pictures from the International Affective Pictures System (IAPS). Valence and arousal ratings of these pictures show a quadratic relationship, such that positive and negative stimuli are typically highly arousing and neutral stimuli low arousing (Lang et al., 2008). To ascertain that the pictures induced a physiological response we used pupillometry. Recent work by Bradley, Lang, and co-workers has validated this approach (Bradley et al., 2008). In that study, both negative and positive IAPS pictures were shown to produce pupil dilation, a response reflecting emotional arousal which is associated with increased sympathetic nervous activation. By means of this setup we were able to contrast two competing hypotheses. If more attentional selectivity in affectively laden circumstances would be driven by nonspecific arousal, the difference in saccadic reaction time (RT) between anti- and prosaccades should be reduced following negative as well as positive arousing pictures as compared to the non-arousing neutral pictures. Alternatively, if more attentional selectivity is specific to threatening situations, this latency cost should be reduced following negative stimuli but comparable for positive and neutral stimuli.

Methods

Participants

Eleven students from Leiden University (18-22 years old; 2 males; 1 left-handed) participated for either payment (5 Euros) or course credits.

Materials

Thirty-two highly arousing negative, 32 neutral, and 32 highly arousing positive pictures were selected from the IAPS set (Lang et al., 2008)*. The stimulus set was almost identical to the one used by Bradley et al. (2008). Like that study, negative and positive stimuli could be differentiated on the basis of valence IAPS ratings, whereas they were matched for arousal IAPS ratings (Lang et al., 2008, see Table 1). Neutral pictures had low arousal ratings and intermediate valence ratings. In order to avoid light reflex confounds we used gray-scaled pictures (cf. Bradley et al., 2008); brightness and contrast were adjusted to ensure identical mean luminosity values for all pictures.

Task

Each trial started as soon as participants had successfully looked at the central fixation cross for at least 1 second. Then an IAPS stimulus appeared for 500 ms, which was replaced by the fixation cross for a jittered interval ranging from 1500 to 2500 ms. Following a 200-ms blank gap (cf. Everling & Fischer, 1998), the target stimulus (also a cross) appeared for 500 ms 8° to the left or right to the screen center. Then the central fixation cross appeared for another interval (ranging from 1000 to 2500 ms) before the next trial started. At the beginning of each block an 8-s verbal cue (approximately 5.7° x 1.4°; width x height) indicated whether a pro- (target position) or an antisaccade (mirror position of the target) was to be made to the next target stimulus. The picture (16° x 12°) and the black fixation cross (0.8° x 0.8°) were shown on a gray background with luminosity equal to the mean

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* The library numbers for the IAPS stimuli used in the present study are: Negative: 2120, 2205, 2520, 2590, 2691, 2730, 2750, 2800, 3015, 3030, 3053, 3100, 3170, 3180, 3181, 3400, 3500, 3530, 3550, 6210, 6211, 6212, 6821, 6834, 6838, 9041, 9250, 9300, 9341, 9405, 9800, 9921. Neutral: 2020, 2190, 2200, 2210, 2214, 2215, 2220, 2221, 2235, 2240, 2270, 2272, 2278, 2383, 2393, 2410, 2441, 2491, 2493, 2514, 2579, 2620, 2749, 2752, 2810, 2850, 2870, 2890, 3210, 5455, 7550, 9210. Positive: 2208, 2250, 2260, 2501, 2560, 2650, 4611, 4617, 4640, 4650, 4653, 4658, 4659, 4689, 5621, 8041, 8080, 8090, 8116, 8120, 8161, 8180, 8200, 8280, 8300, 8320, 8330, 8370, 8380, 8400, 8420, 8465.

of the pictures. In rare cases (0.2% of the time), eye tracker recording problems delayed the trial presentation (inter-trial intervals > 9 seconds). Because the interruption of the ongoing presentation sequence by either delayed presentation or by the onset of a new block is likely to compromise the experimental manipulation of the arousal and valence, the first five trials after such events were excluded.

Procedure

Participants were instructed to attend to the emotional pictures and to make pro- and antisaccades to the target as fast and accurate as possible. They were also asked to avoid eye blinks during picture and target presentation. After informed consent and eye tracker calibration, subjects practiced with 6 prosaccade and 6 antisaccade trials preceded by neutral IAPS pictures and followed by accuracy feedback for 1 second. Calibration and/or practice were repeated in case of eye tracking problems or when the subject did not follow the instructions. The task consisted of 6 alternating prosaccade and antisaccade blocks (counterbalanced order), with two self-paced breaks in between. Each block consisted of 48 trials, and every chosen IAPS picture appeared three times in randomly chosen trials. Participants were debriefed after the experiment.

Data acquisition and analysis

Saccadic behavior and pupil diameter were recorded at 120 Hz using a Tobii T120 eye tracker, which was integrated into a 17-inch TFT monitor. Participants were seated at a distance of approximately 60 cm from the monitor while their head was stabilized by using a chin rest. Artifacts and blinks as detected by the eye tracker were corrected by using a linear interpolation algorithm. A saccade was considered to begin as soon as the horizontal angle exceeded 2° and speed passed a 30°/sec threshold. For all analyses, we excluded the following trials: trials including and following recording-related delays (see above), trials following performance errors, trials with saccadic reaction time outliers (< 80 ms or > 500 ms), and trials where no saccades could be detected. Repeated-measures ANOVAs with the factors picture content (negative, neutral, positive) and task (pro versus anti) were run on pupil dilation and saccadic behavior measures. Paired t-tests were used for post-hoc tests.

Results

Pupil dilation

Following Bradley et al. (2008), pupil dilation to the picture content was measured after the initial light reflex. Dilation was defined as the mean pupil diameter in a window from 2 to 2.5 seconds after picture onset, using a 200 ms pre-picture baseline. As Table 1 shows, both negative and positive pictures caused dilation in comparison to neutral pictures. Analyses revealed a main effect of picture content ($F(2,20) = 4.74$, $p < .05$, $MSE = .005$), independent of task ($F(2,20) = 1.02$, n.s., $MSE = .003$). Replicating Bradley et al. (2008), planned t-tests confirmed that arousing pictures increased pupil diameter ($t(10) = 2.49$, $p < .05$). As in that study, there was also a trend for negative pictures to induce more dilation than positive pictures ($t(10) = 1.822$, $p = .09$).

Saccadic behavior

See Table 1 for details. As usually found, correct saccadic reaction times were slower during anti blocks than during pro blocks ($F(1,10) = 77.08$, $p < .001$, $MSE = 1073.76$). More importantly, this task effect interacted with picture content (F(2,20 $= 3.82$, $p < .05$, $MSE = 112.48$). Planned t-test showed that the latency cost (anti-

Table 1. *Emotion and performance measures as a function of picture content*

Measure	Picture content					
	Negative		Neutral		Positive	
Self report						
Valence rating	2.4	(.11)	5.0	(.11)	7.0	(.11)
Arousal rating	5.9	(.16)	3.6	(.16)	5.5	(.16)
Physiology						
Pupil diameter (mm)	4.25	(.040)	4.19	(.026)	4.23	(.033)
Behavior						
Pro-saccadic RT (ms)	196	(8.3)	185	(7.5)	189	(7.4)
Anti-saccadic RT (ms)	257	(12.7)	260	(10.8)	265	(9.8)

Note: Table shows means with standard errors between brackets.

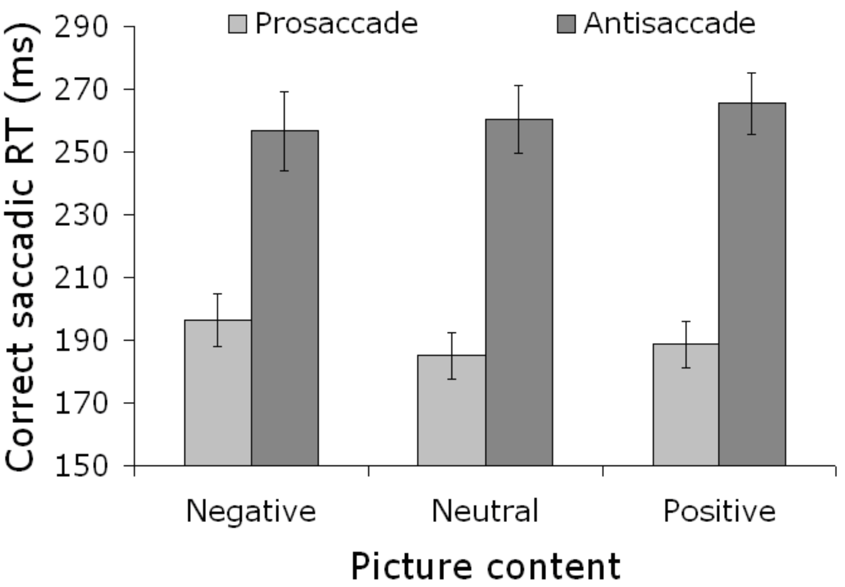

Figure 1. *Correct saccadic RT as a function of picture content and task context.*

RT minus pro-RT) was reduced following negative pictures ($t(10) = 2.84$, $p < .02$) in comparison to neutral pictures, but not for positive pictures ($t(10) = .21$, n.s.). As Figure 1 illustrates, relative to the neutral baseline, negative pictures slowed down prosaccadic reaction time (11 ms; $t(10) = 3.34$, $p < .01$) but did not significantly speed up antisaccadic reaction times (3 ms; $t(10) = .71$, n.s.), whereas positive pictures did not make any reliable difference (4 ms and 5 ms, respectively, all n.s.).

Task also affected the error rates ($F(1,10) = 17.90$, $p < .01$, $MSE = .025$): subjects committed 18% erroneous saccades in antisaccade blocks but only 1.5% in prosaccade blocks. This effect did not interact with picture content ($F(2,20) = .97$, n.s., $MSE = .006$).

To further test whether arousal might mediate any of these negative emotion effects we re-ran the analyses of correct saccadic reaction times with strong vs. weak pupil dilation as an additional factor. For this purpose, we categorized the trials following emotional pictures by means of a median split of the corresponding dilation measures. However, even though we replicated the task effect and its interaction with picture content, the dilation factor was not involved in any main effect or interaction (*F*s < 1).

Discussion

The aim of our study was to test whether attentional narrowing is due to general arousal or is selectively triggered by negative affective events. Although pupil dilation data confirmed that both negative and positive pictures increased the arousal level – a finding replicating Bradley et al. (2008) – attentional narrowing was observed following negative pictures only. This indicates that attentional narrowing is not caused by emotional arousal per se, at least as it can be measured by pupil dilation following the presentation of high-arousing pictures. In other words, increased emotional arousal may be a necessary condition, but it is not a sufficient condition for increased attentional selectivity. The same conclusion is suggested by the lack of impact of pupil dilation in the combined analysis. Hence, our observations do not provide any evidence for a role of arousal in driving attentional narrowing. Instead, the attentional focus seems to narrow whenever individuals are encountering events of negative affective valence.

How may negative affect regulate attentional narrowing? According to one account, dangerous situations may mobilize executive functions that protect against interference from disruption by irrelevant, distracting information (Norman & Shallice, 1986). Neuroimaging studies have suggested that these adjustments in cognitive control are implemented in the prefrontal cortex (Miller & Cohen, 2001), probably via signaling from the anterior cingulate cortex, a brain region involved in the detection of demanding and aversive situations (Botvinick et al., 2001; Shackman et al., 2011). Frontal cortex modulation, in turn, may modulate saccadic eye movements via the basal ganglia (Munoz & Everling, 2004). Thus, the reduced latency costs triggered by the negative pictures may originate from affect-driven modulation of cognitive control. This interpretation also fits earlier work that has used the antisaccade task to assess inhibitory control (cf. Munoz & Everling, 2004). A similar explanation may also apply to earlier published studies such as effects on Stroop tasks usually attributed to attentional narrowing (e.g., Agnew & Agnew, 1963; Callaway, 1959; cf. Wachtel, 1967).

However, it is important to emphasize that the reduced latency cost with negative pictures was driven by a slowing of RT during the prosaccade block rather than a speeding of RT during the antisaccade blocks. This indicates that processes other than improved control may also play a role in the affective modulation of behavior. For example, although it is likely that negative emotions increased control and attentional selectivity, which inhibits the visuo-motor grasp reflex resulting in delayed prosaccadic RTs (Kristjansson, 2007), this effect may have become attenuated during the antisaccade blocks. Because a state of high cognitive control is known to attenuate the effects of negative emotions (Ochsner & Gross, 2005), it might be that the effects of emotions on cognitive control were less pronounced in situations of higher task demands. Alternatively, it could be that the possible speeding of antisaccades is masked by an overall slowing effect induced by the negative pictures. Indeed, several studies suggest that the processing of negative events may compete for perceptual and/or executive resources, which may slow down performance on a subsequent task (e.g., Cohen, Henik, & Mor, 2011; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Notebaert et al., 2009; Pessoa, 2009). It remains an important aim for future studies to disentangle the role of these bidirectional interactions between emotions, perception, and executive function (cf. Vuilleumier, Armony, & Dolan, 2003).

Our study demonstrates for the first time that increased emotional arousal is not a sufficient condition to produce focused attention: prosaccadic slowing presumably reflecting attentional narrowing was observed for negative affect, but not for positive affect. Consistent with this finding, and in contrast to a common misinterpretation, Easterbrook's (1959) original hypothesis attributed attentional narrowing not to general arousal but to a drive or motivation to withdraw. Given that positive emotions with approach-motivation have been shown to increase attentional focus (e.g., Gable & Harmon-Jones, 2008; for a review, see Gable & Harmon-Jones, 2010b), it is an important challenge for future research to determine which affective dimension, other than arousal accurately predicts attentional narrowing induced by positive emotions. In line with very recent discussions (cf. Friedman & Forster, 2011; Harmon-Jones, Gable, & Price, 2011), our results imply that it is now time to start research programs that search for emotional dimensions beyond valence and arousal that are responsible for tuning one's attentional scope.

Acknowledgments

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5

Mood and Conflict Adaptation

"A mood is a way, not merely a form or a mode, but rather a manner, like a melody, which does not float above the so-called actual being occurrent of a person, but rather sets the key of this being, that is, it attunes and determines the manner of his being."

Martin Heidegger

This chapter is based on:

van Steenbergen, H., Band, G.P.H., & Hommel, B. (2010). In the mood for adaptation: How affect regulates conflict-driven control. *Psychological Science, 21*, 1629-1634.

Abstract

Cognitive conflict plays an important role in tuning cognitive control to the situation at hand. On the basis of earlier findings demonstrating emotional modulations of conflict processing, we predicted that affective states may adaptively regulate goal-directed behavior that is driven by conflict. We tested this hypothesis by measuring conflict-driven control adaptations following experimental induction of four different mood states that could be differentiated along the dimensions of arousal and pleasure. After mood states were induced, 91 subjects performed a flanker task, which provided a measure of conflict adaptation. As predicted, pleasure level affected conflict adaptation: Less pleasure was associated with more conflict-driven control. Arousal level did not influence conflict adaptation. This study suggests that affect adaptively regulates cognitive control. Implications for future research and psychopathology are discussed.

Introduction

Emotions seem to have evolved to guide organisms and their conspecifics in their struggle for survival, and affective states are assumed to facilitate behavior that is adaptive to the current situational context (Morris, 1992). In particular, it has been suggested that negative mood stimulates the processing of stimuli that have a negative valence and, therefore, deserve priority. Indeed, low pleasure levels seem to induce negative-information biases in attention and memory. Although it has been suggested that these biases systematically change the way people cope with negative events (cf. Gendolla, 2000), it has yet to be demonstrated how affect may play this regulating role in cognitive-control adaptations.

The main function of cognitive control is to adapt the cognitive system to situational demands. It has been proposed that this adaptation is driven by the detection of cognitive conflict (Botvinick et al., 2001). Evidence supporting this view comes from conflict tasks, such as the flanker task. Subjects respond more slowly to target information if distracting flanker information suggests a different response. On trials following this conflict, however, flanker interference is reduced (Egner, 2007; Gratton et al., 1992), which indicates that facing conflict enhances control (Botvinick et al., 2001).

Numerous studies have shown that low-pleasure affect facilitates neural conflict monitoring (e.g., Luu et al., 2000). They illustrate that moods that are congruent with the negative valence inherent to conflict (Botvinick, 2007) facilitate conflict registration (cf. Rusting, 1998). Given that conflict registration is important for tuning goal-directed behavior (cf. Kerns et al., 2004), affective states that prioritize conflict processing should also strengthen behavioral adaptations to cognitive conflict. We therefore predicted that people in a low-pleasure mood would adapt more strongly to cognitive conflict, and thus would be more likely to recruit control, than people in a high-pleasure mood. Some authors have postulated that, independently of pleasure, changes in arousal level may also influence conflict adaptation by altering the signal-to-noise ratio of conflict information (Verguts & Notebaert, 2009). If so, conflict-driven cognitive control may be influenced by the arousal level of the current affective state.*

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* Recent work has suggested a relationship between pleasure increases and shifts toward more flexible behavior at the cost of goal maintenance (Dreisbach & Goschke, 2004). The hypothesis that higher pleasure levels reduce conflict adaptation is in line with such a framework because

Given that pleasure and arousal are the two fundamental dimensions on which mood is assumed to vary (Yik et al., 1999), we investigated four groups of participants who underwent a standard mood-induction manipulation before performing a conflict-evoking flanker task. Each mood group occupied one of the four quadrants derived by crossing the dimensions of pleasure and arousal (see Fig. 1; cf. Jefferies, Smilek, Eich, & Enns, 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). We predicted stronger conflict-driven adaptation effects (i.e., reductions of flanker-induced interference after conflict trials) for participants with low pleasure levels (anxious and sad participants) than for participants with high pleasure levels (calm and happy participants).

Method

Participants and design

Ninety-eight students participated either for payment or for course credits (age range: 18–30 years; 24 males, 74 females; 11 left-handed). They were randomly assigned to one of the four mood-induction groups: anxious, sad, calm, and happy. Data from 7 subjects were excluded from analyses because of response omissions on more than 20% of the trials (n = 2), chance-level task performance (n = 3), or noncompliance with instructions (n = 2). All subjects completed a mood induction, the flanker task, and a manual color-word Stroop task.

Mood induction and assessment

We used a standard mood-induction procedure that combines music with imagination and is known to induce reliable mood changes (Eich, Ng, Macaulay, Percy, & Grebneva, 2007). Subjects used headphones to listen to specific classical music

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conflict adaptation facilitates task maintenance at the cost of flexible switching (e.g., Notebaert & Verguts, 2008). Cumulating evidence suggests a role for neurotransmitter modulation in these effects. For example, pharmacological studies suggest that raised tonic dopamine levels reduce phasic dopamine responses to conflict (for a review, see Jocham & Ullsperger, 2009). However, other neurotransmitter systems involved in mood changes (e.g., serotonin and norepinephrine) may also play a role (Posner, Russell, & Peterson, 2005). The mutual interactions and causal role of these systems is complex and remains a hot topic for future investigation.

samples whose efficacy in inducing the intended moods was validated by previous research (Jefferies et al., 2008). They were instructed to develop a particular mood by imagining and writing about a mood-appropriate event in detail; they were free to either focus on a written vignette they were given or to recall a similar event from their past. Music continued to play throughout the remainder of the experiment. To check the induction manipulation, we asked subjects to rate their mood on a 9 × 9 Pleasure × Arousal grid (Russell, Weis, & Mendelsohn, 1989) with values ranging from –4 to 4. Subjects were instructed to rate their mood whenever the grid appeared on the computer monitor during the experiment.

Flanker task

We used a computerized version of the classic flanker task (Eriksen & Eriksen, 1974) in which, on each trial, a central target stimulus is vertically flanked by four response-compatible or four response-incompatible stimuli, two on either side. Dutch color words were used as targets and flankers, and were randomly drawn from one of two sets of words ("brown," "gray," "yellow," and "red" or "purple," "green," "orange," and "blue"); the other set of words was used for the Stroop task, with assignment of word set to task counterbalanced within mood groups. Subjects were instructed to respond using their index fingers, pressing a key with their left index finger when the central target was either of two specific words and pressing a different key with their right index finger when the target was either of the other two words (stimulus-response mapping was counterbalanced within mood groups). A reminder of the stimulus-response mapping was shown for 15 s before the start of each of the two blocks of 72 trials.

All trials started with a fixation cross (randomly varying duration of 800, 1,000, or 1,100 ms), followed by the stimulus, which was presented until response registration, or for a maximum of 1,500 ms. In half of the trials, the target and flanker stimuli called for different responses (response-incompatible condition: I), whereas in the other half, physically identical target and flanker stimuli called for the same response (response-compatible condition: C). All trials were presented in an unconstrained random sequence. Stimuli appeared in black, lowercase Arial bold font and were presented on a gray background. The stimulus array was 3.5 cm wide and 5.4 cm high. Participants viewed the stimuli on a 17-in. monitor from a distance of approximately 60 cm.

Procedure

After giving informed consent, subjects were instructed about the mood ratings and told how to perform the flanker and Stroop tasks.* Instructions for both tasks emphasized both speed and accuracy. Following 16 practice trials and a 10-min mood induction, subjects performed a block of 72 trials for each task. After a short, 3-min mood booster, another block of each task was presented. The order of tasks was counterbalanced within mood conditions. Following completion of a questionnaire in which subjects were asked to rate how genuinely they had experienced their mood (9-point scale), subjects were instructed to return to baseline mood levels. Negative-mood subjects received a candy to facilitate return to their baseline mood. During the experiment, nine mood ratings were obtained at the following time points: at the beginning of the experiment (baseline), following the practice trials, halfway through and at the end of the mood-induction procedure, after the first half of the tasks, following the mood booster, after the second half of the tasks, following the questionnaire, and at the end of the experiment.

Data analysis

Analyses of variance were used to test our hypotheses. Arousal and pleasure grid ratings served as a mood-manipulation check. We analyzed absolute reaction times (RTs) and error rates, as well as interference effects (I minus C), on correct trials as a function of mood condition. Standard conflict-adaptation effects, for both RTs and error rates, were calculated by subtracting the interference effect following a correct conflict, or incompatible, trial (i) from the interference effect following a correct no-conflict, or compatible, trial (c) (i.e., (cI – cC) – (iI – iC)). The first trial of each block (1.4%) and outlier trials (RT > 2 SD from the condition-specific mean, calculated for each subject separately; 4.7%) were excluded from all analyses.

