

INFLUENCE OF POSITIVE EMOTION ON ATTENTIONAL BREADTH:

AN EXPERIMENTAL APPROACH

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Influence of positive emotion on attentional breadth: An experimental approach

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GENERAL INTRODUCTION

Imagine you are sitting on the beach, watching the sunset with a warm breeze on your skin and a cocktail in your hand. Or imagine seeing your child happily play in the garden with friends on a sunny day in spring. Experiencing such moments might fill you with joy, but can this happiness also influence the way you actually perceive the sunset or the scene of your playing child? While it has become widely accepted that how you perceive the world can influence the way you feel, an idea reflected in cognitive reappraisal, mindfulness exercises and other therapeutic techniques, much less is known about whether and how the way you feel can shape your perception. Presumably, emotion and mood are not simply byproducts of the mind that add a specific color to perception, but they may dynamically alter it. In this PhD project, we investigated if and how positive mood can change the way people select, inhibit and attend to specific visual information in their environment, as well as if it may change their thinking style. For example, when feeling happy, you might have many (and often original) research ideas, come up with interesting interpretations of your new empirical results, or experience a rewarding ‘flow’ when writing a manuscript (Csikszentmihalyi, 1999). By contrast, when you feel rather neutral, you may not experience such broadening of the action-thought repertoire and boost in creative thinking. Although we might intuitively associate a change in creative thinking to the transient experience of positive mood, it is likely that this specific affective state already influences more fundamental cognitive processes, including selective attention and inhibition. Moreover, gains in general cognitive functioning and well-being associated with positive mood might arise *thanks to* the modulation of such lower cognitive functions. These questions lie at the heart of this PhD project. Importantly, to gain a better insight into the modulatory effects of positive mood on cognitive functions is not only important in the context of cognitive and affective neuroscience, where research on negative affect still prevails. It might also contribute to our understanding of the conservation and improvement of mental health, as well as the prevention (and relapse) of mood disorders. If confirmed by empirical results, this framework might have a number of important implications for the prevention and treatment of disorders associated with a break-down in positive affect (e.g., anxiety and depression).

Evidence in favor of beneficial effects of positive affect on cognition and well-being mainly comes from the influential broaden-and-build theory (Fredrickson, 2001,

2004). This theory proposes that positive and negative emotions have opposite but complementary functions on information processing: whereas negative emotions narrow attention, cognition and the behavioral repertoire, positive emotions broaden them. According to this theory, the broadened attention and cognition associated with positive affect contributes to the 'building' of long-term personal resources over time (Fredrickson, Cohn, Coffey, Pek, & Finkel, 2008), on a psychological (Cohn, Fredrickson, Brown, Mikels, & Conway, 2009; Fredrickson, Tugade, Waugh, & Larkin, 2003; Tice, Baumeister, Shmueli, & Muraven, 2007), intellectual (Isen, 2000), physical (Burton & King, 2009), and social level (Gable, Gonzaga, & Strachman, 2006; Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008). Moreover, the enhancement of personal resources makes future experiences of positive affect more likely, creating an upward spiral (Burns et al., 2008; Fredrickson & Joiner, 2002; Garland et al., 2010, see Fig. 1).

