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

Steenbergen, H. van

Citation

Steenbergen, H. van. (2012, January 17). *The drive to control : how affect and motivation regulate cognitive control*. Retrieved from https://hdl.handle.net/1887/18365

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).

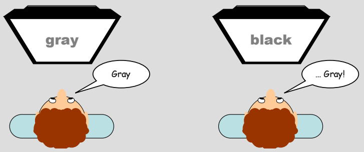
Affective valence and cognitive control

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

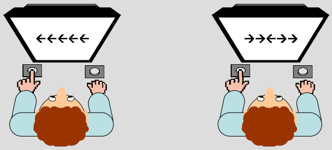
Box 1: Cognitive control paradigms

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).*

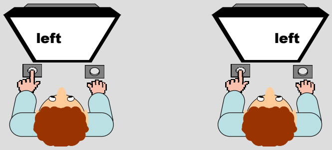
A. Stroop task



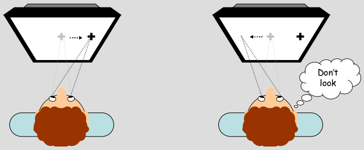
B. Flanker task



C. Simon task



D. Anti-saccade task



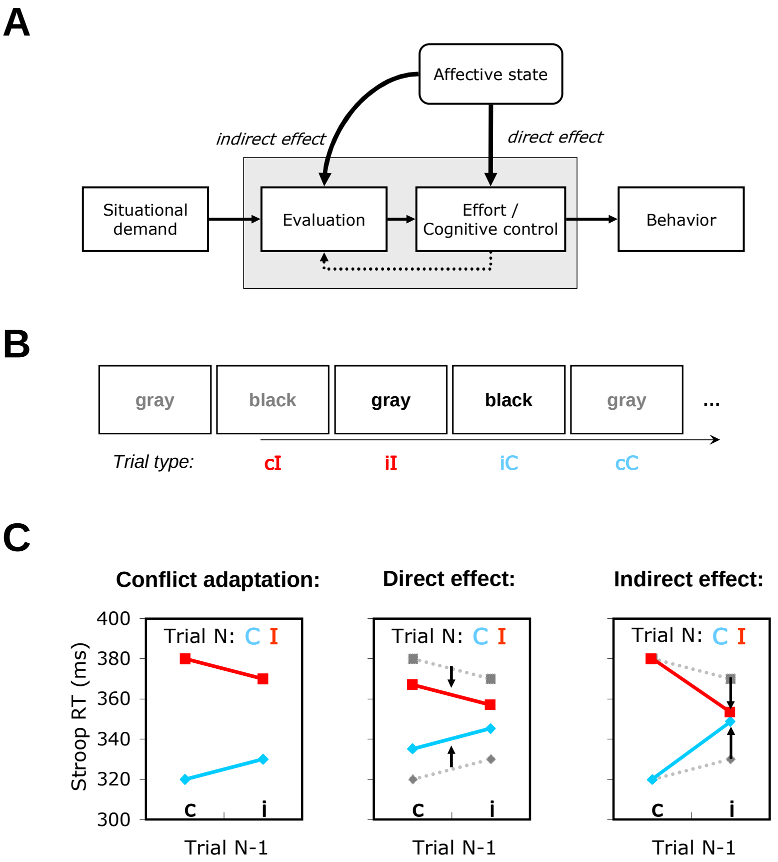


Figure 1. A. *Demands drive behavior via the mobilization of effort and cognitive control. Affective states may influence effort and cognitive control either directly or indirectly. Whereas direct effects can have immediate consequences for behavior, indirect effects are mediated via the evaluation or 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

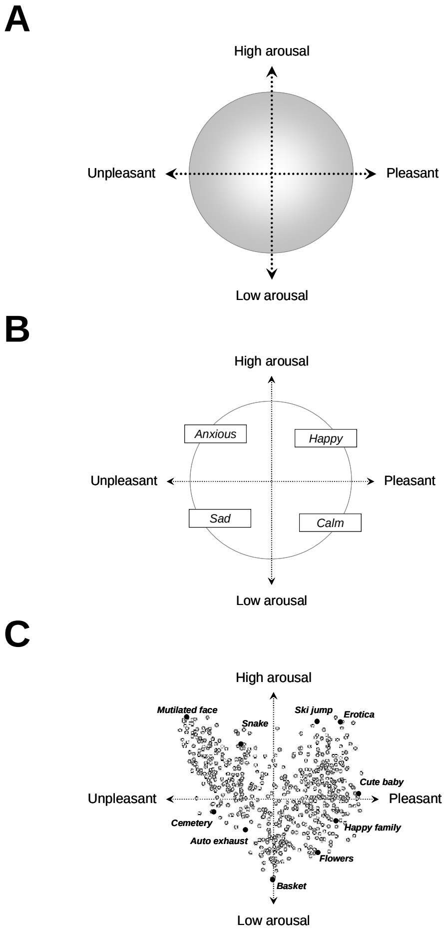


***Figure 2. A**. Core affect as defined by a Cartesian space that includes the dimensions valence and arousal. **B.** Core affect as reflected in possible mood states. **C.** Core affect as reflected in emotional states induced by pictures from the IAPS set*

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).*

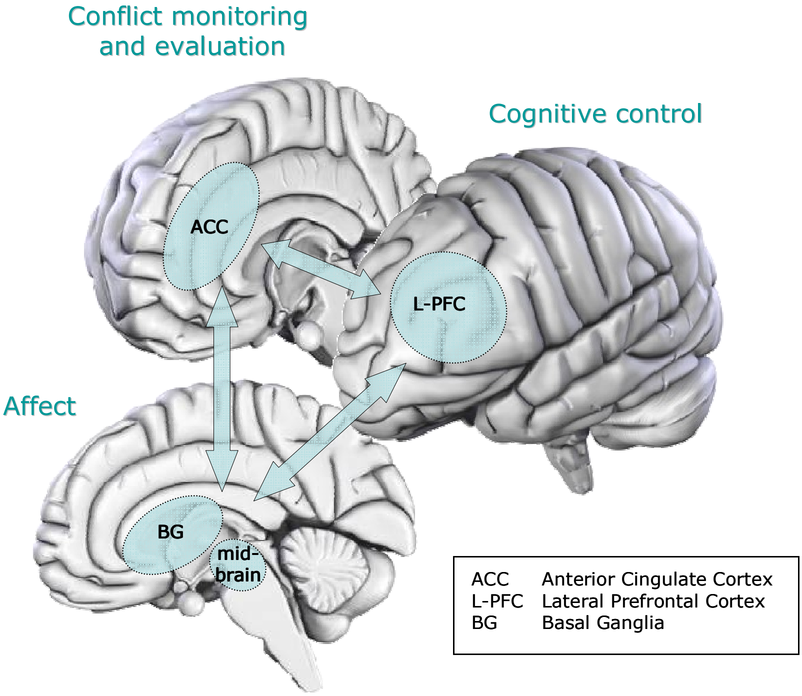


Figure 3. *Brain areas involved in the interactions between affect and cognitive control.*

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