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* We could not use reaction time data from the Stroop task to test our hypothesis, given that no overall conflict-adaptation effect was observed in Stroop reaction times, $F(1, 87) = 1.37$. As expected, mood effects on this measure were not observed, $F(1, 87)$s < 2.31. In line with the flanker task, this task did produce a reliable interference effect, $F(1, 87) = 70.60$, $p < .001$, which was not modulated by mood, $F(1, 87)$s < 1.

Task-specific characteristics, such as task difficulty, may account for differences in the size of conflict-adaptation effects (e.g., Fischer et al., 2008). In a new series of experiments including Stroop and flanker tasks similar to those used in the current study, we indeed demonstrated that high task demands eliminate conflict-adaptation effects (see Chapter 8).

Results

Mood-induction manipulation check

Table 1 presents subjects' mean affect ratings at all nine assessment points. Participants began the experiment in a slightly positive (M = 0.59, SE = 0.14) and slightly aroused (M = 0.15, SE = 0.16) mood. Baseline ratings did not differ across the mood-induction groups, F(1, 87)s < 1.70. Participants reported the expected changes in arousal and pleasure following the mood induction. Average self-reported affect during task performance (ratings given at the beginning and end of the task blocks; i.e., at Times 3–6 in Table 1) indicated that the sad (M = –1.8, SE = 0.25) and anxious (M = –1.5, SE = 0.23) groups reported lower pleasure scores than the calm (M = 1.5, SE = 0.24) and happy (M = 1.7, SE = 0.25) groups, F(1, 87) = 181.14, p < .001, MSE = 1.33. Similarly, arousal scores were higher for the anxious (M = 1.7, SE = 0.31) and happy (M = 0.9, SE = 0.34) groups than for the sad (M = –0.5, SE = 0.34) and calm (M = –1.0, SE = 0.32) groups, F(1, 87) = 40.05, p < .001, MSE = 2.42, although the unpleasant-mood subjects reported slightly higher arousal than the pleasant-mood subjects, F(1, 87) = 4.30, p = .041. As in earlier studies (e.g., Eich et al., 2007), subjects judged their reported moods as genuine at the end of the task (M = 7.0, SE = 0.14), and this rating did not depend on mood condition, F(3, 87) = 2.69. Across mood conditions, comparisons between ratings given at baseline and at the end of the tasks suggest that the tasks themselves induced some reduction in pleasure, F(1, 90) = 7.78, p < .01, MSE = 2.30, but no change in arousal, F(1, 90) < 1.

Table 1. *Mean self-report mood scores per mood induction group*

Dimension	Induction group	Time point								
		Baseline	1	2	3	4	5	6	7	8
Pleasure	Anxious	0.42	0.54	-1.69	-1.69	-1.27	-1.96	-1.19	-0.04	0.77
	Sad	0.57	0.57	-2.05	-2.38	-1.57	-2.10	-1.14	0.14	0.71
	Calm	0.57	0.61	1.96	2.04	1.13	1.74	1.04	1.09	1.09
	Happy	0.81	0.33	2.62	2.33	1.62	1.62	1.29	1.24	1.14
Arousal	Anxious	0.12	0.92	1.58	1.46	1.85	2.00	1.65	0.73	0.65
	Sad	0.14	1.29	-0.52	-0.91	-0.14	-0.76	-0.19	-0.14	0.43
	Calm	-0.22	1.00	-0.61	-1.48	-0.57	-1.26	-0.74	-0.74	-0.22
	Happy	0.57	1.29	1.38	1.19	1.48	0.67	0.24	0.05	0.33

Table 2. *Behavioral data per mood induction group*

Trial type / Effect	Mood induction group							
	Anxious (N = 26)		Sad (N = 21)		Calm (N = 23)		Happy (N = 21)	
Overall	593	(9.3%)	619	(5.6%)	596	(2.9%)	604	(4.8%)
Compatible (C)	580	(8.6%)	600	(4.4%)	577	(1.9%)	587	(4.7%)
Incompatible (I)	607	(10.1%)	638	(6.8%)	616	(3.8%)	620	(5.0%)
Interference effect	27	(1.6%)	37	(2.3%)	39	(1.8%)	33	(.3%)
cC	572	(3.7%)	578	(3.0%)	568	(1.2%)	580	(2.8%)
cI	611	(8.8%)	631	(6.9%)	612	(4.0%)	613	(4.4%)
iC	587	(7.4%)	617	(3.5%)	582	(1.2%)	595	(3.1%)
iI	597	(8.1%)	637	(6.8%)	613	(2.3%)	619	(4.1%)
Conflict-adaptation effect	29	(4.5%)	33	(.5%)	13	(1.7%)	8	(.6%)

Note: Latency data in ms for all conditions with error rate between brackets.
Interference effect = I–C, Conflict-adaptation effect = (cI – cC) – (iI – iC)

Mood and conflict-adaptation effects

Reliable overall RT conflict-adaptation effects, $F(1, 87) = 16.83$, $p < .001$, $MSE = 2{,}303.02$, were observed for the flanker task, and, as Figure 1 shows, this effect was modulated by pleasure level, $F(1, 87) = 4.241$, $p < .05$, $MSE = 2{,}303.02$. This predicted effect of pleasure was not accompanied by an effect of arousal or by a Pleasure × Arousal interaction, $F(1, 87)$s < 1. Overall, interference effects were smaller if conflict was experienced on the previous trial (21 ms vs. 42 ms), and, as predicted, these conflict-driven interference reductions were larger for subjects in a low-pleasure mood (anxious and sad groups: $M = 29$, $SE = 9.4$, and $M = 33$, $SE = 10.5$) than for subjects in a high-pleasure mood (happy and calm groups: $M = 8$, $SE = 10.5$, and $M = 13$, $SE = 10.0$). This effect could not be accounted for by mood-induced differences in overall RT or interference effects, $F(1, 87)$s < 2.23 (see Table 2 for details on RTs, interference effects in RTs, and conflict-adaptation effects in RTs). Correlations between self-reported affect during task performance and individual conflict-adaptation effects across mood groups were not significant (pleasure: $r = -.161$, $p = .13$; arousal: $r = -.134$, $p = .21$).

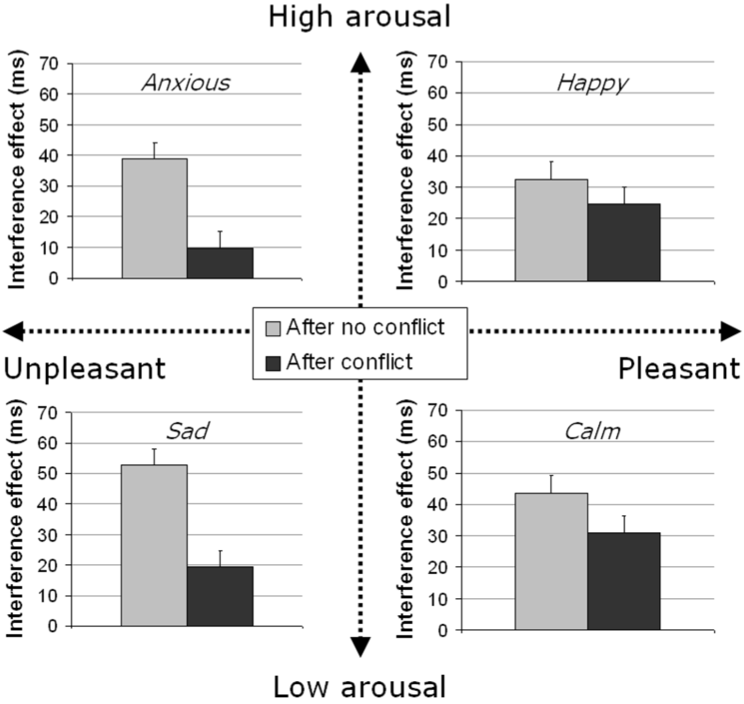

Figure 1. Conflict-adaptation effects as a function of mood induction group. Groups were defined by a crossing of the pleasure (horizontal) and arousal (vertical) dimension. Subjects in a low-pleasure mood show stronger conflict-adaptation effects (interference reduction after conflict) in comparison to subjects in a high-pleasure mood. Arousal does not modulate conflict-adaptation effects. Graph shows means and standard errors.

Overall, conflict-adaptation effects for error rates were not reliable, F(1, 87) = 3.13 (see Table 2 for details on error rates, interference effects in error rates, and conflict-adaptation effects in error rates). Overall interference effects in error rates, F(1, 87) = 10.03, $p < .01$, MSE = 0.002, were not modulated by mood condition, F(1, 87)s < 1.57, though subjects with low pleasure levels, F(1, 87) = 6.741, $p < .05$, MSE = 0.004, and subjects with high arousal levels, F(1, 87) = 4.267, $p < .05$, MSE = 0.004, made slightly more errors in general than their high-pleasure and low-arousal counterparts.

Discussion

This study provides substantial evidence for the hypothesis that conflict adaptation is sensitive to modulations in pleasure level. After a successful mood manipulation, both sad and anxious people showed stronger adaptation following conflict trials than did people in a happy or calm mood (see Fig. 1). This effect was not accompanied or modulated by effects of arousal level; subjects with high-activation moods (anxious and happy groups) did not show differences in conflict-adaptation effects in comparison with subjects in low-activation moods (sad and calm groups). These findings thus suggest that affect helps to regulate goal-directed behavior in response to cognitive conflict.

Our observations show an interesting parallel to the seminal work of Festinger (1957) on cognitive dissonance. Cognitive dissonance is thought to be triggered by conflicting cognitions and to be reduced by either avoiding the inducing perceptual events or changing one's attitude. Dissonance reduction and conflict adaptation may thus both reflect adaptive avoidance responses to situations of incompatibility and rely on the same neural mechanism (Harmon-Jones, Amodio, & Harmon-Jones, 2009; van Veen, Krug, Schooler, & Carter, 2009). In line with our findings, dissonance reduction through attitude change increases when people are in a negative mood (e.g., Rhodewalt & Comer, 1979). Low pleasure levels thus increase cognitive control after conflict situations only, rather than improving control in general (cf. van Steenbergen et al., 2009). Thus, we observed only context-sensitive, dynamic effects, probably because moods—unlike short-term affect manipulations used in other studies (e.g., Kuhl & Kazen, 1999)—are thought not to have stable, motivational consequences leading to improved sustained control (Gendolla, 2000; for a recent motivational account of emotions influencing cognitive control, see Gable & Harmon-Jones, 2010b).

We believe that our findings may also provide insight into the way cognitive-control processes are impaired in psychopathological individuals. Mood disorders such as depression and anxiety have been associated with increased negativity biases (Leppanen, 2006). Indeed, sensitized conflict-monitoring processes have been observed in people with internalizing mood disorders (Olvet & Hajcak, 2008). Whether conflict-driven adaptations are also changed in these people has yet to be investigated, because mood-disorder studies using cognitive-control measures usually overlook conflict-adaptation effects, reporting main interference effects only (but cf. Holmes & Pizzagalli, 2007).

Altogether, our findings suggest that conflict-driven control adaptations are highly dependent on one's emotional state, with pleasure level being more important than arousal level. Our results demonstrate that the influence of affect is not limited to conflict processing per se, but modulates subsequent behavioral adaptation as well. This suggests that affect is highly important not only in biasing perception and signaling environmental conflict, but also in adaptively regulating goal-directed behavior.

Acknowledgements

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6

Humor and Conflict Adaptation: a Neural Mechanism

> "One happiness scatters a thousand sorrows."
>
> Chinese proverb

This chapter is based on:

van Steenbergen, H., Band, G.P.H., Hommel, B., Rombouts, S.A.R.B., & Nieuwenhuis, S. (submitted for publication). Keep smiling! Humor reduces neurocognitive adjustments to conflict.

Abstract

Positive emotional states are known to reduce the impact of cognitive demands and information-processing conflict on human behavior, but the underlying neural mechanism of this modulation is unknown. We used functional magnetic resonance imaging to examine how pleasure induced by funny cartoons regulates behavioral control and neural adaptations to cognitive conflict. Humor activated hedonic hotspots in the basal ganglia, which attenuated the rostral anterior cingulate cortex (ACC) response to conflict. This reduced subsequent conflict adaptation as observed in behavior and monitoring-related dorsal ACC activation. Our observations reveal the neural mechanism by which positive emotions regulate adaptive goal-directed behavior.

Introduction

Positive emotions do not only feel good, they may also help to counter the impact of stressful events on our behavior and health (Garland et al., 2010). The claim that pleasure reduces the impact of events evoking information-processing conflict and negative performance outcomes (Gendolla, 2000; Botvinick, 2007) is supported by physiological measures, subjective evaluations, and behavioral adjustments to such events (de Burgo & Gendolla, 2009; Mayer, Gaschke, Braverman, & Evans, 1992; van Steenbergen, Band, & Hommel, 2010). An important aim of neuroscience is to understand how pleasure-related neuromodulation produce adaptive behavior (Kringelbach & Berridge, 2009). Neuroimaging studies suggest that hedonic tone attenuates demand-related conflict signaling in the anterior cingulate cortex (ACC; Luu et al., 2000; van Wouwe et al., 2011), a brain region in which cognitive and affective information converge (Botvinick et al., 2001; Paus, 2001; Bush et al., 2000). Here we provide evidence that pleasure-induced ACC attenuation regulates behavioral adjustment to conflict, and that this modulation is driven by subcortical reward systems.

Pleasant emotions may regulate cognitive-control optimization to behavioral demands via neural interactions between ACC and the basal ganglia. According to an influential neurobiological theory, the ACC supports adaptive behavior to the situational value at hand via dopaminergic teaching signals from the basal ganglia (Holroyd & Coles, 2002). Several observations in humans confirm the involvement of such interactions between cortex and basal ganglia: nucleus accumbens recordings have revealed a negative functional coupling with monitoring-related ACC activity (Munte et al., 2008), pharmacological studies have found that elevated baseline dopamine levels reduce conflict-related ACC activity (Jocham & Ullsperger, 2009), and lesion studies have demonstrated that ACC activity depends on intact basal ganglia (Ullsperger & von Cramon, 2006). Neuromodulatory projections to the ventral striatum (VS) and the ventral pallidum (VP) – the central components of the neural reward circuit (Haber & Knutson, 2010) – may allow hedonic states to modulate this network. Earlier studies have shown that stimulation of the VS and VP can generate hedonic 'liking' reactions in the rat. fMRI studies in humans have also strongly implicated these regions in the processing of reward and positive emotions (Kringelbach & Berridge, 2009).

To investigate the impact of pleasant emotional states on conflict processing, we used fMRI to record brain activation while measuring participants' behavioral adjustments to a demanding conflict task. Pleasure was induced by funny cartoons; stimuli that are known to increase hedonic tone (Abel & Maxwell, 2002) and to activate the reward system (Mobbs, Greicius, bdel-Azim, Menon, & Reiss, 2003). Following cartoon presentation, participants performed the arrow-flanker task, an established paradigm for inducing and measuring reactive cognitive control adjustments to conflict (Gratton et al., 1992; Egner, 2007; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; see Figure 1A and 1B). In each flanker trial, a central target indicates whether the left or right-hand response is required, and flanking distracters introduce either no conflict (compatible information) or conflict (incompatible information). Because conflict trials are more demanding than no-conflict trials, responses in these trials are commonly slower; this compatibility effect can be taken as an index of attentional interference. The critical

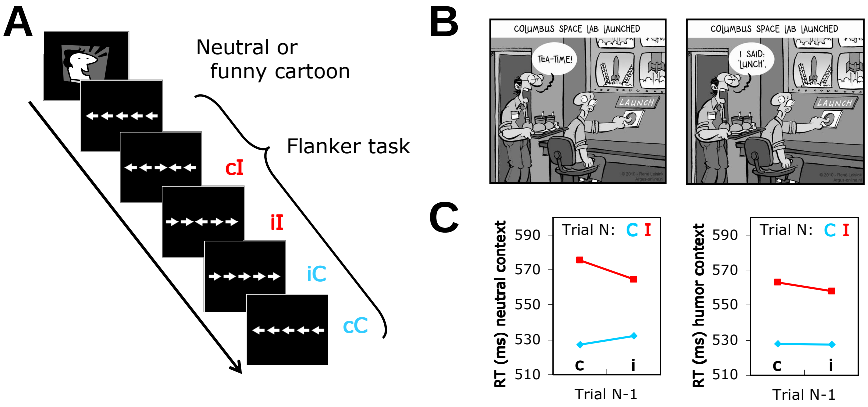

Figure 1. A. *Example of a trial. Neutral and funny cartoons were presented in random order. Each cartoon was followed by a block of five randomly selected flanker trials being either compatible (C) or incompatible (I). Sequential-effect analyses compared Trial N compatibility (as indicated by upper-case letters C and I) as a function of the compatibility of the preceding trial (Trial N-1; indicated by lower-case letters c and i).* ***B.*** *Example of a funny cartoon (right) and the same cartoon with funny cues omitted presented as neutral cartoon (left). © 2010 René Leisink, reprinted with permission.* ***C.*** *Standard conflict-driven behavioral adjustment was observed following neutral cartoons (left). This effect was cancelled out by humor (right).*

moment of adaptation in this task occurs on trials that follow conflict trials, in which the compatibility effect is reduced (Figure 1C, left panel). This indicates that conflict detection leads to reactive increases in cognitive control in the subsequent trial (Egner, 2007; Gratton et al., 1992). Previous studies have suggested that this often-replicated behavioral post-conflict adjustment is driven by ACC activation (Botvinick et al., 1999; Kerns et al., 2004) and is reduced when hedonic tone increases (van Steenbergen et al., 2010). We tested whether such affective regulation of conflict adaptation depends on modulation of ACC, driven by pleasure-related activation of VS and VP.

Methods

Participants

Twenty-two healthy right-handed volunteers (age 18 - 29) with normal or corrected-to-normal vision participated in the study. In order to optimize the detection of humor-induced reward circuit activation, we tested only females. Earlier studies have shown stronger mesolimbic reward responses to funny cartoons in females than in males (Azim, Mobbs, Jo, Menon, & Reiss, 2005). The volunteers gave written informed consent for participation in the study, and they received a monetary incentive. The experiment was approved by the medical ethics committee of the Leiden University Medical Center.

Stimuli

Thirty-two funny cartoons were selected from a set of approximately 130 cartoons, on the basis of funniness ratings and simplicity ratings (i.e., how easy the jokes were to comprehend) provided by participants matched to the age and background of the experimental subjects. Adopting the same approach as earlier studies (Azim et al., 2005; Mobbs et al., 2003), a closely matched set of 32 non-funny, neutral cartoons was created by omitting funny cues of humor cartoons through visual and/or textual changes. Both gray-scaled sets were matched on visual clarity, geometrical complexity and mean luminosity. All cartoons were presented once during the experiment.

Task and procedure

Before entering the MRI scanner, participants were informed about the task to perform. They were encouraged to enjoy the content of the funny cartoons even during subsequent flanker trials and to avoid head movements. Instructions emphasized fast and accurate responses to the direction of the central target arrow of the flanker task. Optical response-button boxes (positioned on the upper leg) recorded index finger responses of the left and right hand. Participants performed two practice trials with performance feedback before the experiment started. Experimental data were then acquired in two consecutive runs of 32 trials.

Stimuli were presented against a black background (1024 x 768 pix). Funny and neutral cartoons (500 x 500 pix) were presented in a quasi-random order for 6 seconds each. Following each cartoon, a fixation cross (jittered duration between 2-6 seconds), a block of five flanker trials and another fixation cross (1 second) were presented. Each trial in the block consisted of an imperative flanker stimulus (a row of five black arrows pointing either left or right; 100 x 7 pix), presented for 1 second, followed by a fixation cross (jittered, 3 – 5 seconds). In order to provide an index of neural distracter-related activation measurable in the visual motion area of the brain, the flankers were always moving vertically (using a triangle function with T = 200 ms and A = 10 pix). We used the same number of compatible (flankers in same direction as the central target) and incompatible (flankers opposite to central target) trials. A quasi-random trial sequence was created, ensuring that all possible sequential combinations occurred equally often during the experiment. Data were collected in one test session including two consecutive runs, each lasting about 20 min. In a final functional scan a motion localizer task was presented. Participants passively viewed moving flanker trials and still flanker trials in 12 alternating runs of 15 seconds, separated by 10-seconds fixation periods. In each of these localizer runs, 15 random flanker stimuli were presented for 800 ms, separated by an inter-stimulus interval of 200 ms.

After the scan session, participants rated the funniness of each cartoon they saw in the scanner (9-points scale). Participants were fully debriefed at the end of the experiment.

Behavioral data analysis

Inspection of the post-experimental ratings revealed that a few cartoons were given funniness ratings that did not match the intended funny/nonfunny category. Cartoons with such extreme outlier ratings (more than 3 interquartile ranges below/above the 25/75th percentile; on average 1.8 cartoons per participants) and its subsequent block of flanker trials were marked as rating outliers and were excluded from all analyses. On initial inspection of the behavioral flanker task data, two participants turned out to have made more than 5% response omissions. These participants were excluded from further analyses.

Correct reaction time (RT) and error rate were analyzed with repeated measures ANOVAs that included the factors current-trial compatibility (Compatible vs. Incompatible; abbreviation: C vs. I), previous-trial compatibility (compatible vs. incompatible; abbreviation: c vs. i), and humor context (funny vs. neutral cartoon). Standard sequential compatibility effects (i.e., the conflict-adaptation effect), for both RTs and error rates and separately for both humor contexts, were calculated by subtracting the compatibility effect following a correct incompatible (conflict) trial (i) from the compatibility effect following a correct compatible (no-conflict) trial (c) (i.e., (cI – cC) – (iI – iC)). The first trial of each block, trials following errors, trials following cartoons with outlying ratings, and behavioral outlier trials (RT > 2 SD from the condition-specific means, calculated for each participant separately) were excluded from all analyses.

fMRI data acquisition

Scanning was performed with a standard whole-head coil on a 3-T Philips Achieva MRI system (Best, The Netherlands) in the Leiden University Medical Center. For both task runs 532 T2*-weighted whole-brain EPIs were acquired, including two dummy scans preceding each scan to allow for equilibration of T1 saturation effects (TR = 2.2 sec; TE = 30 msec, flip angle = 80°, 38 transverse slices, 2.75×2.75×2.75 mm(+10% interslice gap)). During the motion localizer task, 141 of these EPIs were acquired. Visual stimuli were projected onto a screen that was viewed through a mirror at the head end of the magnet. After the functional runs, a high-resolution EPI scan and a T1-weighted anatomical scan were obtained for registration purposes (EPI scan: TR = 2.2 msec; TE = 30 msec, flip angle = 80°, 84 transverse slices, 1.964×1.964×2 mm; 3D T1-weighted scan: TR = 9.717 msec; TE = 4.59 msec, flip angle = 8°, 140 slices, .875×.875×1.2 mm, FOV = 224.000×168.000×177.333).

fMRI data analysis

Data analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.FMRIb.ox.ac.uk/fsl (Smith et al., 2004). The following pre-statistics processing was applied: motion correction (Jenkinson, Bannister, Brady, & Smith, 2002), non-brain removal (Smith, 2002), spatial smoothing using a Gaussian kernel of FWHM 8.0 mm, grand-mean intensity normalization of the entire 4D data set by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100.0 seconds). Functional scans were registered to high-resolution EPI images, which were registered to T1 images, which were registered to standard MNI space (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

In native space, the fMRI time series were analyzed using an event-related approach in the context of the general linear model with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Models were high-pass-filtered (Gaussian-weighted least-squares straight-line fitting, with sigma=100.0 seconds). All regressors used square-wave functions to represent stimulus duration and were convolved with a canonical HRF and its temporal derivative.

Exactly equivalent to the trials included for RT analysis, a first model analyzed trial-to-trial adaptation in conflict-related ACC activation by comparing iI and cI trials following neutral and funny cartoons. This model included all eight possible combinations of current-trial compatibility (Compatible vs. Incompatible), previous-trial compatibility (compatible vs. incompatible), and humor context (trials following neutral cartoons vs. following funny cartoons) as separate regressors. Additional confound regressors included funny cartoon and neutral cartoon presentation, as well as events representing the first flanker trial of each block, errors, trials following errors, and outliers.

In order to reveal modulating effects of pleasure on the conflict trials preceding adaptation, we ran a second model that included regressors for incompatible (conflict) trials and compatible (no-conflict) trials (i.e., irrespective of subsequent-trial compatibility) as well as for cartoon presentations. These events were modeled separately for both humor contexts. Separate confound regressors included events of the last flanker trial of each block, errors, trials before errors, and trials before outliers.

Two additional variants of the previous model were also analyzed. One analysis examined whether ACC activity during conflict trials predicted trial-to-trial adjustments in the subsequent conflict trial. This model included all eight possible combinations of current-trial compatibility (Compatible vs. Incompatible), subsequent-trial compatibility (compatible vs. incompatible), and humor context (neutral vs. funny cartoons). These events were added as two series of eight regressors. The first series used standard fixed weights to account for invariant BOLD responses to stimulus presentation. The second series of regressors used a weighting vector determined by condition-specific standardized RT values of the subsequent trial. This allowed us to reveal any conflict-related BOLD responses in the

ACC that predicted subsequent adaptation in iI trials. All remaining events were modeled as confound regressors.

The second variant modeled interactions in functional connectivity between subcortical reward areas and ACC during conflict trials. Two psychophysiological interaction (PPI) analyses Friston et al., 1997 were run separately for the ventral striatum (VS) seed and the ventral pallidum (VP) seed. Physiological regressors used the extracted time-course information from the VS (2, 20, -4) and the VP (14, -10, -8), based on a sphere of radius 4 mm around the peak-activation voxel in the respective region using the funny vs. neutral cartoon contrast. The convolved psychological regressor represented the contrast incompatible trials after funny cartoons (FI) – incompatible trials after neutral cartoons (NI). In order to mop out shared variance, a FI + NI regressor was also added. Compatible trials following funny and neutral cartoons were modeled separately. The PPI regressor was computed as the product of the demeaned physiological timecourse and the centred psychological regressor. Again, all remaining events were modeled as confound regressors.

For all analyses, the relevant contrasts were combined across the two runs on a subject-by-subject basis using fixed-effects analyses (Beckmann, Jenkinson, & Smith, 2003; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). Second-level contrast images were submitted to third-level mixed-effects group analyses. All resulting statistical parametric images were thresholded using clusters determined by $Z > 2.3$ and a cluster-corrected significance threshold of $p < 0.05$ (Worsley, 2001). Given the a priori hypotheses about conflict-related ACC activation triggered by incompatible flanker stimuli, analyses for these contrasts were constrained to an anatomical mask defining the anterior cingulate cortex proper (using the anterior division of the cingulate cortex as defined by the Harvard-Oxford structural atlas, 70%-likelihood threshold). ROI analyses used individual mean z-scores from second-level analyses extracted with Featquery.

Table 1. *Behavioral data*

	After neutral cartoon				After funny cartoon			
	RT (ms)		Error rate		RT (ms)		Error rate	
Trial Type	Mean	SD	Mean	SD	Mean	SD	Mean	SD
cC	527	67	0.2%	0.7%	528	68	0.5%	1.2%
cI	576	72	2.2%	3.5%	563	75	2.9%	3.8%
iC	532	69	0.8%	2.1%	527	67	0.5%	1.3%
iI	565	65	1.3%	2.1%	558	66	1.2%	1.7%
Compatibility effect = ((cI + iI) - (cC + iC)) / 2	40	18	1.3%	2.4%	33	18	1.5%	1.7%
Conflict-adaptation effect = (cI - cC) - (iI - iC)	16	27	1.5%	2.6%	4	26	1.7%	4.5%

Note: The table reports mean response times (RTs), error rates, and the corresponding flanker compatibility effects and conflict-adaptation effects. cC = compatible trials following compatible trials; cI = incompatible trials following compatible trials; iC = compatible trials following incompatible trials; iI = incompatible trials following incompatible trials.

Results

Behavioral results

The flanker task produced robust current-trial compatibility effects in reaction time (F(1,19) = 116.7, p < .001, MSE = 455.7), indicating that it successfully induced performance conflict. An interaction between current-trial and previous-trial compatibility, indicating standard conflict adaptation, was observed in the neutral condition (F(1,19) = 7.0, p < .02, MSE = 182.6), but not in the humor condition (F(1,19) = 0.5, p = .50, MSE = 173.0) (Figure 1C). Thus, in line with predictions and replicating earlier findings (van Steenbergen et al., 2010; van Steenbergen et al., 2009), participants adjusted their behavior in response to conflict only in the neutral, low-pleasure condition: incompatible trials preceded by incompatible trials (iI) were faster than incompatible trials preceded by compatible trials (cI), presumably because the preceding conflict trial evokes increased cognitive control (effect = 11 ms, t(19) = 2.2, p < .05). (Similarly, compatible trials preceded by incompatible trials (iC) were numerically slower than compatible trials preceded by compatible trials (cC) (effect = 5 ms, t(19) = 1.3, N.S.), probably because increased control decrease flanker facilitation). A planned comparison confirmed that humor reduced the conflict-adaptation effect (t(19) = 1.9, p < .05).

Note that humor did not modulate overall flanker interference (t(19) = 1.6, N.S.), suggesting that it did not change general motivation (Gable & Harmon-Jones, 2010b). Furthermore, there were no modulating effects of humor on error rate, indicating that the effects on reaction time cannot be attributed to speed-accuracy tradeoff (Fs(1,19) < 1; see Table 1). Post-experimental cartoon ratings (9-points scale) outside the scanner confirmed that funny cartoons were funnier than their neutral counterparts (M = 6.1 versus M = 2.3, t(19) = 13.0, p < .001).

fMRI results

In keeping with conflict monitoring theory (Botvinick et al., 2001) and previous observations (Kerns et al., 2004; Botvinick et al., 1999), we predicted that behavioral adjustment to conflict on a given trial should concur with reduced cognitive

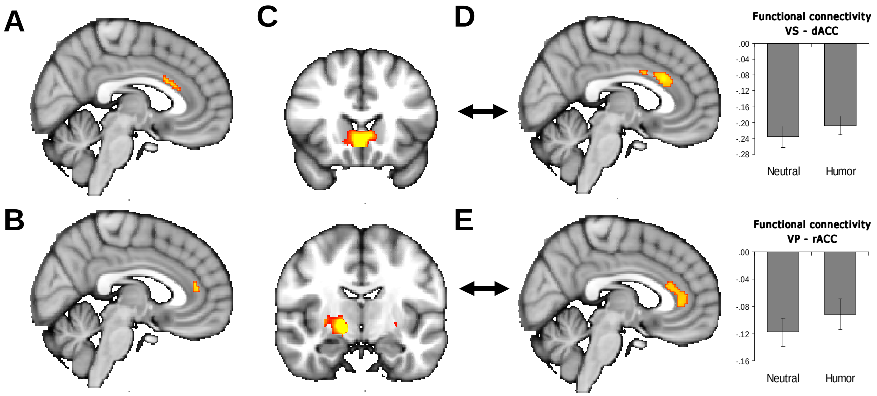

Figure 2. A. *Trial-to-trial adaptation in dorsal ACC (peak voxel in MNI coordinates: 2, 22, 20) for the cI > iI contrast of flanker trials following neutral cartoons. Confirming behavioral findings, there was no evidence for conflict adaptation in the ACC following funny cartoons, even when lowering the threshold to z = 1 (p = .15, uncorrected).* ***B.*** *Deactivation in the rostral ACC (2, 42, 12) for conflict trials following funny cartoons (versus neutral cartoons).* ***C.*** *In comparison to neutral cartoons, funny cartoons increased reward system activation in the ventral striatum (top slice, 2, 20, -4) and right posterior ventral pallidum (bottom slice, 14, -10, -8). Images are in radiological convention (left hemisphere to viewer's right). Activations in other regions are reported in Table 2.* ***D.*** *Psychophysiological interaction between ventral striatum and dorsal ACC (4, 24, 26) during conflict trials. This region overlaps with the activation cluster displayed in A.* ***E.*** *Psychophysiological interaction between ventral pallidum and rostral ACC (0, 40, 8) during conflict trials. This region overlaps with the activation cluster displayed in B.*

conflict registered in the ACC on the subsequent trial. This trial-to-trial adaptation effect should not be observed in the funny condition, in which behavioral conflict adaptation was cancelled out. Confirming predictions, activity in the dorsal ACC (dACC) decreased during iI as compared to cI trials following neutral cartoons, but not following funny cartoons (Figure 2A). This demonstrates that pleasure eliminates not only the behavioral adjustment to conflict but also the resulting adaptations of conflict monitoring activity in dACC.

To test the hypothesis that this reduction of conflict adaptation originates from general pleasure-driven ACC attenuation during conflict, we compared ACC activity elicited by conflict trials following neutral and following funny cartoons. Pleasure-related deactivation to conflict was observed in the affective, rostral part of the ACC (rACC; Figure 2B), presumably reflecting reduced negative appraisal of conflict when participants are in a hedonic state (Bush et al., 2000; Taylor et al., 2006). To test the hypothesis that rACC under neutral conditions plays a pivotal role in subsequent behavioral adjustment, we used intra-individual fluctuations in behavior adaptation during iI trials as a regressor to model predictive brain activity in the preceding conflict trial. Using an ROI analysis focusing on the dACC and rACC activation clusters, we found that neural conflict-related increases in the rACC were a successful predictor of subsequent behavioral adaptations following neutral cartoons ($t(19) = 2.7$, $p < .02$), but not following funny cartoons ($t(19) = -1.0$, $p = .30$). This suggests that the pleasure-driven reduction of activation in the rACC eliminated the implementation of conflict-driven cognitive control increases observed under normal, emotionally neutral conditions. No predictive brain activation was observed for the dACC ($|t|$s < 0.5).

We compared brain activation related to funny and neutral cartoons to determine the neural antecedents of conflict-related ACC attenuation. Replicating earlier findings (Mobbs et al., 2003), funny cartoons recruited a large network of brain areas involved in the representation of language, semantic, and motor aspects of humor (see Table 2). More importantly, we also replicated the involvement of mesolimbic reward circuitry. As predicted, funny cartoons elicited more activation than neutral cartoons in the VS and VP (Figure 2C) – the only two regions currently known to play a direct causal role in hedonic liking reactions (Kringelbach & Berridge, 2009). To investigate the modulatory role of activity in these regions during conflict processing, we carried out a psycho-physiological interaction (PPI) analysis, which provides a measure of condition-specific functional connectivity between two brain regions. This allowed us to test whether the negative coupling between ventral basal ganglia and ACC, as should be observed during conflict processing under affectively neutral conditions (Holroyd & Coles, 2002; Munte et al., 2008), is attenuated by pleasure. Confirming predictions, a PPI analysis using the VS as seed region revealed the dACC (Figure 2D), overlapping with the region earlier identified as cognitive conflict area (cf. Figure 2A). This network showed reduced conflict-related negative coupling in the funny condition. A similar interaction was observed between the VP and the rACC (Figure 2E), which overlaps with the rACC region identified earlier as being involved in the subjective emotional evaluation of conflict (cf. Figure 2B).

Additional fMRI analysis: breadth of attention

Earlier studies have suggested that conflict-driven behavioral adaptation reflects the neural enhancement of task-relevant information, whereas the behavioral compatibility effect may reflect susceptibility to task-irrelevant information related to increases in attentional breadth (Egner & Hirsch, 2005). Replicating earlier findings (van Steenbergen et al., 2009; van Steenbergen et al., 2010), our data suggest that pleasure can reduce conflict adaptation independently of modulations in the compatibility effect. However, it might still be argued that the small, though non-significant, decrease in the behavioral flanker compatibility effect following funny cartoons indicates that humor tends to reduce the susceptibility to task-irrelevant information. This effect might be driven by changes in motivation that are known to change attentional breadth (Rowe, Hirsh, & Anderson, 2007; Gable

Table 2. *Brain areas activated by funny versus neutral cartoons*

Regions	Left/ Right	Brodmann area	Cluster size (voxels)	Z-score	MNI coordinates		
					X	Y	Z
Temporal pole*, fusiform gyrus, ITG, MTG, STG, MTL, IFG, cerebellum, insula, amygdala, midbrain, thalamus, ventral pallidum	L/R	20, 21, 28, 36, 38, 44, 45, 48	15,238	6.27	-52	8	-20
Supplementary motor area*	L/R	6	462	3.98	-10	4	56
Sensorimotor cortex*	L	3	148	4.46	-48	-16	42
Sensorimotor cortex*	R	3	68	3.63	44	-16	36
Lateral occipital cortex*, angular gyrus, temporo-occipital junction	L	39, 21, 37	5,187	5.53	-42	-72	38
Lateral occipital cortex*, angular gyrus	R	39, 21	1,106	5.10	46	-68	40
Anterior cingulate gyrus*, medial frontal cortex	L/R	10, 24, 32	4,118	5.20	-2	18	24
Posterior cingulate gyrus*, precuneus	L/R	23, 31	2,105	4.47	-12	-52	22
Ventral striatum*	L/R	_	126	3.83	2	20	-4

* Denotes peak activation . Table shows activation clusters for the Funny cartoon > Neutral cartoon contrast, thresholded at $z > 3.1$; $p < 0.001$; > 50 contiguous voxels. Abbreviations: ITG, inferior temporal gyrus; MTG, middle temporal gyrus; STG, superior temporal gyrus; MTL, medial temporal lobe; IFG, inferior frontal gyrus.

& Harmon-Jones, 2010b; Schmitz, De Rosa, & Anderson, 2009). To investigate this possibility we analyzed neural activation in the visual cortex representing distracter-related information. Because the distracters in our flanker task were moving, we could use motion-related brain activity as a neural index of distracter activation.

In order to analyze individual distracter-related brain activation, a motion localizer task was used to identify each subject's MT+ complex, an area in the dorsal visual cortex that has consistently been implicated in human motion processing (Tootell et al., 1995). Epochs of moving flankers and still flankers were compared to identity motion-specific activation. Using this contrast, subject-specific MT ROIs were defined by spheres of radius 6 mm around the peak-activation voxel in the left and the right motion-related MT+ complex. Average activation in these two spheres was then used for individual ROI analyses.

MT ROI analyses were carried out in the trial-to-trial adaptation model earlier used to identify behavior-related conflict adaptation in the ACC. The moving flanker stimuli presented during the experiment were shown to reliably activate MT ($F(1,19) = 99.6$, $p < .001$, $MSE = 16.3$). However, paralleling the unreliable effect of humor on the behavioral compatibility effect, there was no effect of humor on distracter activation as measured in MT ($F(1,19) = 0.002$). This corroborates our conclusion that the breadth of attention is not reliably modulated by humor. The effects of current-trial compatibility, previous-trial compatibility or (higher-order) interactions were not significant ($Fs(1,19) < 1.7$). This is consistent with earlier findings showing that conflict-adaptation does not involve neural adaptation to task-irrelevant information (Egner & Hirsch, 2005).

Discussion

Altogether, our data demonstrate how pleasure induced by funny cartoons affects conflict processing: pleasure attenuates the rACC response to conflict and cancels out the resulting standard conflict adaptation as observed in behavior and monitoring-related dACC activation under neutral conditions. ACC was found to be functionally connected with hedonic hotspots in the VP and VS. Pleasure-related activation in the VP may have inhibited rACC activation, a region which in the neutral condition predicts subsequent behavioral adaptation. This finding implies that the rACC, presumably involved in the negative emotional evaluation of conflict (Bush et al., 2000; Taylor et al., 2006), drives subsequent cognitive control.

This suggestion is corroborated by recent observations from lesion studies showing that conflict-driven activation and behavioral adjustment crucially depends on intact VP and rACC (di Pellegrino, Ciaramelli, & Ladavas, 2007; Ullsperger & von Cramon, 2006). Subsequent adaptations in control were shown to be registered by the dACC, a region well-known for its role in the cognitive monitoring of conflict (Botvinick et al., 2001). Feedback signals for future behavioral optimization processed in the dACC appeared to be conveyed through the VS to become integrated with hedonic state information.

The functional network identified in this study converges with well-known cortico-basal ganglia anatomical connections, looping between ACC and VS through the VP and thalamus (Alexander, Delong, & Strick, 1986). This 'limbic' loop may have played an important role in the affective regulation of conflict-driven behavior observed. Modulation of functional coupling between the basal ganglia (BG) and ACC is probably driven by neuromodulatory input via dopamine and opioid receptors (Holroyd & Coles, 2002; Kringelbach & Berridge, 2009). Conflict-driven motivation and behavioral adjustment may depend on phasic dopamine fluctuations (Holroyd & Coles, 2002; Jocham & Ullsperger, 2009; van Steenbergen et al., 2009). Hedonic liking modulation is probably mediated by tonic opioid input (Barbano & Cador, 2007; Kringelbach & Berridge, 2009). Future research is needed to further understand the neurochemical basis of this BG-ACC network modulation.

This study provides an initial answer to the question why humor and jokes are so central to humanity: they appear to be adaptive means to transiently reduce the impact of cognitive demands on our behavior through activation of the neural reward system. One important goal for future research is to investigate how positive emotions can also promote beneficial neural effects in the long term. Such advances in the cognitive neuroscience of pleasure are necessary to further extend our understanding of how positive emotions can protect and improve our mental and physical health (Garland et al., 2010).

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7

Depression and Conflict Adaptation

"A depressed man lives in a depressed world."

Ludwig Wittgenstein

This chapter is based on:

van Steenbergen, H., Booij, L., Band, G.P.H., Hommel, B., & van der Does, A.J.W. (in press). Affective regulation of conflict-driven control in remitted depressive patients after acute tryptophan depletion. *Cognitive, Affective, & Behavioral Neuroscience.*

Abstract

Negative affect in healthy populations regulates the appraisal of demanding situations, which tunes subsequent effort mobilization and adjustments in cognitive control. We hypothesized that dysphoria in depressed individuals similarly modulates this adaptation, possibly through a neural mechanism involving serotonergic regulation. We tested the effect of dysphoria induced by Acute Tryptophan Depletion (ATD) in remitted depressed patients on conflict adaptation in a Simon task. ATD temporarily lowers the availability of the serotonin precursor L-Tryptophan and is known to increase depressive symptoms in approximately half of remitted depressed participants. We found that depressive symptoms induced by ATD were associated with increased conflict adaptation. Our finding extends recent observations implying an important role of affect in regulating conflict-driven cognitive control.

Introduction

One of the defining symptoms of depression is a depressed mood. Although a depression is certainly undesirable and maladaptive, normal and pathological mood states of sadness lie on a continuum and may actually play an important role in adaptive behavior (e.g., Andrews & Thomson, 2009; Mayberg et al., 1999). The Mood-Behavior-Model (MBM; Gendolla, 2000) proposes that negative affect helps to regulate resource mobilization and behavior via a biased appraisal of situational demands (cf. Ach, 1935; Hillgruber, 1912). Indeed, several studies using mood induction procedures in healthy populations have shown that negative affect increases demand appraisals of difficult situations, which improves subsequent effort mobilization as measured by cardiovascular adjustments (for a review, see Gendolla & Brinkmann, 2005). Recent evidence suggests that behavioral adaptation to fluctuating task difficulty is also subject to this affective regulation. We have recently shown that dynamic behavioral adjustments after demanding, conflict trials in a flanker task are stronger following the induction of a sad or anxious mood than following a happy or calm mood (van Steenbergen et al., 2010). These data suggest that negative affect may facilitate conflict-driven recruitment of cognitive control, as can be measured by trial-to-trial adaptations in conflict tasks that use randomized presentation of compatible and incompatible trials (Gratton et al., 1992; for a review, see Egner, 2007).

Here, we hypothesize that – analogous to these negative mood effects in healthy samples – dysphoria in remitted depressed individuals also improves demand-driven behavioral adaptation. Recent work has demonstrated enhanced demand-driven effort recruitment in depression using cardiovascular measures (Brinkmann & Gendolla, 2007), but no study has yet demonstrated such effects of depressed mood on behavioral adjustments in cognitive control tasks. It is important to note that the majority of past research on the link between depression and cognitive control has compared attentional interference effects only (i.e., calculating main compatibility effects, such as the Stroop effect), and did not address the modulation of trial-to-trial adaptations in control (i.e., a sequential modulation of interference effects). Although this literature has yielded some evidence for depression-related general deficits in cognitive control (for reviews, see Levin, Heller, Mohanty, Herrington, & Miller, 2007; Rogers et al., 2004), it has been proposed that such deficits are mainly driven by factors other than mood state, e.g., increased rumination (e.g., Nolen-Hoeksema, Wisco, & Lyubomirsky, 2008; Philippot & Brutoux, 2008). Mood induction studies in healthy populations actually support this suggestion, showing that sad mood in itself does not modulate effort mobilization or interference effects (Chepenik, Cornew, & Farah, 2007; van Steenbergen et al., 2010). These findings are also consistent with the notion that a negative mood in itself does not have general motivational implications, but can regulate effort adaptation via modulated demand appraisals, thus producing context-sensitive effects in tasks using fluctuating task demands (Gendolla, 2000). Thus, in contrast to the analysis of main attentional interference effects, sequential effect analysis may provide a measure that is much more sensitive to depressed-mood modulation.

Increased demand-driven behavioral adaptation in depression may arise from the negativity bias and its associated amplified neural reactivity to adverse and demanding events typically observed in this disorder (Beck, 1976; Olvet & Hajcak, 2008; Pizzagalli, Peccoralo, Davidson, & Cohen, 2006). It has been proposed that these neural effects are driven by central serotonin (5-hydroxytryptamine; 5-HT) regulation (Jocham & Ullsperger, 2009; Cools et al., 2008). The impact of central 5-HT on mood and cognition has been investigated with Acute Tryptophan Depletion (ATD), a manipulation that temporarily lowers the availability of L-Tryptophan (Trp), the precursor of serotonin. ATD leads to a transient increase in depressed mood in individuals who are vulnerable to depression (e.g., former patients and first-degree relatives), but not in healthy non-vulnerable individuals (cf. Booij, van der Does, & Riedel, 2003; Ruhe et al., 2007; van der Does, 2001). Some studies have shown that ATD can lower attentional interference independent of mood changes, that is, in both non-vulnerable and depression-vulnerable individuals (Booij et al., 2005; Schmitt et al., 2000; for a review, see Mendelsohn, Riedel, & Sambeth, 2009). However, it is still an open question whether ATD-induced mood changes may modulate conflict adaptation. Recent neuroimaging studies provide some initial support for this hypothesis (for reviews, see Alexander, Hillier, Smith, Tivarus, & Beversdorf, 2007; Fusar-Poli et al., 2006). For example, ATD-induced depressed mood correlates with activity in the Anterior Cingulate Cortex (ACC; Evers, van der Veen, Jolles, Deutz, & Schmitt, 2009), a region playing a prominent role in the generation of adaptive control to demanding situations (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Serotonin polymorphisms have also been linked to changes in post-conflict behavioral adjustments (Holmes, Bogdan, & Pizzagalli, 2010; Osinsky et al., 2009). However, the role of 5-HT accounting for the link between negative mood and conflict adaptation is not known yet.

This study investigates the putative link between conflict adaptation, 5-HT function, and depressed mood. Focusing on trial-to-trial adjustments in performance, we reanalyzed data from an earlier published ATD study (Booij et al., 2005) that only reported overall response-conflict effects, as measured with a Simon task (Simon & Rudell, 1967), in a group of remitted depressed patients after they received ATD. In that study, ATD increased depressive symptoms in about half of the investigated sample and thus provides an excellent design to investigate the associations between depressive symptoms, 5-HT, and conflict adaptation. Similar to the better-known Stroop and flanker tasks, the Simon paradigm is a conflict-inducing task that requires speeded responses to targets that randomly appear in locations that correspond (compatible trial) or do not correspond (incompatible trial) to the location of the correct response key. Incompatible, demanding trials evoke response conflict, which is thought to generate increased cognitive control on subsequent trials (Botvinick et al., 2001). This adaptation to conflict is manifested by reduced compatibility effects in trials following conflict (incompatible) trials as compared to trials following nonconflict (compatible) trials (Gratton et al., 1992; for a review, see Egner, 2007). Given previous theory and evidence for enhanced demand-driven effort mobilization in dysphoria (Gendolla, 2000; Brinkmann & Gendolla, 2007) and after negative mood inductions (Gendolla, 2000; van Steenbergen et al., 2010), and neural evidence suggesting potentiated conflict responses in individuals who show a depressed mood response to ATD (Evers et al., 2009), we hypothesized that ATD may increase conflict adaptation, especially in individuals in whom ATD transiently induced depressive symptoms.

Methods

Twenty-three patients were administered a high-dose and low-dose ATD mixture (100 vs. 25 g amino acids) in a double-blind randomized crossover design with two sessions, separated by at least four days (Booij et al., 2005; Booij, van der Does, Spinhoven, & McNally, 2005). The 100 g and 25 g ATD mixture have previously been shown to lower plasma Trp levels by approximately 90% and 50%, respectively, in this sample (Booij et al., 2005) as well as in other samples (e.g., Booij, van der Does, Haffmans, & Riedel, 2005). The study was approved by an independent medical ethics committee (METIGG, Utrecht), and performed according to their guidelines and regulations. All patients were informed about the study by their clinician and in detail by one of the investigators (LB), and provided written informed consent.

Participants

The sample has been described in detail previously (Booij et al., 2005). Eligible patients were selected outpatients of a mood disorders clinic. Inclusion criteria were: age between 18 and 65 years; ongoing treatment with an SSRI or a serotonin noradrenaline reuptake inhibitor for at least 4 weeks, meeting DSM-IV criteria for depression in full or partial remission, Hamilton Depression rating Scale (HRSD, 17-items) (Hamilton, 1960) lower than 15 (Frank et al., 1991). Exclusion criteria were: substance abuse within the past 3 months, psychosis (lifetime), major physical illness, lactation, pregnancy. After excluding two drop-outs and two statistical outliers, 19 participants remained for statistical analyses (cf. Booij et al., 2005).

Diagnoses and symptoms

As described in the original paper (Booij et al., 2005), depressive symptoms were assessed with the 10-item Montgomery Asberg Depression Rating Scale (MADRS) (Montgomery & Asberg, 1979). The sleep items were omitted, as this could not change within an ATD session. Diagnoses, demographic and clinical background variables were verified with the Structured Clinical Interview for DSM-IV (SCID-I) (First, Spitzer, Gibbon, & Williams, 2005).

Conflict adaptation

The Simon task consisted of 64 trials presented in two consecutive blocks in which the stimulus interval differed (2250 ms fixed versus 2250–5500 ms variable). The word ‘left’ or ‘right’ was presented in randomized order either at the left or the right side of the screen. Participants were instructed to respond to the meaning of the word (target) and to ignore its location (distracter), as fast as possible. The same number of compatible (distracter location matches the target word) and incompatible (distracter location conflicts with the target word) stimuli was used.

Procedure

Venous blood (10 ml) was taken in the morning, 6 h after ATD and the next day (t+24) and analyzed for total plasma Trp and the other large neutral amino acids (Fekkes, Vandalen, Edelman, & Voskuilen, 1995). Mood was assessed 1 h before ATD (t−1), 6.5 h later (t+6.5), and the next morning (t+24). The Simon task (“left/right task”) was administered (Booij et al., 2005) approximately 5.5 h after administration of the ATD mixture. Cognitive performance was also assessed at a separate intake and a post-intervention session. The average of these two assessments was taken as baseline measurement (cf. Booij et al., 2005).

Data analysis

Repeated measures ANOVAs were used for sequential analysis of Simon performance, separately for correct reaction time (RT) and percent accuracy. In order to measure sequential adjustments in Simon task performance, we not only included the factor compatibility of the current trial as is usually done, but we also added the factor "compatibility of the previous trial". Standard conflict-adaptation, i.e., the modulation of the compatibility effect as a function of previous-trial compatibility (cf. Figure 1A), should yield an interaction effect between current and previous trial compatibility (Gratton et al., 1992; Egner, 2007).

To analyze direct effects of the ATD manipulation on conflict adaptation, intervention (baseline versus low-dose versus high-dose ATD) was added as a within-subject factor. The effect of mood state on conflict adaptation, for the low-dose ATD and high-dose ATD sessions separately, was analyzed by using mood scores (measured at +6.5 h) as a covariate. To visualize the hypothesized association between mood and conflict adaptation, we calculated standard individual conflict-adaptation scores by subtracting the interference effect following a correct conflict (incompatible) trial from the interference effect following a correct nonconflict (compatible) trial (cf. Figure 1A). Before averaging sequential conditions for each individual, the first trial of each block, trials following an error, and trials with RTs not fitting the outlier criterion (deviating more than 2.5 SD from the individual condition-specific mean) were excluded from analyses.

Results

As described in detail elsewhere (Booij et al., 2005), high-dose ATD but not low-dose ATD led to a both statistically and clinically significant induction of depressive symptoms as measured by MADRS scores 6.5 h after depletion (7.9 ± 7.8 vs. 3.7 ± 3.8, mean ± standard deviation; $t(18) = 3.34$, $p < .005$). The Simon task produced a standard interference effect: incompatible trials produced longer RTs than compatible trials ($F(1,18) = 23.47$, $p < .001$, $MSE = 1933.65$). The analysis also revealed a robust conflict-adaptation effect as indicated by an interaction between current- and previous-trial compatibility ($F(1,36) = 38.27$, $p < .001$, $MSE =$

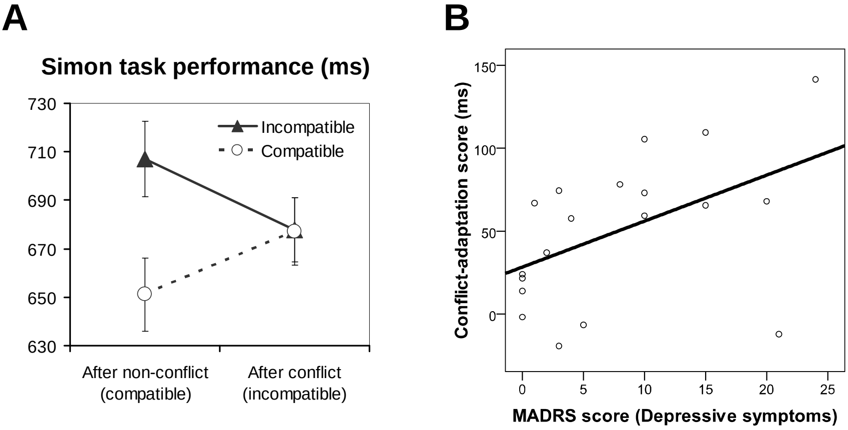

***Figure 1. A.** Conflict adaptation in the Simon task as evidenced by a reduced compatibility effect after conflict trials vs. non-conflict trials. Graphs show mean RT (ms) and standard errors. **B.** More depressive symptoms (MADRS score) after the high-dose ATD intervention are associated with increased conflict adaptation.*

1143.45). As Figure 1A shows, the interference effect was eliminated after conflict (incompatible) trials but not after non-conflict (compatible) trials, indicating standard conflict adaptation, that is, reduced interference after conflict trials. This reduction in interference was driven by both post-conflict speeding of incompatible trials (illustrating that increased conflict-driven control reduces interference; $t(18) = -4.2$, $p < .001$) and by post-conflict slowing of compatible trials (illustrating that increased conflict-driven control reduces facilitation; $t(18) = 4.5$, $p < .001$). Analyses of error rates also showed standard interference ($F(1,18) = 5.38$, $p < .05$, $MSE = 0.001$) and conflict adaptation ($F(1,36) = 6.30$, $p < .05$, $MSE = 0.001$) effects. In addition, it revealed a main effect of previous compatibility ($F(1,18) = 4.46$, $p < .05$, $MSE = .002$) indicating improved accuracy after conflict. Notably, no main effects or interactions with congruency or conflict-adaptation in RT or accuracy were observed for ATD intervention. Thus, ATD did not have an effect on interference (as reported earlier by Booij et al., 2005) and it also did not directly modulate conflict adaptation.

An ANCOVA using mood score as covariate confirmed our hypothesis: depressed-mood scores during the high-dose ATD condition predicted increased conflict adaptation in RT as indicated by a significant three-way interaction between mood, current-trial compatibility, and previous-trial compatibility (F(1,18) = 5.30, $p < .05$, MSE = 396.75). As Figure 1 shows, individuals with more depressive symptoms after the ATD intervention showed more conflict adaptation in the Simon task. As is typically observed (Chepenik et al., 2007; van Steenbergen et al., 2010), mood did not have effects on interference or overall reaction time. Moreover, no mood effects were found for accuracy, thus showing that the effect on conflict adaptation could not be attributed to a speed-accuracy tradeoff. Because the low-dose ATD session did not lead to any mood changes (Booij et al., 2005), data from this session were used for a control analysis: no association between mood and performance emerged.

Discussion

We report the first evidence for a link between low tryptophan concentrations, depressed mood and conflict adaptation in remitted depressed patients: Individuals with higher levels of depressive symptoms following high-dose ATD showed increased conflict adaptation. The ATD manipulation in itself exerted no direct effect on conflict adaptation. This finding is in line with predictions derived from MBM theory (Gendolla, 2000), with earlier behavioral and physiological observations from mood-induction studies in healthy populations (e.g., Gendolla, Abele, & Krusken, 2001; Gendolla & Krusken, 2002; van Steenbergen et al., 2010), and with neural evidence (e.g., Evers et al., 2009). Our study demonstrates for the first time that extra demand-driven recruitment of cognitive control is not limited to conditions of sad mood as induced in healthy volunteers (van Steenbergen et al., 2010), but can also be observed in people with depressive symptoms.

Our observation has important implications for understanding how depressive affect regulates cognitive control. In line with MBM theory (Gendolla, 2000), our data illustrate that depressed mood per se does not have motivational implications (as would be indicated by a modulation in attentional interference effects), but may facilitate increased cognitive control after a behavioral challenge. Interestingly, this effect was observed in a relatively low-demanding Simon task where people were merely instructed to do their best (see also Brinkmann & Gendolla, 2007) and in the context of depression scores that were mainly below the cut-off value for a depression diagnosis, but that were still clinically relevant and much larger than the effect of mood inductions in healthy participants.

However, it is important to note that MBM theory also predicts situations where a negative mood may actually lead to demand-driven disengagement, namely in cases where a demand is perceived as too high to actively cope with (cf. Brehm & Self, 1989). 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 & Gendolla, 2008). We think that these findings may also provide an interesting account for the recent observation of decreased conflict adaptation when participants received negative feedback concerning their task performance, an effect especially strong in subclinically depressed participants (Holmes & Pizzagalli, 2007). Interestingly, a very recent study by Meiran and colleagues (Meiran, Diamond, Todor, & Nemets, 2011) has reported a reversal of the conflict-adaptation effect in currently depressed patients, which suggests that conflict-driven control may actually break down when people become clinically depressed. In other words, there might be an inverted-U relationship between depressive symptoms and conflict adaptation (cf. Brehm & Self, 1989). It is an important aim for future studies to understand the generalizablilty 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. MBM theory assumes that the interaction between both factors determines the actual appraisal of the demand, which in turn modulates effort mobilization. This hypothesis now ripe for further testing in other studies using sequential analyses of conflict-task performance.

At the neural level, the joint impact of depressed mood and demand evaluation on subsequent effort mobilization and cognitive control may be associated with (hyper)activation of the anterior cingulate cortex (ACC), a region important for signaling the need for more cognitive effort to the dorsolateral prefrontal cortex (DLPFC) (Botvinick et al., 2001; Davidson, Pizzagalli, Nitschke, & Putnam, 2002; Olvet & Hajcak, 2008; Pizzagalli et al., 2006). It has been suggested that dysfunction of this ACC-DLPFC circuit in unipolar depression also produces catastrophic reactions to errors (for a review, see Pizzagalli, 2011). Further study is needed to understand the exact neuromodulating role that 5-HT may play in this affective regulation (cf. Jocham & Ullsperger, 2009). Future studies that combine neuroimaging methods with effort-related physiological and behavioral measures will advance our understanding of the functional role of the ACC in the affective (dys)regulation of adaptive control to fluctuating task demands.

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8

Task Difficulty and Conflict Adaptation

> "Face a mirror, look at your eyes and invent a mathematical problem, such as 81 times 17. Try to solve the problem and watch your pupil at the same time (...) After a few attempts, almost everyone is able to observe the pupillary dilation that accompanies mental effort."
>
> Daniel Kahneman (1973)

This chapter is based on:

van Steenbergen, H., Band, G.P.H., & Hommel, B. (in preparation). Dynamic control adaptations depend on task difficulty: Evidence from behavior and pupillometry.

Abstract

Sequential modulation of congruency effects in conflict tasks show that cognitive control and effort quickly adapt to changing task demands. We investigated how this behavioral congruency-sequence effect interacts with different levels of task difficulty in a flanker and a Stroop task. In addition, online measures of pupil diameter were used as a physiological index of effort mobilization. Consistent with the notion that task difficulty increases effort mobilization up to a certain limit, dynamic conflict-driven adjustment in behavior was observed only if task difficulty was moderate, whereas congruency effects in behavior and pupil dilation were unaffected. Furthermore, high difficulty levels induced a conflict-driven reduction in pupil dilation, presumably reflecting a physiological marker of mental overload.

Introduction

In a constantly changing environment, cognitive control helps to adaptively respond to task demands. Paradigms such as the flanker task (Eriksen & Eriksen, 1974) and the Stroop task (Stroop, 1992) have been designed to probe cognitive control processes. In the flanker task, for example, people respond to a central target while ignoring flanking distracters. The reaction-time difference between trials with target-congruent and -incongruent flankers has been called congruency effect and been considered a measure of sustained cognitive control. On the other hand, dynamic adjustments in control are reflected in trial-to-trial adaptations. This sequential effect typically shows that the congruency effect on the current trial is reduced when it follows an incongruent as compared to a congruent trial (Gratton et al., 1992; Greenwald & Rosenberg, 1978).

According to the conflict monitoring theory, the congruency-sequence effect occurs because incongruent trials evoke response conflict, which triggers control improvements and thus reduces interference on subsequent trials (Botvinick et al., 2001). Indeed, numerous studies have found evidence for this so-called conflict-adaptation effect, an adaptation that has been demonstrated across flanker, Stroop, and Simon tasks (for a review, cf. Egner, 2007). Accumulating neuroimaging data has demonstrated a possible neural mechanism involving the medial prefrontal cortex as a conflict monitoring system that helps to adapt control by enhancing task-goal representations in more lateral prefrontal areas (e.g., Egner & Hirsch, 2005; Kerns et al., 2004).

Although the congruency-sequence effect typically is investigated in the context of the conflict monitoring theory (Botvinick et al., 2001), it probably reflects a more general effect that Ach and colleagues have coined the ‘difficulty law of motivation’ (Ach, 1935; Hillgruber, 1912). According to this law, increasing the difficulty of a task automatically makes people to try harder. That is, the amount of mental effort –here defined as the mobilization of energy resources to carry out behavior (Gendolla & Richter, 2010) – invested in the task is thought to be proportional to the level of perceived task difficulty (cf. Kahneman, 1973; Brehm & Self, 1989). This increased mental effort, in turn, may also improve goal-directed behavior as measured in reaction times. Although the majority of the available studies have provided physiological and self-report evidence for effort mobilization in difficult situations (for reviews, see Gendolla, Wright, & Richter, 2011; Wright & Kirby, 2001), a recent study by Dreisbach & Fischer (2011) has shown that adjustments in effort mobilization can also be observed in behavior. In that study, sequence effects in reaction times were observed in a perceptual fluency task using different levels of task difficulty, demonstrating that sequential behavioral adaptation can occur even in the absence of conflict.

The aim of the current study is to investigate how behavioral congruency-sequence effects in conflict tasks interact with different levels of task difficulty. Although – as outlined above – conflict-driven improvement of control is likely to reflect a momentary increase in effort driven by the difficulty of the previous trial, it is important to understand what happens if difficulty further increases. Given the limited nature of processing resources, one would expect that task difficulty can increase effort mobilization only up to some upper limit, after which it reaches asymptote. Likewise, dynamic conflict-driven increases in effort can only occur if there is some room left for improvement. In other words, conflict adaptation may only occur in cases where overall task difficulty is not too high. The present study put this prediction to empirical test.

A first indication that congruency-sequence effects indeed become smaller when resources come close to their limits has been provided by two recent studies. Comparing Simon-task performance under single and dual-task situations, Stürmer and colleagues (Sturmer, Seiss, & Leuthold, 2005) observed smaller congruency-sequence effects in the dual-task context, indicating that the secondary task may have consumed resources needed for conflict-driven improvements in control. In another study by Fischer and coworkers (Fischer et al., 2008), processing demands and response conflict were manipulated within the same trial, using a numerical judgment task in the context of a Simon paradigm. Consistent with a limited resources account, difficult number judgments reduced the subsequent congruency-sequence effect in Simon performance.

The present study aims to find evidence for task-difficulty effects on cognitive control adaptations in a series of three experiments. In Experiment 1 and 2, we compared how task-demand differences between a Stroop and a flanker task may account for the size of conflict-adaptation effects observed. In Experiment 3 an explicit manipulation of task difficulty was used to further investigate the possibility of a difficulty-driven reduction in the congruency-sequence effect.

Experiment 1: Re-analysis of Van Steenbergen et al. (2010)

In a first attempt to test whether demand differences between tasks can account for differences in conflict-adaptation effects, we re-analyzed an earlier published data set (van Steenbergen et al., 2010) by comparing congruency-sequence effects as a function of the level of task demands participants reported. Given that increased task difficulty may increase effort mobilization up to its limits, we expected that no further improvements in cognitive control by previous-trial conflict will be observed under conditions of high task difficulty. That is, we predicted that a task that is associated with high task demands may show smaller congruency-sequence effects.

Methods

For detailed methods, see van Steenbergen et al. (2010).

Participants

Ninety-eight students participated either for payment or course credits (18-30 years old; 24 males; 11 left-handed). Data from seven participants were excluded from analyses because of response omissions on more than 20% of the trials (2), chance level task performance (3), or incompliance with instructions (2). Data were pooled across four different mood induction groups, as the mood conditions were irrelevant for the purpose of the current study.

Tasks

Two variants of a classic cognitive-control paradigm were used to measure conflict adaptation. An adapted version of the flanker task (Eriksen & Eriksen, 1974) consisted of centrally presented target stimuli which were vertically flanked on either side by two identical response-congruent or response-incongruent stimuli. An adapted version of the Stroop task (Stroop, 1992) consisted of a column of five identical stimuli presented in response-congruent or response-incongruent ink colors. Flanker and Stroop stimuli were carefully matched by using sets of Dutch color words. Each task used a counterbalanced unique set of four words. Two of these stimuli were mapped to a left hand response, and the other two stimuli were mapped to a right hand response.

E-prime software was used for stimulus presentation and response recording. All trials started with a fixation cross (randomly varying intervals of 800, 1000, or 1100 ms), followed by the stimulus, which was presented until response registration or, in the case of omission, for 1500 ms. In half of the trials the stimuli would call for different responses (Incongruent [I] condition; e.g., the word “green” surrounded by the words “yellow” in the flanker task and the word “blue” printed in red in the Stroop task) whereas in the other half identical target and distracter dimensions would call for the same response (Congruent [C] condition; e.g., the word “green” surrounded by the words “green” in the flanker task and the word "blue" printed in blue in the Stroop task). All trials were presented in an unconstrained random sequence. Stimuli appeared in lower-case in Arial bold font (3.5 cm wide and 5.4 cm high) and were presented on a grey background. Flanker stimuli used black ink color. Participants viewed the stimuli on a 17" monitor from about 60 cm.

Procedure

Instructions emphasized both speed and accuracy. Following 16 practice trials, and a 10-minute mood induction, participants performed a flanker and a Stroop task block (in counterbalanced order), which were repeated after a short 3-minute mood booster. A textual reminder of the stimulus-response mapping was shown for 15 seconds before the start of each of the four blocks of 72 trials. At the end of the experiment, participants evaluated the flanker and Stroop task in terms of weariness, unpleasantness and difficulty on a 6-points scale.

Results

Subjective ratings

Task difficulty ratings showed that the Stroop task was associated with higher demands than the flanker task (4.1 versus 3.7; t(90) = 2.6, p < .05). Weariness and unpleasantness scores were not different for the tasks (t(90)s < 1.6, ps > .12).

Behavioral results

The first trial of each block (1.4%) and trials not complying with the outlier criterion (2 SDs; 4.7%) were excluded from all analyses. ANOVAs on correct Reaction Time (RT) data revealed significant basic congruency effects for both the flanker task (31 ms; F(1,90) = 137.9, p < .001) and the Stroop task (35 ms; F(1,90) = 71.9, p < .001) confirming that both paradigms can reliably measure cognitive control. However, as Figure 1A shows, a congruency-sequence effect, i.e., a reduction of the congruency effect following conflict, was only found for the flanker task (21 ms; F(1,90) = 17.2, p < .001) but not for the (more difficult) Stroop task (7 ms; F(1,90) = 1.4, p > .2). Accuracy data confirmed the basic congruency effects for the flanker task (2.5%; F(1,90) = 22.3, p < .001) and the Stroop task (2.5%; F(1,90) = 18.5, p < .001). There was a trend for a congruency- sequence effect in the flanker task (2.0%; F(1,90) = 3.68, p = .058). In addition to the congruency-sequence effect in the flanker task, participants showed a tendency to slow their response following conflict (F(1,90) = 11.4, p < .005) (cf. Ullsperger, Bylsma, & Botvinick, 2005).

Discussion

Experiment 1 provides initial support for the hypothesis that task difficulty may be an import factor that accounts for reduced congruency-sequence effects: a Stroop task that was reported to be more demanding yields less conflict adaptation than a matched version of the flanker task. That is, while a reliable congruency-sequence effect was observed in the flanker task, the much smaller effect observed in the Stroop task was not statistically significant, despite the large sample (N = 91).

Experiment 2

Even though Experiment 1 provided initial evidence for task-difficulty effects on conflict adaptation, these data were pooled over several mood induction groups which produced different adaptation effects in the earlier published study (see van Steenbergen et al., 2010). It might thus be argued that the absolute size of conflict-adaptation effects cannot be generalized to emotionally neutral situations. This motivated us to design a replication study.

In addition, the follow-up study recorded pupillary dilation to provide a measure of effort mobilization (cf. Kahneman, Hess & Polt 1964). Although pupil size is also determined by other variables, it has been repeatedly shown that task-related pupil dilation systematically increases as a function of task difficulty or processing load and thus “provides a powerful analytic tool for the experimental study of processing load and the structure of processing resources” (Beatty, p 291 1982; Beatty & Lucero-Wagoner, 2000). Interestingly, when task demands overload the resources, no further dilation occurs and dilation may either reach asymptotic value or decline (Cabestrero, Crespo, & Quiros, 2009; Granholm & Steinhauer, 2004; Peavler, 1974; Poock, 1973). The decline in pupil diameter under conditions of mental overload exclusively occurs when people keep trying to work on the task (Granholm, Asarnow, Sarkin, & Dykes, 1996).

In the context of cognitive control tasks, numerous pupillometry studies have already shown that incongruent Stroop trials increase pupil dilation (Brown et al., 1999; Siegle, Steinhauer, & Thase, 2004; Laeng, Orbo, Holmlund, & Miozzo, 2011), which is consistent with the central assumption that incongruent trials, like other difficult situations, automatically recruit effort. Given that behavioral congruency effects are observed across different paradigms, flanker tasks may produce similar congruency effects on dilation as has been observed in Stroop tasks. However, it is not clear yet how trial-to-trial adaptations are related to effort recruitment on a temporal scale (cf. Scherbaum, Fischer, Dshemuchadse, & Goschke, 2011). Whereas the original computational conflict-monitoring model suggests that conflict from a previous trial starts to recruit effort in the subsequent trial (across-trial adaptation; Botvinick et al., 2001), other models suggest that the adaptation of control may already start to develop within the previous conflict trial itself (within-trial adaptation; e.g., Brown, Reynolds, & Braver, 2007). According to this within-trial adaptation account, conflict adaptation in the current trial is mainly due to a carryover of the adjusted control state from the previous trial. Although recent findings from frequency-tagged EEG responses (Scherbaum et al., 2011; cf. Goschke & Dreisbach, 2008) indeed support this within-trial adaptation account, the pupil dilation signal probably is too slow to accurately index such subtle effort-related adaptation within the previous trial. On the other hand, if conflict adaptation mainly stems from across-trial adaptation (Botvinick et al., 2001), pupil dilation may shown an overall increased dilation in the current trial after conflict in the previous trial. Task difficulty manipulations that reduce adaptation may then decrease this conflict-driven dilation increase in the subsequent trial.

In order to test the effects of task difficulty on sequence effects in cognitive control and effort mobilization, we conducted two new experiments that included a flanker and a Stroop task while pupil data were acquired during task performance. Experiment 2 included a flanker and a Stroop task similar to those used in Experiment 1. We expected to replicate the behavioral finding that, in comparison to the Flanker task, increased task demands in the Stroop task lead to smaller or absent conflict-adaptation effects. Pupil dilation data were acquired to explore sequential effects in effort mobilization.

Methods

Participants

Twenty-eight healthy right-handed Dutch students participated either for payment or course credits (18-30 years old; 7 males). All participants indicated not to use medication (other than anti-conception pills) and were not color blind. Four participants were excluded from analysis because of technical problems during the data acquisition. After initial data screening, two other participants were excluded because of random performance in one or more of the task blocks.

Tasks

The flanker and Stroop tasks were identical to those used in the pilot study with a few exceptions. First, the Stroop task only included one stimulus rather than a column of five identical stimuli in order to prevent potential dilution-effect confounds (cf. Kahneman & Chajczyk, 1983). Second, both tasks used a fixed set of color words in order to match Stroop ink color luminance levels. To specify, the flanker task always used the words “brown”, “gray”, “yellow”, and “red” whereas the Stroop taks always used the words “purple”, “green”, “orange”, and “blue” (all words were presented in Dutch translations). Isoluminant ink colors from the Teufel colors set were used for the Stroop task (Teufel & Wehrhahn, 2000) whereas the flanker task stimuli were printed in black. Finally, in order to avoid pupil light reflexes produced by stimulus presentation (cf. Beatty & Lucero-Wagoner, 2000) a scrambled picture of the average stimulus was used as a baseline fixation stimulus (for both tasks separately).

Procedure

After informed consent was given, participants were seated in a dimly lit room where the eye tracker was calibrated. Following a data quality check, participants performed 28 practice trials for both tasks which were repeated until they sufficiently learned the task to start the experiment proper. Flanker and Stroop trials were presented in 12 alternating blocks (in counterbalanced order). Before each block started, a self-paced textual reminder of the stimulus-response mapping was shown for a maximum of 15 seconds. Each block consisted of 36 consecutive fast test trials (see under Tasks) and 18 consecutive filler trials with a constant inter-trial interval of 4 seconds (test and filler sequence in random order). For both the flanker and Stroop task, 216 test trials were available for sequential analyses of reaction time and pupil dilation. The 108 filler trials were used to validate the timing of the pupil dilation response in the short test trials.

Following each block, participants received accuracy feedback about their performance in a line graph showing their accuracy per block over time. Feedback was given for the flanker and Stroop task separately. Participants were required to make errors within a target range of 5-10%, and if the participant reached this target they received positive feedback which still encouraged both speed and accuracy. If the error rate dropped below 5%, participants received the following text feedback: “You are not doing your best. Please increase speed. You are allowed to make more errors.” If the error rate exceeded 10%, participants received the following text feedback: “You are not doing your best. You are making too many errors. Please improve accuracy but keep responding fast.” A reminder of the feedback given earlier was provided again at the start of the next task block. Visual feedback was verbally reinforced by the experimenter. Short self-paced breaks (for a maximum of 30 seconds) were provided following each pair of two blocks. Participants had a fixed 1-minute break halfway the experiment.

Pupil data acquisition and analysis

Pupil diameter was recorded at 60 Hz using a Tobii T120 eye tracker, which is integrated into a 17-inch TFT monitor. Participants were seated at a distance of approximately 60 cm from the monitor. Pupil data were processed and analyzed using custom-made macros programmed in Brain Vision Analyzer. Artifacts and blinks as detected by the eye tracker were corrected using linear interpolation. Trials including extremely unreliable interpolated values (< 20% data points obtained in the intervals of interest) were excluded from analyses. After visual inspection (see below), pupil dilation was defined as the mean pupil diameter during a 700 to 1300 ms period following stimulus onset. A 200-ms pre-stimulus interval was used as baseline.

Results

All analyses reported for Experiment 2 and Experiment 3 were performed after the following trials were excluded: the first trial of each block, trials following an error, trials with RTs not fitting the outlier criterion (2.5 SDs deviating form the individual condition-specific mean), and trials including unreliable pupil-data interpolations.

Behavioral results

Correct reaction time data are shown in Figure 1B. Replicating our pilot study, both the flanker and the Stroop task yielded a congruency effect (F(1,21) = 67.7, p < .001, MSE = 184.9 and F(1,21) = 17.1, p < .001, MSE = 1538.0), which was modulated by previous trial conflict in the flanker task (F(1,21) = 9.7, p < .01, MSE = 213.6), but not in the Stroop task (F(1,21) = 0.4, p = .52, MSE = 456.0). Error rate data revealed congruency-effects for the flanker (F(1,21) = 6.1, p < .03, MSE = .003) and the Stroop task (F(1,21) = 4.4, p < .05, MSE = .001) but no indications of conflict adaptation for both tasks (Fs < 1). These behavioral results replicate the finding in Experiment 1: the Stroop task produced smaller congruency-sequence effects than the flanker task.

Pupil data validation

In order to explore whether effort mobilization as measured by pupil dilation is different between the flanker and the Stroop task, we measured pupil dilation in response to stimulus onset. As is shown in Figure 2A (upper panels), the long-interval filler trials showed a pupil dilation for both the flanker and the Stroop task, which reached its peak value around 1 second after stimulus onset. More importantly, in the same time interval dilations were found for the test trials with the short inter-trial intervals, which validates the analytic approach to define maximum pupil dilation as the mean pupil diameter during a 700 to 1300 ms period following stimulus onset (Figure 2A, lower panels).

The pupil dilation data yielded congruency effects in dilation for both the flanker task (F(1,21) = 14.5, p < .001, MSE = .001) and the Stroop task (F(1,21) = 4.3, p = .052, MSE = .001), irrespectively of the inter-trial interval used (Fs < 1). Thus, pupil diameter could reliably be used as an index of effort mobilization during the test trials with their short inter-trial intervals.

Pupil results

In order to test differential effort mobilization effects on the Stroop versus the flanker task, we analyzed pupil dilation during test trials as a function of congruency of the current trial and congruency of the previous trial, using task (flanker versus Stroop) as an additional within-subject factor. As shown in Figure 1C, both tasks showed more dilation during incongruent trials in comparison to congruent trials (F(1,21) = 10.1, p < .005, MSE = .001). Independent of this, a trend for a main effect of previous-trial congruency was observed: decreases in current-trial dilations were observed when the previous trial was incongruent (F(1,21) = 3.4, p = .08, MSE = .001). This effect was moderated by a significant Task x Previous-Trial Congruency interaction (F(1,21) = 4.7, p < .05, MSE =.0004) showing that the decrease in overall dilation following conflict was only significant in the Stroop task (F(1,21) = 4.9, p < .05, MSE = .001) but not in the flanker task (F(1,21) = .30, p = .60, MSE = .0004). Task did not significantly interact with other (combinations of) factors. Because the Task x Previous-trial Congruency effect was not observed in the preceding baseline interval (F(1,21) = .55, p = .47, MSE = .002), the effect in dilation cannot be attributed to a carry-over effect from a dilation starting in the preceding trial.

Discussion

Experiment 2 replicated the behavioral effect in Experiment 1: conflict adaptation was reduced in the – presumably more demanding – Stroop task in comparison to the flanker task. Pupil data across the flanker and Stroop task showed that incongruent trials produced more dilation than congruent trials. Thus, replicating and extending earlier studies on the Stroop task, both Stroop and flanker conflict induced pupil dilation, which probably reflects conflict-driven effort mobilization.

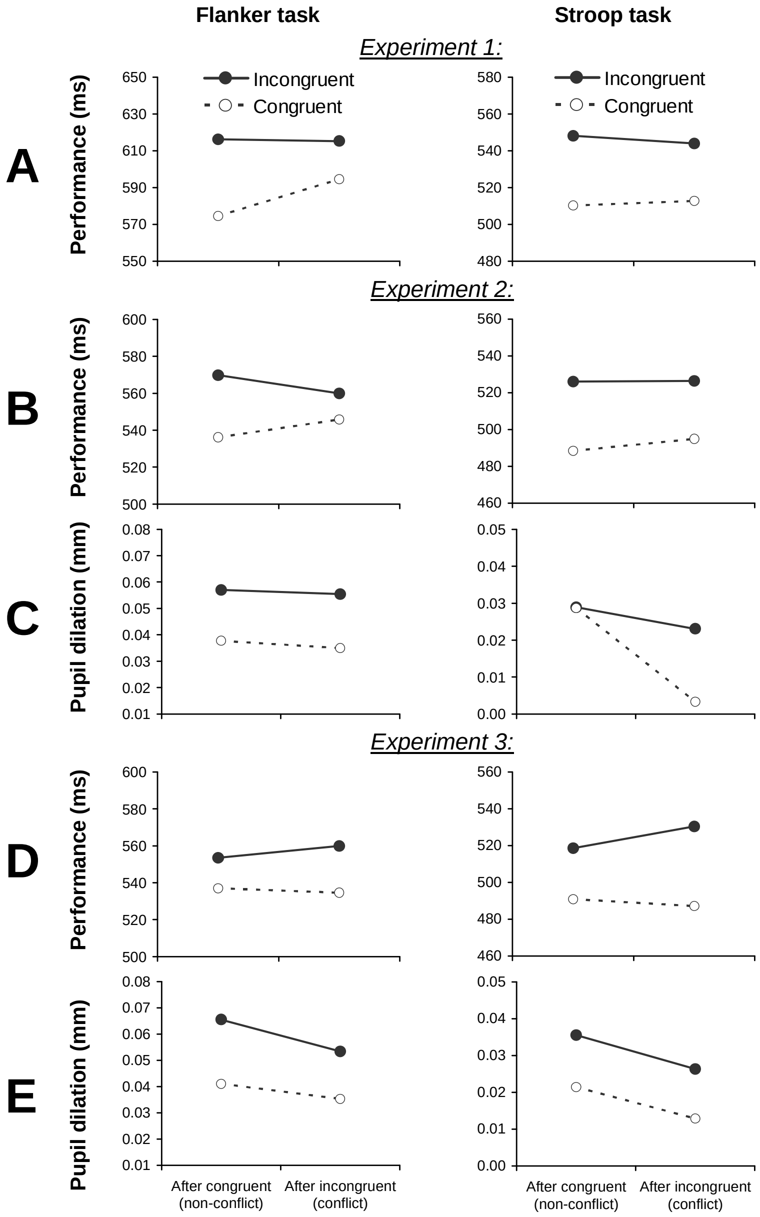

Figure 1. *Flanker task (left column) and Stroop task (right column) performance (**A, B,** and **D**) and pupil dilation (**C** and **E**) across Experiment 1, 2, and 3, as a function of current-trial congruency and previous-trial congruency.*

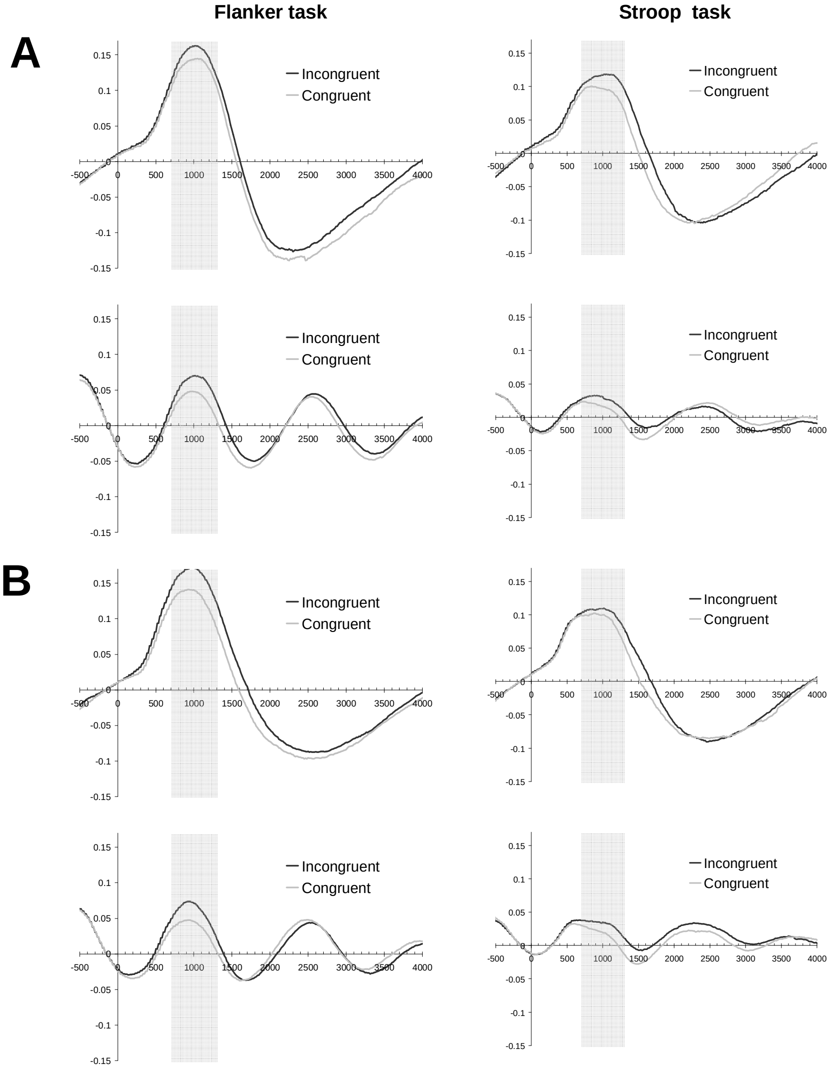

__Figure 2.__ Pupillary response (mm) as a function of time (ms) and current-trial congruency for Experiment 2 (__A__) and Experiment 3 (__B__). Both graphs depict baseline-corrected pupil dilation in the Flanker (left column) and Stroop (right column) task for filler trials (upper row) and test trials (lower row).

Even more importantly, sequential analyses of pupil dilation indicated a main effect of previous trial congruency in the Stroop task, but not in the flanker task. The absence of increased dilation in Trial N after conflict in Trial N-1 for the flanker task, observed in combination with the conflict-adaptation effect in behavioral data, suggests that the behavioral adaptation effect might have been driven by within-trial rather than across-trial adaptation of mental effort. In other words, the conflict-adaptation effect observed at Trial N may reflect a carry-over effect of conflict-driven recruitment of effort that mainly took place within Trial N-1. Interestingly, a conflict-driven reduction in pupil dilation was observed for the Stroop task in the absence of behavioral adaptation. Demand-driven decline of pupil dilation has been reported earlier for overload conditions in other paradigms, including a reaction time task using extreme presentation rates (Poock, 1973) and a digital span recall task using excessive load (Granholm et al., 1996). In line with these findings, the effect observed on pupil dilation may thus represent a physiological marker of resource overload, which in our case is driven by increased task difficulty in combination with the conflict in the previous trial.

Although subjective reports from Experiment 1 support our claim that the Stroop task was experienced to be more difficult than the flanker task, we can only speculate about a possible cause. Importantly, both tasks were carefully matched in terms of stimulus material. That is, both paradigms required a similar manual response to similar verbal information (i.e., color words). Moreover, both the Stroop and the flanker task are thought to induce conflict between relevant and irrelevant stimulus dimensions (Egner, 2008; Kornblum, Hasbroucq, & Osman, 1990), and pupillary responses and behavior confirmed different effects for incongruent trials in comparison to congruent trials. However, the source of this conflict might be different. For example, according the Dimension-Action model (Magen & Cohen, 2007) the Stroop effect is driven by conflict between relevant and irrelevant verbal codes (following the translation from color to word), whereas conflict in the flanker task takes place between relevant and irrelevant stimulus elements in a visual dimension. In addition, Stroop interference stems from two features of the same visual object, whereas flanker interference stems from features of different visual objects (Magen & Cohen, 2002). This may differently impact task demands. Processing the relevant word color in a Stroop stimulus inevitably is accompanied by the processing of the irrelevant color word (Chen, 2003; Duncan, 1984), which may induce task conflict even in congruent trials (Goldfarb & Henik, 2007). In contrast, selective processing of central target relative to surrounding stimuli in the flanker task is simply possible through a spatial narrowing of attention (Laberge, Brown, Carter, Bash, & Hartley, 1991). One or more of these factors might have produced an increase in task difficulty for the Stroop task.*

Nevertheless, it is important to stress that conflict-adaptation effects have been demonstrated in numerous studies on Stroop and Stroop-like effects. To the best of our knowledge, however, the Stroop-like tasks usually reported were not as demanding as the task used in our experiment, which mapped four different stimulus features to two responses. Moreover, previous studies used simple categorization responses and/or a low ratio of incongruent trials (e.g., Kerns et al., 2004), which may well have inflated adaptation effects (cf. Purmann, Badde, & Wendt, 2009). To our knowledge, the few publications that did use a standard color-word Stroop tasks and demonstrate conflict adaptation (Egner & Hirsch, 2005; Naccache et al., 2005) exclusively used a low-demanding two-color version, where participants simply can base their response on the presence or absence of a color change rather than on color identity. Previous work is thus not inconsistent with our claim that increased task difficulty in the Stroop task may eliminate conflict-adaptation effects.

However, given that Experiment 1 and 2 only provide correlational rather than causal evidence for a link between task difficulty and conflict-adaptation reductions, and because it is not the paradigm (Stroop versus flanker) itself thought to be responsible for this effect, Experiment 3 used an experimental manipulation of task difficulty to demonstrate that difficulty effects can occur independently of the particular paradigm.

Experiment 3

In order to increase overall effort, tasks difficulty in Experiment 3 was further increased using a time-pressure manipulation (cf. Kahneman, 1973). A new group of participants performed exactly the same tasks as used in Experiment 2 but with different instructions. Specifically, participants were forced to try improving their

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* The somewhat counterintuitive finding that responses were faster on the Stroop task may also have been driven by quicker processing in phases prior to response selection, e.g., perceptual processes. Moreover, because we used fixed response-stimulus intervals, this may have increased stimulus pacing, which in turn increased task difficulty. Note that faster responses have also been observed as a consequence of the participant's adaptation to higher levels of task difficulty (cf. Washburn & Putney, 2001).

speed over time while maintaining accuracy. We hypothesized that this extra increase in task difficulty should further reduce congruency-sequence effects. That is, in comparison to Experiment 2, we expected to find an additional reduction of conflict adaptation irrespective of the particular task. We recorded pupil diameter in order to find converging evidence for the sequential previous-trial congruency effect observed for pupil dilation (i.e., during the Stroop task in Experiment 2) when behavioral conflict adaptation was absent.

Methods

Participants

Twenty-seven healthy right-handed Dutch students participated either for payment or course credits (18-30 years old; 8 males). All participants indicated not to use medication (other than anti-conception pills) and were not color blind. After initial data screening, three participants were excluded because of random performance in one or more of the task blocks.

Tasks

See Experiment 2.

Procedure

Procedures were identical to Experiment 2, except for the performance feedback and instructions that participants received. Like in Experiment 2, after each block, participants received both accuracy and correct reaction time feedback about their performance in a line graph showing their accuracy and speed per block over time. Feedback was given for the flanker and Stroop task separately. Participants were required to continuously improve speed over time, while keeping errors within a target range of 5-10%. If the participant attained the accuracy target they received positive feedback, which still instructed to further increase speed without reducing accuracy. If the error rate dropped below 5%, participants received the following text feedback: "You are not doing your best. Please increase speed. You are allowed to make more errors.” If the error rate exceeded 10%, participants received the following text feedback: "You are not doing your best (or you respond TOO fast). You are making to many errors. Please try as hard as you can and improve accuracy.” A reminder of the feedback given earlier was provided again at the start of the next task block. Visual feedback was verbally reinforced by the experimenter.

Pupil data acquisition and analysis

See Experiment 1.

Results

Behavioral results

Consistent with predictions, the increased task difficulty reduced conflict adaptation across tasks (see Figure 1D), as no evidence for congruency-sequence effect was found for the flanker task (F(1,23) = .66, p = .43, MSE = 701.6), whereas the Stroop task even showed a reversal of the congruency-sequence effect (F(1,23) = 7.7, p < .02, MSE = 187.1). Congruency effects (F(1,23) = 27.1, p < .001, MSE = 385.8 and F(1,23) = 13.9, p < .001, MSE = 2166.2) were similar to those reported for Experiment 2. As in Experiment 2, error rate data revealed significant flanker and Stroop congruency-effects (F(1,23) = 6.5, p < .02, MSE = .002 and F(1,23) = 9.6, p < .005) but no indications of conflict adaptation for both tasks (Fs < 2). In addition, the Stroop task produced a previous-trial congruency effect on accuracy (F(1,23) = 4.6, p < .05, MSE = .001), showing an increase in error rate after conflict in the previous trial.

Pupil data validation

As Figure 2B shows, the dilation patterns in Experiment 3 mirrored the effects observed in Experiment 2. Congruency effects were observed in the flanker task (F(1,23) = 26.5, p < .001, MSE = .001) and in the Stroop task (F(1,23) = 4.0, p = .059, MSE = .002), irrespectively of the inter-trial interval used (Fs < 1).

Pupil results

As shown in Figure 1E, both tasks caused more dilation to incongruent than to congruent test trials (F(1,23) = 16.3, p < .001, MSE = .001). Independent of this, previous-trial congruency also influenced current-trial dilations: decreases in dilation were observed when the previous trial was incongruent (F(1,23) = 8.8, p < .01, MSE = .0004), irrespectively of task type (F < 1).

Discussion

As expected, conflict-adaptation effects in Experiment 3 were eliminated for both tasks when performed under conditions of increased task difficulty using time pressure. Standard congruency effects in RT and pupil dilation confirmed that these tasks still induced conflict and effort mobilization. Moreover, as observed for the Stroop task in Experiment 2, the absence of behavioral adaptation in both tasks was accompanied by a conflict-driven reduction in pupil dilation in both tasks.

General Discussion

We provided converging evidence for task-difficulty effects on dynamic control adaptations in three experiments. Experiment 1 and 2 showed that a more difficult Stroop task produced smaller congruency-sequence effects than a less demanding flanker task (see Figure 1A and 1B). Experiment 3 showed that, when task difficulty was manipulated experimentally, these congruency-sequence effects were further reduced for both tasks (see Figure 1D). Altogether, our behavioral findings support our prediction that extreme task difficulty put effort mobilization at its limits, leaving no room for further improvements in cognitive control by previous-trial conflict. As a result, no conflict-adaptation effects were observed in conditions of high task difficulty across three experiments.

In addition, Experiment 2 and 3 demonstrates that pupillary measures provide an interesting tool to index effort mobilization in cognitive control paradigms. Although a few studies already have shown pupil dilation increases to incongruent Stroop trials (Brown et al., 1999; Siegle et al., 2004), we demonstrated (see Figure 2) that this congruency effect occurred independently of the specific paradigm used (i.e., both in the Stroop and the flanker task) and occurred even during fast trial pacing (inter-trial intervals around 1.5 seconds).

Apart from this methodological contribution, pupil data also provided additional insight in how and when difficult situations may automatically trigger effort mobilization. Firstly, behavioral conflict adaptation was not reflected by a temporary increase in effort in the subsequent trial (Figure 1C, left figure), which suggests that conflict-driven mobilization of effort mainly takes place earlier – presumably within the previous conflict trial itself (Scherbaum et al., 2011) rather than across trials (Botvinick et al., 2001). Secondly, during difficult task conditions in Experiment 2 (Figure 1C, right figure) and Experiment 3 (Figure 1E) where no conflict adaptation was observed, pupil dilation data showed a conflict-driven drop of dilation, most likely a physiological marker of mental overload (cf. Granholm et al., 1996). Taken together, behavioral and pupil data reinforced our interpretation why conflict adaptation did not occur during high levels of task difficulty: subjects spent maximum effort already. Rather than being adaptive, additional conflict thus may simply overload the cognitive system under these conditions.

One important aim for future studies is to further test the impact of task difficulty at the most extreme levels. As has been suggested by the motivation intensity theory (Brehm & Self, 1989; Brehm, Wright, Solomon, Silka, & Greenberg, 1983) effort mobilization is proportional to task difficulty as long as success is viewed as possible and worthwhile. In cases where a demand is perceived as too high to actively cope with, effort mobilization may drop. In other words, there might exist an inverted-U relationship between task difficulty and effort mobilization (Gendolla et al., 2011). Thus far, evidence for the motivation intensity theory has mainly been provided by cardiovascular and subjective measures of effort, and it is an important aim for future studies to further investigate the link with behavioral measures of loosened control after extreme demands. However, it might actually be speculated that the small reversal of conflict adaptation of Stroop performance under time pressure in Experiment 3 illustrates this drop of effort mobilization driven by previous-trial conflict in a very demanding situation. If this is true, reduced conflict-driven pupil dilation in this situation may well indicate a reduced mobilization of effort in this situation, rather than a physiological signal of mental overload. However, given that the effect was small and not anticipated, future experiments are needed to further investigate this possibility.

An important take-home message of this study is that too difficult conflict tasks may not produce the typical congruency-sequence effect. Our findings explain why some researchers using difficult tasks (e.g., using high incongruent-to-congruent ratios) have failed to observe normal conflict-adaptation effects (e.g., Wendt, Heldmann, Munte, & Kluwe, 2007). Moreover, our work contributes to the cumulating evidence that various factors like trial pacing (e.g., Notebaert, Gevers, Verbruggen, & Liefooghe, 2006), time on task (Mayr & Awh, 2009), incongruent-congruent ratio (Purmann et al., 2009), "correction" for binding effects (e.g., Akcay & Hazeltine, 2007, but see Spape & Hommel, 2008), and type of conflict involved (Verbruggen, Notebaert, Liefooghe, & Vandierendonck, 2006) all may influence the size of congruency-sequence effects. Given that all these factors are likely to change task difficulty and motivation, it as an important future challenge to understand how these factors determine effort mobilization and cognitive control, and which emotional and motivational neural systems are responsible for this modulation.

Acknowledgments

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9

Romantic Love and Focused Attention

"There is always some madness in love. But there is also always some reason in madness."

Friedrich Nietzsche

This chapter is based on:

van Steenbergen, H., Langeslag, S.J.E., Band, G.P.H., & Hommel, B. (submitted for publication). Reduced cognitive control in passionate lovers.

Abstract

Passionate love is associated with intense changes in emotion and attention which are thought to play an important role in the early stages of romantic relationship formation. Although passionate love usually involves improved, near-obsessive attention to the beloved, anecdotal evidence has suggested that the lover's concentration for daily tasks like study and work may actually be impaired. We systematically investigated a link between passionate love and cognitive control in a sample of students who had recently become involved in a romantic relationship. Intensity of passionate love as measured by the Passionate Love Scale was shown to predict decreased individual efficiency in cognitive control as measured in Stroop and flanker task performance. This study provides the first systematic empirical evidence that impaired cognitive control is an important characteristic of passionate love.

Introduction

Falling in love is an experience that involves very intense emotional changes including euphoria and overwhelming joy, increased arousal and energy, emotional dependency on the partner, craving for emotional union with the beloved, and obsessional thoughts about and focused attention on the special other (Fisher, 1998). Passionate love has been recorded in all contemporary human cultures for which data are available and it can be traced back to ancient historical and literary sources (Jankowiak & Fischer, 1992). Systematic psychological investigation has shown that this attraction-related emotional state – also referred to as limerence (Tennov, 1979) or infatuation – can be distinguished from lust and attachment, aspects of romantic love that are driven by dissociable affective systems (Fisher, 1998; Hatfield & Sprecher, 1986; Reis & Aron, 2008).

Cumulating neuroscientific evidence has recently led to the formulation of biologically and evolutionarily informed theories that aim to understand why love is so important in human behavior (Fisher, Aron, & Brown, 2006). According to one influential proposal, passionate love originates from an phylogenetically old mechanism that boosts courtship attraction via neurochemical modulation (Beach, 1976; Fisher et al., 2006). Extending earlier evidence from animal studies, neuroimaging studies in humans have shown that the euphoria and near-obsessive attention devoted to the beloved is associated with reward circuitry activation (Bartels & Zeki, 2000) which varies as a function of passionate love intensity (Aron et al., 2005). In line with evolutionary theory, infatuation and the associated, often demanding and wasteful behavior (Miller, 2000) rarely last much longer than until sexual reproduction has been achieved (Tallis, 2005a; Tallis, 2005b).

In the light of these considerations, passionate love might be suspected to deplete cognitive resources needed for the control of goal-directed behavior in everyday life. Effects of that sort have indeed been reported for the processing of high arousing emotional stimuli, which impairs cognitive control by exhausting resources shared with executive functions (Pessoa, 2009). Anecdotal evidence suggests that something similar may hold for passionate love. People who are madly in love may find it more difficult to concentrate on daily tasks like study and work, a feature that passionate love is proposed to share with mental disorders (Tallis, 2005b). However, until now, systematic empirical evidence for a link between passionate love and diminished executive functioning is lacking. We aimed to provide such evidence, if possible, by testing whether the individual efficiency in a standard cognitive-control task can be predicted by the intensity of passionate love exhibited by participants involved in the early stage of a romantic relationship.

This prediction might be tested by comparing performance of infatuated people to a control group of individuals who are not involved in a romantic relationship. However, given that the majority of people in late adolescence have a romantic relationship (Collins, Welsh, & Furman, 2009), this approach would inevitably result in distorted comparisons, e.g., by biasing the control group towards individuals with uncommon traits and inappropriate social skills to engage in relationships (which in itself may be related to altered executive functions; Beauchamp & Anderson, 2010). Moreover, this design would make insufficient use of the fact that individual differences in the intensity of passionate love is likely to account for a substantial part of the variance; indeed, people who are madly in love may show much stronger dysfunction in cognitive control than mildly loving people (cf. Tallis, 2005b).

Given these considerations, we decided to adopt a correlational approach that relates individual differences in infatuation to individual differences in control efficiency. We used the standard Passionate Love Scale (PLS), a questionnaire developed by Hatfield and Sprecher (1986) to quantify passionate love. Cognitive control was measured by versions of two classical conflict-inducing tasks: the flanker task (Eriksen & Eriksen, 1974) and the Stroop task (Stroop, 1992). These two tasks assess the individual ability to attend to relevant information while filtering out distracting, irrelevant spatial and verbal information, respectively. This allowed us to test whether the possible link between passionate love and cognitive control generalizes across tasks or whether it is task-specific. A balanced number of male and female subjects were included to test for generalizability across gender.

Method

Participants

Fifty-one healthy heterosexual students who had recently (at most 6 months ago) fallen in love participated either for payment or course credits. Based on initial screening of the behavioral data, eight participants were excluded from further analyses because of random performance during at least one of the experimental task blocks. The age range of the remaining 43 participants (23 females; 20 males) was 18 – 27 years (mean = 20.9 years), four participants were left-handed. All participants had a relationship with their beloved (mean duration = 2.8 months). The reported duration of being in love ranged between 1 and 6 months (mean = 3.4 months). All participants were Dutch native speakers, not color blind, and without a psychiatric history.

Tasks

Two variants of a classic cognitive control paradigm were used. The flanker task (Eriksen & Eriksen, 1974) consisted of centrally presented target stimuli which were vertically flanked on either side by two identical response-compatible or response-incompatible stimuli. The Stroop task (Stroop, 1992) consisted of a column of five identical stimuli presented in response-compatible or response-incompatible ink colors. Flanker and Stroop stimuli were carefully matched by using two non-overlapping sets of Dutch color words (“brown”, “gray”, “yellow”, and “red” or “purple”, “green”, “orange”, and “blue”). Each task used a counterbalanced unique set of four words. Two targets were mapped to a left hand response, whereas the other two targets were mapped to a right hand response.

E-prime™ software was used for stimulus presentation and response recording. All trials started with a fixation cross (randomly varying intervals of 800, 1000, or 1100 ms), followed by the stimulus, which was presented until response registration or, in the case of omission, for 1500 ms. In half of the trials the stimuli would call for different responses (incompatible condition; e.g., the word “green” surrounded by the words “yellow” in the flanker task and the word “blue” printed in red in the Stroop task) whereas in the other half identical target and distracter dimensions would call for the same response (compatible condition; e.g., the word “green” surrounded by the words “green” in the flanker task and the word “blue” printed in blue in the Stroop task). All trials were presented in an unconstrained random sequence. Stimuli appeared in lower-case in Arial bold font (3.5 cm wide and 5.4 cm high) and were presented on a grey background. Flanker-task stimuli used black ink color. Participants viewed the stimuli on a 17” monitor from about 60 cm.

Procedure

After giving informed consent, subjects received task instructions that emphasized both speed and accuracy. Both the flanker and the Stroop task were practiced in 16 trials that included performance feedback. Participants then filled out a Dutch translation of the PLS (a unidimensional scale that includes 30 items on a 9-points scale; Hatfield & Sprecher, 1986; Langeslag, Jansma, Franken, & Van Strien, 2007) and were instructed to develop a romantic mood by imagining and writing about an appropriate romantic event from their past or to focus on a romantic vignette they were given. During this 10-min period, subjects listened via headphones to their own favorite love-related music which they had brought with them. This procedure is known to evoke intense feelings of romantic love (Mashek, Aron, & Fisher, 2000). Participants then performed a block of 72 trials for each task. After a short, 3-min romantic mood booster (again using imagination and music), another block of each task was presented. The order of tasks was counterbalanced across participants. Participants rated their current mood state using a computerized affect grid (measuring mood valence and arousal; Russell et al., 1989) occasionally provided throughout the experiment.

Results

Correct reaction time (RT) and accuracy measures of interference were calculated for the Stroop and flanker tasks by subtracting average performance on compatible trials from average performance on incompatible trials. Both tasks produced robust RT interference scores (flanker task: 29 ms, $t(42) = 8.17$, $p < .001$; Stroop task: 38 ms, $t(42) = 5.24$, $p < .001$), indicating that they successfully induced decision conflict. These interference scores were submitted to a repeated-measures analysis of covariance (ANCOVA) using the factors Task (within subjects: flanker versus Stroop), Sex (between subjects: female versus male), and PLS-score (between-subjects covariate). As Figure 1 shows, higher PLS-scores were found to be a reliable predictor of interference effect increases ($F(1,39) = 5.18$, $p = .028$, MSE = 974.54, partial eta squared = .117), a correlation that was independent of Task ($F(1,39) = 1.252$, $p = .270$, MSE = 1263.70, partial eta squared = .031) and Sex ($F(1,39) = .147$, $p = .704$, MSE = 974.54, partial eta squared = .004). Main effects of Task and Sex or higher-order interactions were not observed either (Fs < 1.44). A predictive effect for PLS-score was not found for interference effects measured in accuracy ($F(1,39) = 0.26$, $p = .611$, MSE = .004, partial eta squared = .007), indicating that the RT results could not be accounted for by a speed-accuracy trade off. A separate analysis on overall RT showed that the effect of PLS on attentional interference could not be accounted for by a scaling effect due to RT slowing ($F(1,39) = 1.25$, $p = .270$). We re-ran analyses to ensure that the effects on interference were not exclusively driven by three particular PLS items that explicitly refer to obsessional thoughts and intrusive thinking (i.e., items 5, 19, and 21). A PLS sumscore that did not include these items, was also shown to be a reliable predictor of interference effect increases (F(1,39) = 5.22, p = .028, MSE = 972.63, partial eta squared = .118).

As control analyses, we also tested whether the effect of PLS on interference might have been mediated by mood effects. We analyzed average arousal and valence ratings (9-points scale) across ratings provided just before and after the task blocks. Arousal was positively associated with PLS scores (r = .326, p = .033), but not with the interference effect (r = .185, p = .235). Valence was not related to PLS (r = .019, p =.902) nor to interference (r = -.134, p = .393). This shows that arousal may share some variance with PLS scores, but that neither mood valence nor arousal played a reliable mediating role in the relation between romantic love and attentional interference.

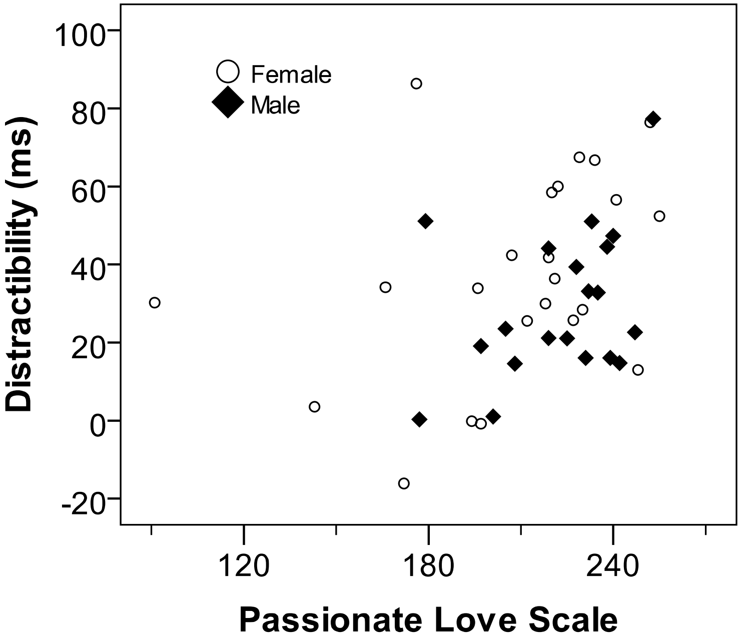

Figure 1. Positive correlation between Passionate Love Scale scores and distractibility as measured by a composite score of interference effects pooled across the Stroop and flanker tasks.

Discussion

This study provides the first evidence to suggest a systematic link between passionate love (as measured by the PLS) and impaired cognitive control (as measured by flanker and Stroop task performance). Passionate love was associated with increased distractibility in a sample of students involved in the early stage of a romantic relationship. This effect did not interact with the specific task employed, suggesting that intense passionate love is associated with a general loss of cognitive control. Furthermore, the link between passionate love and executive control was independent of gender, which implies that the underlying mechanism related to attraction probably does not interact with, or rely on sex-specific systems involved in attachment and sex drive (Fisher, 1998).

This finding is consistent with the assumption that infatuation becomes costly when daily life demands goal-directed behavior and cognitive control (Tallis, 2005b). It might be speculated that such effects are related to love-induced neurochemical effects. Elevated neurotransmitter levels, such as dopamine, have consistently been related to mating preference in animals (Fisher et al., 2006), and a recent study in humans has shown that PLS scores correlate positively with activity in the striatum (Aron et al., 2005). Increases in striatal dopamine are known to deplete prefrontal dopamine (Cools, 2008), which might have caused the impaired cognitive control observed. However, future research is required to corroborate such speculations.

Our study shows that passionate love, notwithstanding the positive feelings it is usually associated with, has negative effects for the goal-directed control of one's behavior. Such downsides of passionate love have long been suspected and anecdotal evidence traces back to ancient times (cf. Tallis, 2005b). We provided the first systematic empirical evidence suggesting that impaired cognitive control is an important characteristic of passionate love. The fact that love distracts people away from conventional civilized behavior motivated Plato even to depict love as a kind of madness, a possibility which psychologists should begin to take more seriously (cf. Tallis, 2005a).

Acknowledgments

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10

Discussion

"To every thing there is a season, and a time to every purpose under the heaven: A time to weep, and a time to laugh; a time to mourn, and a time to dance."

Ecclesiastes 3: 1 and 4, King James translation

The studies described in this thesis aimed to investigate how affect and motivation impact cognitive control. As summarized in Table 1 of Chapter 1, six out of the eight empirical studies found support for indirect effects on cognitive control, as measured with sequential trial-to-trial adaptations in cognitive control tasks. Only two studies resulted in evidence for a direct modulation of cognitive control. The implications of these results are discussed below. This chapter begins with a discussion of the sparse evidence found in our experimental work for direct effects of emotion on cognitive control, and of the question how the effects observed relate to earlier theorizing and empirical work in the field. This is followed by a summary of the abundant evidence for indirect effects on cognitive control, and a discussion of their implications. Next, on the basis of the neuroimaging data obtained, a theory about the neural mechanism that might be responsible for the indirect effects on behavior is proposed. A comment on the adaptive value of emotions concludes this chapter.

Direct effects of emotions

One important aim of this thesis was to investigate how emotions, as manipulated by short-term affect inductions, may directly improve or impair cognitive control. In Chapters 2 and 3 we reported that we did not find any evidence for a direct effect of positive and negative feedback on cognitive control in a flanker task. That is, contrary to existing theories (Fredrickson, 2001; Schwarz, 1990), we did not observe valence effects on attentional scope. The role of arousal was further investigated in the study described in Chapter 4. Here, we showed that in comparison to neutral pictures, negative high-arousing pictures with threatening content led to improved subsequent anti-saccade task performance, whereas positive high-arousing pictures did not produce this effect. Importantly, pupil dilation data confirmed that both positive and negative pictures successfully induced a state of increased sympathetic activation, so that the null-effect for positive pictures could not be attributed to an unsuccessful manipulation of emotional arousal.

Taken together, these studies using short-term affect manipulations confirm Derryberry and Tucker's (1994) interpretation of Easterbrook's (1959) hypothesis that high-arousal negative emotional states improve selective attention (Chapter 4). On the other hand, negative valence alone, as manipulated by feedback (Chapters 2 and 3), appears insufficient to modulate cognitive control directly, and hence contradicts theories by Schwarz (1990) and Fredrickson (2001) predicting valence-only effects. Interestingly, we did not observe that positive emotions led to reduced selective attention – even when these emotions induced physiological arousal – which supported neither valence-only theories (Fredrickson, 2001; Schwarz, 1990), nor the theory that positive arousal causes attentional broadening (Derryberry & Tucker, 1994).

It is interesting to note that recent findings from other studies also have consequences for earlier theorizing. Experimental work by Gable and Harmon-Jones (for a review, see Gable & Harmon-Jones, 2010b), has shown that positive emotions broaden attention only when they are accompanied by a low approach motivation (e.g., contentment), but that they will narrow attention when accompanied by a high approach motivation (e.g., desire). Similar effects have been observed for negative emotions: sadness, a negative emotion with low withdrawal motivation, broadens attention, whereas disgust, a negative emotion with high withdrawal motivation, narrows attention. Taken collectively these findings indicate that it is the motivational intensity as such, i.e., the strength of the drive to approach or avoid an object or goal, that determines one's attentional scope. Hence, as described by the motivational dimensional model (Gable & Harmon-Jones, 2010b) the degree of motivational intensity can be orthogonal to the dimension of motivational direction or affective valence. However, as motivationally intense states have been associated with greater sympathetic nervous system activation, they may often be reflected in arousal effects. Nonetheless, as has been carefully pointed out in earlier work (e.g., Kahneman, 1973), arousal is determined by several factors and does not necessarily constitute an index of motivational intensity. For example, amusement is a positive high-activating emotion, but unlikely to urge one to approach something in the environment (Gable & Harmon-Jones, 2010b). Indeed, our findings do not support the notion either that high-arousal positive emotions by themselves narrow attention.

If motivational intensity is indeed a better predictor of attentional narrowing than arousal or valence, the core affect model we used as a heuristic in our research needs to be replaced. Future studies, then, should make use of new dimensional frameworks that are better able to capture the fundamental affective processes driving focused attention, preferably those that have been shown to have a sound empirical basis. A recent study by Fontaine, Scherer, Roesch, & Ellsworth (2007) provides an excellent example of such an approach. These authors have shown that, besides the dimensions of valence and arousal, at least two other emotional dimensions can be identified, namely 'unpredictability' and 'potency / control'. Together, these four dimensions were shown to provide a very adequate description of emotional states across three different languages. The ‘potency / control’ factor may be of particular relevance for effects on attentional scope. This factor is characterized by action tendencies, such as wanting to take an initiative versus being apathetic. The description of this dimension actually comes close to the motivational intensity factor proposed by Harmon-Jones and Gable (2010b). Interestingly, this factor also captures parasympathetic forms of activation, and it might be argued that these effects are more important for motivation than the sympathetic activation usually associated with arousal (Fontaine et al., 2007).

The use of stimulus sets such as those validated by Fontaine et al. (2007) may also overcome another major shortcoming of previous studies. Some of the studies by Harmon-Jones and Gable apparently involved an ad-hoc inclusion of stimulus material, and it might be argued that the level of motivational intensity induced by these stimuli depends more on the introspective qualities of the researcher than on objectively measurable standards (cf. Friedman & Forster, 2011). For example, Gable & Harmon-Jones (2008) attribute different attentional focus effects induced by film clips showing scrumptious desserts versus clips presenting cats in humorous situations to differences in approach motivation. However, it has been argued that these obviously cute animals may induce a similar drive to approach them and hug, pet, or play with them, as the drive induced by the desserts to approach and eat them (as discussed by Friedman & Forster, 2011). For this reason, future studies should provide proper independent indices of motivational intensity. This is also important to ensure that the motivation intensity theory is falsifiable, and to prevent circular argumentation (e.g., observation: a stimulus narrows the attentional scope; conclusion: it apparently had motivational intensity).

Direct effects of mood?

In contrast to theories predicting that emotions and moods do not differ in the way they impact behavior (Derryberry & Tucker, 1994; Fredrickson, 2001; Schwarz, 1990), the Mood-Behavior-Model (MBM; Gendolla, 2000) states that moods do not have direct effects on cognitive effort. According to the MBM, moods, unlike emotions, are usually not related to any particular goal or object. Because of this, moods may lack the specific action tendencies and stable motivational implications that emotions have. Accordingly, mood may not have a direct effect on cognitive control, but may affect behavior in a context-sensitive, indirect way only. That is, the recruitment of effort depends on how a particular situational demand is evaluated, and affect regulates this appraisal. Our data are entirely consistent with this suggestion, as mood was found to have an indirect effect (see next section), but lacked a direct effect on cognitive control. This was repeatedly shown in our experiments. First, using a standard mood induction procedure that combined imagination with music, we found (Chapter 5) that neither mood valence nor arousal directly impacted cognitive control as measured in a flanker and Stroop task. In addition, we did not observe an interactive effect of valence and arousal, as would have been predicted by Derryberry and Tucker's framework. Similarly, we found (Chapter 6) that sustained positive affect induced by funny cartoons did not directly reduce cognitive control. Finally, depressive symptoms after ATD, a pharmacological manipulation known to induce depressed mood in this population of remitted depressive patients, were not associated with cognitive control deficits or improvements either, as described in Chapter 7.

Altogether, our null findings regarding direct mood effects suggest that the influence of mood on sustained effortful processing as measured in standard cognitive control tasks is limited. Thus, although under certain conditions (cf. Forgas, 1995) moods may have an effect on the way visual stimuli are judged on global versus local features, as measured in Navon tasks (e.g., Gasper & Clore, 2002; Gasper, 2004), this effect might be unrelated to effects on mental effort and cognitive control. This conclusion is also supported by studies showing that moods do not have direct effects on effort-related cardiovascular measures. Moreover, cumulative findings from other labs also show the lack of impact of mood states on direct measures of cognitive control (e.g., Finucane, Whiteman, & Power, 2010; Martin & Kerns, 2011; but see Mitchell & Phillips, 2007; Rowe et al., 2007).

It is important to note that affective states may still impair cognitive control via other, more cognitive, mechanisms. As has long been recognized, processing the emotion-inducing stimulus or problem and the elaborated task-irrelevant thoughts triggered by this stimulus, may deplete resources needed for cognitive control (Mitchell & Phillips, 2007; Schwarz, 1990). This effect may also explain the observation in Chapter 9 concerning passionate lovers who had only recently fallen in love. Participants reporting very high levels of passionate love showed worse performance on a Stroop and flanker task than participants reporting lower levels of infatuation. The extreme, almost obsessive, attention for the other characteristic for these high levels of infatuation may simply have depleted resources needed for cognitive control. However, mood scores in this study were not related to control impairment, which reinforces our conclusion that mood in itself seems not to have direct effects on cognitive control.

Indirect effects: a matter of valence

In contrast to the scant evidence for direct effects on cognitive control, our findings provide a great deal of support for indirect effects of emotional states on cognitive control. These effects occurred on trial-to-trial adaptation in cognitive control tasks involving a random presentation of compatible and incompatible trials. We found that conflict adaptation, the transient improvement of behavioral control after incompatible in comparison to compatible trials (Botvinick et al., 2001), was subject to affective regulation. We found that after incompatible trials, positive emotional states reduced and negative emotional states increased adaptation. These effects occurred for both short-term (Chapters 2 and 3) and long-term affect manipulations (Chapters 5, 6, and 7).

As shown in Chapter 2, short-term positive emotions were found to undo the adaptation triggered by previous conflict. This effect was observed in an arrow flanker task with monetary gain or loss as arbitrary feedback between trials. Unlike monetary loss, gain was shown to counteract conflict adaptation. This finding was replicated in the study described in Chapter 3. Consistent with the notion that effortful situations are aversive (Botvinick, 2007), our findings suggest that incompatible trials evoke a negative emotional state that, unless neutralized by a positive event such as a monetary reward, increases attentional focus. These data provide important initial evidence for the notion that affective valence may play a functional role in the transient adaptation of cognitive control, as measured in sequential effects of reaction time (Cabanac, 1992). They are in line with earlier findings that positive emotions can undo the aftereffects of stressful events (Fredrickson et al., 2000).

As described in the previous section, the MBM (Gendolla, 2000) expects that hedonic tone in sustained affective states predicts demand-driven adaptation. That is, conflict-driven adaptation of control may be improved by negative moods and reduced by positive moods. Several of our studies confirmed this prediction. In Chapter 5 this effect is illustrated in a study involving a flanker task, in which mood was induced using a standard induction procedure that manipulated not only affective valence but also arousal levels. We found that conflict-driven control was regulated only by affective valence. Using both funny and neutral cartoons, the study described in Chapter 6 replicated the effect that hedonic tone reduces conflict adaptation. Moreover, in the next study (Chapter 7) we demonstrated that depressive symptoms, induced by ATD in remitted depressive patients, were correlated with increased conflict adaptation. Taken together, these results strongly imply that hedonic tone regulates conflict adaptation: unpleasant states result in stronger adaptation, and pleasant states result in weaker adaptation.

According to the MBM, hedonic tone effects on demand-driven adaptation are impelled by the informational effect mood has on demand-related judgments. Thus, demands, as triggered by incompatible trials in our studies, are experienced as being more unpleasant and difficult when pleasure levels are low, and this evaluation may in turn drive improved effort mobilization. Although other studies have already found evidence for mood effects on subjective evaluation and effort-related cardiovascular measures (e.g., Gendolla, 2000; de Burgo & Gendolla, 2009), it remains an important aim for future research to integrate such measures with sequential analyses of performance on cognitive control tasks. Such an integrative approach may also enhance our understanding of situations in which adaptation to cognitive demands fails, for example with extremely difficult tasks. As illustrated in Chapter 8, conflict-adaptation effects are eliminated or reversed when task demands are extremely high. Pupil dilation also declined under high task demands, suggesting that demand-driven effort mobilization may drop under conditions of mental overload. How the assumed non-linearity between task demands and the mobilization of effort (Brehm & Self, 1989; Kahneman, 1973; Kukla, 1972) is related to conflict adaptation remains an important issue for further research. Future research into the question how the evaluation of demands influences physiological and neural responses associated with emotions, conflict monitoring, and effort may provide important insights into how these concepts are related.

Another topic for future research is the question how affective modulation of conflict adaptation is related to other measures of adaptation in cognitive psychology paradigms. For example, the conflict monitoring theory suggests that adaptation to demanding events has much in common with another type of adaptation, usually referred to as post-error adaptation (Botvinick et al., 2001): behavioral performance after an error is 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 regulation 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, McDonald, & Simons, 2004; Luu et al., 2000). However, whether effects on post-error slowing reflect an adaptive increase of cognitive control, as conflict adaptation does, has been the subject of serious debate. On the contrary, recent evidence suggests that it is more likely that post-error slowing reflects attentional capture which hinders subsequent performance (Notebaert et al., 2009). Consistent with the suggestion that post-error adjustments are maladaptive, post-error slowing is associated with steeper increases in negative affect and reduced task-focused coping in response to stressors in daily life (Compton et al., 2011).

Recent findings suggest that demand-driven adaptation occurs at a local level. That is, conflict adaptation improves cognitive control in similar tasks, but impairs flexible switching to other task sets (e.g., Notebaert & Verguts, 2008). Since we found that increased pleasure levels left sustained cognitive control unaffected while at the same time reducing conflict adaptation, we might suppose that this effect is adaptive when people have to flexibly switch between other tasks. Although future research will have to address this speculation, a link between positive affect and shifts toward more flexible behavior has indeed been documented earlier (Dreisbach & Goschke, 2004). Interestingly, the combination of the ability to sustain long-term goals with flexibility in the short-term implementation and adjustment of goals has been seen as characteristic of good self-management and self-regulation skills (Baumeister, Heatherton, & Tice, 1994). Thus, positive affect, reduced conflict adaptation, and self-regulation skills may be closely related. Future studies could investigate this possibility. Experience-sampling methods may for instance be used to understand the association between demand-driven adaptation as measured in the lab on the one hand, and the daily-life impact of stressors on motivation, negative emotions, and behavioral control on the other (cf. Compton et al., 2011). Investigating emotion effects on behavior in driving simulators is another way to further investigate the practical applications of our findings (cf. Pecher, Lemercier, & Cellier, 2009).

Neural mechanisms

Direct and indirect effects on cognitive control may reflect different modulatory mechanisms in the prefrontal cortex. On the one hand, direct improvement of cognitive control by emotional or motivational states may directly modulate the more lateral parts of prefrontal cortex, probably via subcortical regions that code the motivational intensity of such states. However, we did not study the neural mechanism of direct effects in this research project, so that this is left for future researchers to investigate. On the other hand, indirect effects may involve not only the lateral but also the more medial parts of the PFC, including the ACC (cf. Figure 1). As summarized below, two of the studies in our project provided direct insight into this neural mechanism.

In Chapter 3 we described evidence for a reward-related inhibition of conflict-related fronto-central theta activity in a flanker task. This neural response observed in the EEG accompanied the reward-driven reduction of conflict adaptation observed in the behavioral data. Consistent with intracranial recordings, this effect in theta power is likely to originate from the ACC and the surrounding medial frontal wall (Cohen et al., 2008). As predicted by the conflict monitoring theory (Botvinick et al., 2001), these data suggest that the ACC represents a signal that indicates the need for more cognitive control. Inhibition of this signal by reward may have counteracted subsequent behavioral adaptation. It seems possible that the opposing influences of conflict and reward that we observed reflect

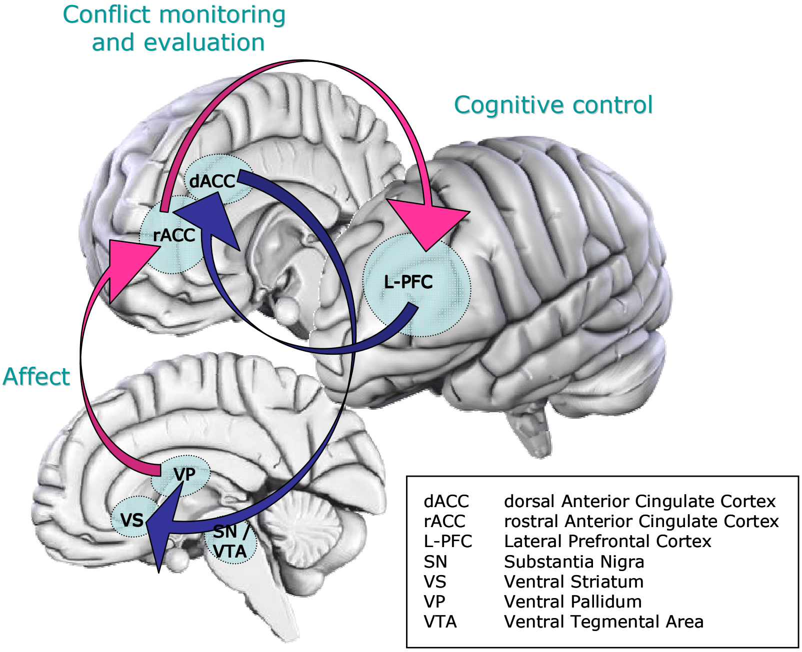

Figure 1. *Neural interactions involved in the indirect affective regulation of cognitive control*

some compensatory effects between conflict and reward at a neurotransmitter level. Consistent with this possibility, Holroyd and colleagues (Holroyd et al., 2008; Holroyd & Coles, 2002) have suggested that negative and positive events interact via dopamine modulation, which drives ACC activity. Conversely, there is also evidence suggesting that the ACC sends feedback signals down to the midbrain, via the striatum, to inhibits dopamine neurons (Frank, 2005).

The role of affective modulation in fronto-striatal interactions was investigated in an fMRI experiment, described in Chapter 6. As summarized in Figure 1, we found that funny cartoons increased neural activity usually associated with the processing of rewards, particularly in the ventral striatum (VS) and ventral pallidum (VP). Animal studies have shown that these basal ganglia (BG) regions include hedonic hotspots that may play a causal role in hedonic states. Reward-related BG activation, in turn, appeared to inhibit the neural response to conflict in a rostral ACC (rACC) region. Because activation in this region proved predictive of conflict-driven control improvement in the emotionally neutral context, it might play an important role in the affective appraisal of demands. Conflict monitoring activity in the dorsal ACC was co-modulated with this behavioral adaptation. Psycho-physiological interaction analyses confirmed functional interactions that were consistent with well-known anatomical connections looping between the VS and ACC through the VP (Alexander et al., 1986). On the basis of these findings we may hypothesize that the VP modulates rostral ACC activation, which in turn drives conflict-driven control. The resulting adaptation is subsequently registered in the dorsal ACC, which then sends feedback signals back to the VS. Within the striatum this feedback signal may become integrated with information concerning the current affective state. One might speculate that the reciprocal loops between the BG and ACC involve different neurotransmitter systems. More specifically, the feedback loop via the dACC and VS is likely to involve dopaminergic mediation, whereas the pleasure-related modulation in the VP and rACC may also involve endogenous opioid modulation (cf. Kringelbach & Berridge, 2009).

An important challenge for future research is to understand the different time scales at which reciprocal interactions between regions identified in this BG-PFC network occur. For example, neural regions coding the hedonic state of an organism may involve tonic signaling, whereas the more short-lived evaluation of incoming events and the associated emotions require faster signaling. Moreover, to ensure constant optimization of the internal homeostatic balance, these signals need to become integrated. However, given the temporal and spatial limitations of neuroimaging techniques a better understanding of these temporal dynamics requires other techniques. Studies using intracranial recordings may be an important tool to gain a better understanding of the temporal dynamics of these networks (cf. for instance Pourtois et al., 2010).

Because neither fMRI nor EEG are able to provide information about the particular neurotransmitters involved, the exact neurochemical basis of affective and motivational regulation requires further investigation. As indicated above, the neural circuitry indentified may involve dopamine and opioid modulation. Nonetheless, the exact role these systems play is not clear. Results from animal studies, for example, have suggested that dopamine is primarily related to motivational aspects, whereas the opioid system is involved in the hedonic aspects of emotions (Barbano & Cador, 2007; Kringelbach & Berridge, 2009). On the basis of this distinction one might propose that direct effects on cognitive control – possibly reflecting motivation – primarily involve dopamine, whereas indirect effects – sensitive to hedonic value – may reflect opioid modulation. To be sure, this is an oversimplified picture. Even within the same neural region or system different neurons have been shown to play different roles. For example, some midbrain dopamine neurons encode motivational values, while others encode motivational salience. These different sets of neurons are assumed to be connected with distinct brain networks, each with its own role in motivational control (Bromberg-Martin, Matsumoto, & Hikosaka, 2010). Similarly, pain and pleasure hotspots have been found in closely adjacent regions in the VS and VP, and release of endogenous μ-opioids is not limited to pleasant events, but can also be observed for painful stimuli. Moreover, the different time courses of neurotransmitter systems cannot be measured by the same technique, making it difficult to compare findings and pin down the actual mechanisms involved. Lastly, the opioid and dopamine systems do not work in isolation but interact with each other in complex, yet ill-understood ways (Leknes & Tracey, 2008).

Taken together, our neuroimaging findings are in line with predictions from the 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 effects of emotions on cognitive control probably involve the modulation of ACC activity via reward-related processing in the BG. However, the exact temporal dynamics and neurochemical basis of this neural circuitry needs further study.

Outlook: the adaptive role of emotions

One of our main conclusions in this dissertation is that hedonic tone helps to counteract the impact of adverse events on the brain and on our behavior. Consequently, positive emotions may help to reduce the impact of stressors and daily hassles, and play an adaptive role in our daily life. From this perspective we may say that our work contributes to the rapidly growing body of psychological literature stressing the beneficial effects of positive feelings. In line with predictions from the broaden-and-build theory (Fredrickson, 2001), numerous studies have shown that positive affect broadens people's thought-action repertoires, and allows individuals to build vital social, physical, and cognitive resources. This line of research follows numerous self-help books, courses, and magazines reflecting the current *Zeitgeist*, which assumes happiness is essential to human flourishing (cf. Seligman & Csikszentmihalyi, 2000).

However, it is important to note that one cannot say that positive affect is always a good thing, whereas negative affect is always a bad thing (Gruber, Mauss, & Tamir, 2011). On the contrary, emotions typically arise as an adaptive response to a particular situation, and as shown in this dissertation negative emotions may also play an important role in improving cognitive control. Thus, hedonic tone may become dysfunctional when a quick adaptation to a dangerous or difficult situation is needed, whereas it can be adaptive in safe situations in which such adaptation is useless. For example, a positive mood might actually impair driving behavior when a maneuver of a vehicle in front of you calls for enhanced control, whereas it may help you to stop being obsessed by a small but annoying computer error when you are on holiday. Likewise, a depressive episode may initially help to prioritize solving the problem that triggered it (Andrews & Thomson, 2009), but after the situation has taken a favorable turn sustained depression will become maladaptive. Thus, the adaptive value of emotions simply depends on their context and their extent. When things are going well, positive emotions can help people to be flexible, increasing resources and form or strengthen social bonds. However, in problematic situations the experience of negative emotions may offer important benefits that positive emotions do not (Gruber et al., 2011).

In conclusion, although the pursuit of happiness is an important component of the good life, there are times when it is better to accept our negative emotions or even let them help guide our behavior. Beneficial emotion effects are not limited to cognitive control, but may also facilitate more complex functions such as those needed in social situations. For example, it has been suggested that expressing negative emotions, such as anger, can be instrumental in social situations involving negotiation (Gruber et al., 2011; Tamir, Mitchell, & Gross, 2008). Moreover, emotions are not “passions”, i.e., “most of our emotions, most of the time, are not entirely beyond our control” (Solomon, 2007, p. 190). On the contrary, people can actively regulate their emotions (Cornelius, 2006; Ochsner & Gross, 2005) and may even make strategic use of them (Tamir, Chiu, & Gross, 2007). Finally, as already indicated long ago by the Greek philosopher Aristotle (Aristotle, 2009), happiness is more than pleasure: life satisfaction and meaning, too, are important ingredients of the good life (Leknes & Tracey, 2008; Waterman, 1993). Notably, when experienced as meaningful, even the most painful events may become rewarding (Leknes & Tracey, 2008). How exactly people find meaning in the pain and pleasures of everyday life is an essential question that only recently has started to be investigated scientifically (Flanagan, 2007; Kesebir & Diener, 2008; Seligman & Csikszentmihalyi, 2000). Formulating answers to this question is crucial to gaining a rich and deep understanding of the intricate link between emotions, well-being, and goal-directed behavior.

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Samenvatting

De drijfveer tot beheersing: Hoe affect en motivatie cognitieve controle beïnvloeden

Helpen emoties in een situatie die vraagt om mentale inspanning? Dat is de centrale vraag die dit proefschrift probeert te beantwoorden. In een moeilijke situatie is cognitieve controle nodig om de aandacht te richten op belangrijke informatie en om irrelevante informatie juist te onderdrukken. In een serie psychologische experimenten is onderzocht hoe affect en motivatie deze cognitieve controle beïnvloeden en welke psychologische processen en neurale mechanismen hieraan ten grondslag liggen.

Om de mate van cognitieve controle te kunnen berekenen heeft het onderzoek beschreven in dit proefschrift gebruikt gemaakt van laboratoriumtaken, zoals de Stroop taak. Deelnemers die de Stroop taak uitvoeren moeten telkens reageren op de inktkleur van het woord terwijl ze het geschreven woord zelf moeten negeren. Het is bekend dat reacties op de Stroop taak vaker traag en fout zijn wanneer deelnemers bijvoorbeeld moeten reageren op de rode inktkleur van het woord "groen" (een zogenaamde incompatibele trial), dan wanneer deze kleur vergezeld gaat van hetzelfde woord "rood" (compatibele trial). Het verschil in reactietijden op incompatibele versus compatibele trials geeft de mate van interferentie (afleiding) van het woord aan. Door dit interferentie-effect te meten kan worden onderzocht hoe affect en motivatie de mate van afleiding door irrelevante informatie beïnvloeden.

Omdat compatible en incompatibele trials normaal gesproken in een willekeurige volgorde worden gepresenteerd, maakt de Stroop taak het ook mogelijk om naar volgorde-effecten in taakprestaties te kijken. Het zogenaamde conflictadaptatie-effect laat zien dat mensen over het algemeen geneigd zijn beter te presteren als men zojuist nog goed op een moeilijke, incompatibele (conflict) trial heeft gereageerd. Over het algemeen zijn mensen dus geneigd zich mentaal sterker in te spannen nadat ze een moeilijke situatie hebben meegemaakt. Ook dit conflictadaptatie-effect kan door affect of motivatie worden beïnvloed. In dit proefschrift wordt onderscheid gemaakt tussen directe en indirecte beïnvloeding. Effecten op interferentie worden 'direct' genoemd omdat ze een aanpassing van algemene, volgehouden mentale inspanning betreffen. Effecten op conflictadaptatie worden 'indirect' genoemd, omdat de modulatie hier afhangt van de context, in dit geval de waargenomen moeilijkheid van de situatie.

In het onderzoek dat is beschreven in dit proefschrift zijn interferentie en conflictadaptatie-effecten gemeten in de Stroop taak en vergelijkbare cognitieve-controle taken. Deze taken zijn gecombineerd met een experimentele manipulatie van affect en motivatie bijvoorbeeld door gebruik te maken van geldbeloning of –straf, stemmingsinductie met muziek, of emotioneel-geladen plaatjes.

Tabel 1 geeft een overzicht van de acht empirische hoofdstukken en de daarbij gebruikte taken en manipulaties. Ook zijn de hoofdbevindingen beschreven die hieronder, na een theoretische inleiding, verder zullen worden uitgewerkt.

Directe effecten

Verschillende psychologische theorieën suggereren dat het interferentie-effect, gemeten in bijvoorbeeld de Stroop taak, door affect kan worden beïnvloed. Sommige theorieën voorspellen dat, in vergelijking met negatieve emoties, positieve emoties leiden tot meer interferentie van afleidende informatie en minder mentale inspanning. Andere theorieën suggereren dat niet alleen de emotionele valentie – bijv. of een emotie positief of negatief is – maar ook het activatie-niveau – de (fysiologische) opwinding op dat moment – een rol speelt. Bovendien zou de tijdsduur van de affectieve toestand een belangrijke factor kunnen zijn: terwijl kortdurende emoties meestal gepaard gaan met een bepaalde motivatie om een situatie te benaderen of juist te ontvluchten, hebben langer durende stemmingen een veel minder duidelijke motivationele component. Verder treedt de invloed van affect op cognitieve controle waarschijnlijk niet altijd op. Doordat emotionele stimuli zelf ook verwerkt moeten worden is het mogelijk dat dit de beschikbare cognitieve capaciteit beperkt, waardoor mensen gevoeliger worden voor afleiding op de taak. Welke factoren precies een rol spelen bij de directe emotionele beïnvloeding van cognitieve controle is nog niet voldoende onderzocht en het onderzoek beschreven in dit proefschrift probeert daarop een antwoord te formuleren.

De empirische hoofdstukken in dit proefschrift geven slechts beperkt bewijs voor directe effecten van emotie op cognitieve controle. Zo wordt er in hoofdstuk 2 en 3 aangetoond dat positieve en negatieve feedback in een flanker taak (een variant van de Stroop taak) niet een direct effect heeft op cognitieve controle. De resultaten in hoofdstuk 4 daarentegen, laten zien dat een negatieve emotie gekoppeld aan een hoog activatie-niveau (zoals gemeten met pupil dilatatie) wel zorgt voor verbeterde cognitieve controle, terwijl een vergelijkbaar hoog-activerende positieve emotionele toestand niet dit effect heeft. Deze resultaten zijn

Tabel 1. *Overzicht van de empirische hoofdstukken*

Deel / Hoofdstuk	Taak	Manipulatie / Instrument	Maat	Effect	Hoofdbevinding
Deel I. Emoties en cognitieve controle:					
2. Beloning en conflictadaptatie	Flankertaak	Geldbeloning en –straf	Manuele RT	indirect	Winst (vs. verlies) vermindert conflictadaptatie
3. De Elektrofysiologie van beloning en conflictadaptatie	Flankertaak	Geldbeloning en –straf	Manuele RT + EEG	indirect	Winst (vs. verlies) vermindert conflictadaptatie
4. Emotie, arousal en aandacht	Anti-saccadetaak	IAPS plaatjes	Oogbewegingen + Pupil dilatatie	direct	Negatieve (vs. neutrale) plaatjes verbeteren cognitieve controle
Deel II. Affect en cognitieve controle:					
5. Stemming en conflictadaptatie	Flanker- en Strooptaak	Stemmingsinductie	Manuele RT	indirect	Positieve (vs. negatieve) stemming vermindert conflictadaptatie
6. Humor en conflictadaptatie: een neuraal mechanisme	Flankertaak	Grappige cartoons	Manuele RT + fMRI	indirect	Positief (vs. neutraal) affect vermindert conflictadaptatie
7. Depressie en conflictadaptatie	Simontaak	Acute Tryptofaan Depletie	Manuele RT + Farmacologie	indirect	Depressieve stemming/ symptomen geassocieerd met versterkte conflictadaptatie
Deel III. Motivatie en cognitieve controle:					
8. Taak moeilijkheid en conflict adaptatie	Flanker- en Strooptaak	Taak moeilijkheid	Manuele RT + Pupil dilatatie	indirect	Toegenomen taakmoeilijkheid vermindert conflictadaptatie
9. Verliefdheid en conflict adaptatie	Flanker- en Strooptaak	'Passionate Love Scale'	Manuele RT	direct	Intensiteit van verliefdheid geassocieerd met verminderde cognitieve controle

vooral consistent met het 'motivational dimension model' van Gable en Harmon-Jones dat voorspelt dat emotionele toestanden met een hoge motivationele intensiteit zorgen voor een verbeterde aandachtsfocus. Onze bevindingen ondersteunen echter niet de theorieën die verbeteringen van aandachtsfocus toeschrijven aan alleen valentie of alleen activatie. Welke rol motivatie precies speelt bij de emotionele modulatie van cognitieve controle is een belangrijke vraag voor vervolgonderzoek.

In tegenstelling tot de emotie-effecten beschreven in hoofdstuk 4, laten de experimenten die gebruik maken van affect manipulaties met een langer durend effect (beschreven in hoofdstuk 5, 6 en 7) geen direct effect op cognitieve controle zien. Deze resultaten komen overeen met het 'Mood-Behavior-Model' van Gendolla dat indirecte maar geen directe effecten van stemming op mentale inspanning voorspelt. In hoofdstuk 9 wordt bovendien aangetoond dat andere factoren dan affect ook een effect kunnen hebben. In deze studie naar de invloed van verliefdheid op cognitieve controle werd een positief verband gevonden tussen het interferentie-effect en de intensiteit van de verliefdheid die gerapporteerd werd. Aangezien er geen relatie was met de gerapporteerde stemming, wordt dit verband mogelijk het best verklaard door de invloed van niet-emotionele factoren. Zo zouden verliefde mensen hun cognitieve capaciteit mogelijk vooral gebruiken om te kunnen denken aan de geliefde in plaats van zich te concentreren op een lastige laboratoriumtaak.

Indirecte effecten

In tegenstelling tot de zogenaamde directe effecten zijn de effecten van emotie en motivatie op het zogenaamde conflictadaptie-effect in het verleden minder vaak onderzocht. Deze indirecte effecten zouden kunnen ontstaan doordat de aanpassing van cognitieve controle na een conflict trial gepaard gaat met negatieve emoties die worden opgeroepen door deze moeilijke situatie. Aangezien eerder onderzoek heeft laten zien dat het effect van stressvolle situaties teniet kan worden gedaan door positieve emoties, zou een dergelijk effect ook op conflictadaptatie van toepassing kunnen zijn. Zoals voorspeld door het 'Mood-Behavior-Model' kunnen op een vergelijkbare manier langetermijn-effecten optreden. Inderdaad laten experimenten vaak zien dat mentale inspanning na een moeilijke situatie wordt afgezwakt door een positieve stemming, een proces waardoor dus ook conflictadaptatie zou kunnen worden gereduceerd. Omgekeerd zou een negatieve stemming het conflictadaptatie-effect kunnen vergroten.

In dit proefschrift is inderdaad veel bewijs gevonden voor een affectieve invloed op het conflictadaptatie-effect. Zo zorgt een positieve feedback gekoppeld aan een geldbeloning (zie hoofdstuk 2 en 3) voor verminderde conflictadaptatie. Deze bevinding suggereert dat positieve emoties de negatieve gevolgen van conflict teniet kunnen doen waardoor een aanpassing in gedrag uitblijft.

Overeenkomstig de voorspellingen van het ‘Mood-Behavior-Model’, wordt in hoofdstuk 5 en 6 aangetoond dat positief affect opgeroepen door middel van een stemmingsinductie (hoofdstuk 5) of grappige cartoons (hoofdstuk 6) leidt tot verminderde conflictadaptatie. Hoofdstuk 7 laat zien dat depressieve symptomen, geïnduceerd met Acute Tryptofaan Depletie in een groep deelnemers hersteld van een depressie, juist geassocieerd zijn met toegenomen conflictadaptatie. Concluderend: deze bevindingen laten een valentie-effect zien; onplezierige stemmingen leiden tot toegenomen conflictadaptatie en plezierige stemmingen leiden juist tot verminderde conflictadaptatie.

Een van de uitdagingen voor toekomstig onderzoek is om metingen van conflictadaptatie te integreren met cardiovasculaire maten van mentale inspanning. Nader onderzoek is ook nodig om de randvoorwaarden waaronder het conflictadaptatie-effect optreedt beter te begrijpen. Zo wordt in hoofdstuk 8 beschreven dat het conflictadaptatie-effect kan verdwijnen of zelfs omdraaien als een taak te moeilijk wordt. Dit effect is al eerder beschreven in de mentale-inspanningsliteratuur die suggereert dat er een niet-lineair verband is tussen taak moeilijkheid en mentale inspanning gemeten met cardiovasculaire maten: mensen geven verdere inspanning op als een taak te moeilijk wordt. Het is interessant om nader te onderzoeken hoe deze effecten samenhangen met fysiologische en neurale reacties op emoties en cognitieve conflicten. Er is ook meer onderzoek nodig om het verband met controle aanpassingen in andere laboratoriumtaken en het dagelijks leven te onderzoeken.

Neurale mechanismen

Naast de effecten op gedragsaanpassingen, is ook onderzocht hoe affect en cognitieve controle de verwerking in de hersenen beïnvloedt. Volgens de zogenaamde 'conflict monitoring theory' van Botvinick en collega's speelt de 'cortex cingularis anterior' (meestal afgekort als ACC) een belangrijke rol bij het registreren van moeilijke situaties en het signaleren van de behoefte aan een toename van mentale inspanning. Vooral de laterale gedeelten van de prefrontale cortex gebruiken dit signaal om cognitieve controle te versterken. Terwijl controleprocessen zich vooral in de hersenschors afspelen, worden positieve emoties juist vooral verwerkt in de meer subcorticale gebieden van het brein, met name in de basale kernen en de middenhersenen. Deze gebieden spelen mogelijk een belangrijke rol in het aanpassen van controle processen doordat ze een regulerende werking hebben op de prefrontale cortex. Neurotransmitters zoals dopamine, serotonine en endogene opioïden spelen daarbij een belangrijke rol.

Twee studies hebben de neurale mechanismen van de invloed van emotie op conflictadaptatie onderzocht. In hoofdstuk 3 is beschreven hoe, vergeleken met negatieve feedback, effecten van positieve feedback gemeten in het EEG samenhangen met de verminderde gedragsaanpassing na conflict. De waargenomen modulatie in oscillaties (binnen de zogenaamde 'theta-band') suggereert dat het conflictsignaal in de ACC inderdaad kan worden geremd door geldbeloning. Mogelijk is deze inhibitie verantwoordelijk voor de waargenomen aanpassing in gedrag op de volgende trial.

Hoofdstuk 6 beschrijft een fMRI studie waarbij grappige cartoons het subcorticale beloningssysteem van het brein activeren, dat vervolgens de reactie van de ACC op conflict doet verminderen. Aanvullende analyses suggereren neurale communicatie tussen de ACC en de beloninggebieden, die weer door de affectieve context wordt beïnvloed. Toekomstig onderzoek is nodig om de temporele dynamiek van deze neurale interacties beter te begrijpen.

Een belangrijke, helaas onbeantwoord gebleven vraag is welke neurotransmitters verantwoordelijk zijn voor de affectieve beïnvloeding van cognitieve controle. Er kan worden gespeculeerd dat het directe effect op cognitieve controle door motivatie vooral gerelateerd moet worden aan het dopamine systeem. Anderszijds worden indirecte effecten op cognitieve controle, die vooral door emotionele valentie worden gereguleerd, mogelijk beter verklaard door een modulatie via endogene opioïden. Het is een grote uitdaging voor toekomstig onderzoek om de rol van deze neurotransmitter systemen beter te begrijpen.

Conclusie

In een breder perspectief geplaatst, laat het onderzoek beschreven in deze dissertatie vooral zien dat een plezierige emotionele toestand de invloed van nare situaties tegengaat. Deze conclusie past bij onderzoek geïnspireerd door de recente 'positieve psychologie' stroming in de psychologie. Volgens deze stroming zijn positieve emoties belangrijk voor een gezond en goed leven. Hoewel positieve emoties inderdaad vaak gewenst zijn en een functionele rol spelen is het echter onjuist te concluderen dat positieve emoties te allen tijde goed zijn en negatieve emoties te allen tijde slecht. Zoals dit proefschrift heeft laten zien, zijn emoties vaak adaptieve reacties op een bepaalde omgeving. Daardoor kunnen negatieve emoties bijvoorbeeld helpen bij mentale inspanning voor een belangrijke taak, terwijl een positieve stemming in een gevaarlijke situatie wel eens disfunctioneel zou kunnen zijn. Of emoties functioneel zijn hangt dus uiteindelijk af van de specifieke situatie en de tijdsduur van de emotionele reactie.

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Curriculum Vitae

Henk van Steenbergen was born in Gorinchem on the 16th of September 1981. He attended secondary and higher technical education (Electrotechnology) in Gorinchem and Den Haag. From 2002 to 2007, he studied Psychology and Philosophy at Leiden University. He received his Bachelor's degree Psychology (cum laude) in 2005 and his Bachelor's degree Philosophy of Psychology in 2007. After completing his Psychology Research Master thesis on a functional magnetic resonance imaging (fMRI) study on action-effect learning, he graduated cum laude in September 2007.

From 2007 to 2011, he did his PhD research which was supervised by dr. Guido Band and prof.dr. Bernhard Hommel (Cognitive Psychology, Leiden University & Leiden Institute for Brain and Cognition). This research focused on the influence of affect and motivation on cognitive control. He used behavioral, physiological, and neuroimaging techniques to study the neurocognitive mechanism of this regulation. The results of his PhD research are described in this thesis.

Henk van Steenbergen is currently working as an assistant professor at Leiden University. Here, he continues to work with prof.dr. Bernhard Hommel. Together with prof.dr. Reinout Wiers and dr. Sanne de Wit (University of Amsterdam) he is going to investigate the cognitive and motivational components of decision making in relation to dopamine and addictive behavior.

List of Publications

Articles submitted or in preparation:

van Steenbergen, H., Band, G.P.H., & Hommel, B. (submitted for publication). Reward counteracts conflict-driven attentional adaptation: Electrophysiological evidence. **(Chapter 3)**

van Steenbergen, H., Band, G.P.H., Hommel, B., Rombouts, S.A.R.B., & Nieuwenhuis, S. (submitted for publication). Keep smiling! Humor reduces neurocognitive adjustments to conflict. **(Chapter 6)**

van Steenbergen, H., Band, G.P.H., & Hommel, B. (in preparation). Dynamic control adaptations depend on task difficulty: Evidence from behavior and pupillometry. **(Chapter 8)**

van Steenbergen, H., Langeslag, S.J.E., Band, G.P.H., & Hommel, B. (submitted for publication). Reduced cognitive control in passionate lovers. **(Chapter 9)**

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van Steenbergen, H., Band, G.P.H., & Hommel, B. (2011). Threat but not arousal narrows attention: Evidence from pupil dilation and saccade control. *Frontiers in Psychology, 2: 281*. **(Chapter 4)**

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