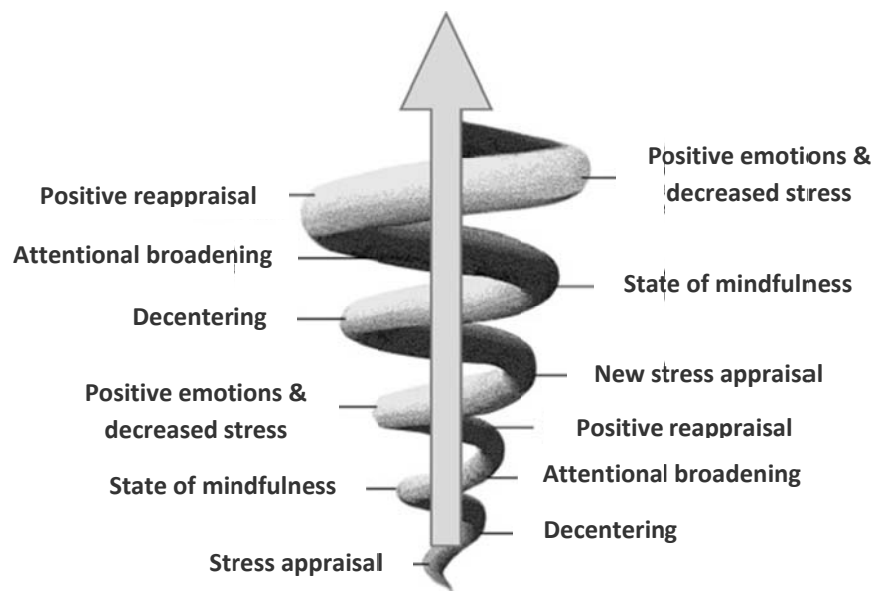


Figure 1. Upward spiral of positive emotions can counteract downward spiral of negative affect. Figure adapted from Garland, 2010

Positive emotions also stimulate resilience (Cohn et al., 2009; Ong, Bergeman, Bisconti, & Wallace, 2006; Philippe, Lecours, & Beaulieu-Pelletier, 2009; Tugade, Fredrickson, & Barrett, 2004), the ability to successfully adapt and recover from hardship (Rutten et al., 2013), contributing to an improved life quality (Cohn et al., 2009). Furthermore, positive mood can enhance mental and physical well-being by counteracting or 'undoing' the detrimental effects of the chronic experience of negative affect and stress, by stimulating emotion regulation and attentional disengagement

from negative information (Fredrickson, Mancuso, Branigan, & Tugade, 2000; Tugade & Fredrickson, 2004). Together, positive emotions and their broadening effects on cognition and behavior stimulate psychological resilience, adaptive coping, mental and physical health and well-being, and might even play a protective role against (relapse of) depression.

Depression is characterized by anhedonia (Pizzagalli, 2014) and is associated with both disturbances in positive mood regulation (Carl, Soskin, Kerns, & Barlow, 2013) and a lack of resilience against stress (Liu & Alloy, 2010; Southwick, Vythilingam, & Charney, 2005). Importantly, it is linked to a narrow scope of attention, memory, thinking and behavior (see Bar, 2009; Desseilles et al., 2009; Desseilles et al., 2011; Nettle & Bateson, 2012; Schmitz, De Rosa, & Anderson, 2009; Whitmer & Gotlib, 2012), and might involve disturbed sensory processing (Fitzgerald, 2013). Hence, it is plausible that positive mood could counteract negative affect and depression by broadening attention and building additional resources that could eventually be engaged to down-regulate the detrimental effects of stress. Strikingly, while several studies provided evidence for modulatory effects of positive mood on higher-order cognitive, resilience and well-being, the putative broadening of attention following the induction of positive mood has received very little empirical validation. A main goal of this dissertation was to establish whether the induction of positive mood in healthy adult participants could lead to a broadening of attention and early changes in visual perception.

In the following sections, we review empirical data and theoretical models related to this question. First, we focus on positive mood per se, its definition and how it is usually induced in standard laboratory conditions. In the second part, we briefly present and discuss several theories put forward in the affective sciences literature that make specific predictions regarding influences of (positive) mood and affect on selective attention and cognition. In the third section, we introduce and define attention, emphasizing the dominant taxonomy for dissociable attention components and delineating the role of positive mood therein. Finally, we outline the main research questions addressed in the five empirical chapters gathered in this dissertation.

1. POSITIVE MOOD

A major issue in the study of effects of positive mood on attention and cognition concerns the way feelings of happiness or pleasantness can be induced and sustained in healthy adult participants in a standard experimental setting. In the past, different mood induction procedures (MIPs) have been described in the literature. However, they reliably differed in their dependence on reward (processing), as well as the intensity of the induced mood. Moreover, mood can refer to multiple and different processes depending on the specific framework embraced by the authors. Hence, as a first step, we define what we refer to as ‘positive mood’ in the present case, how different or similar it is from reward, and describe it in terms of intensity and specificity of the emotional experience. Next, we give a brief overview of the different MIPs often used in the literature and we eventually introduce the MIP we have validated and used systematically throughout the experimental studies reported in this dissertation.

1.1. Defining positive mood

When considering mood, it is necessary to differentiate it from the constructs of affect and emotion, although they are often used interchangeably in the literature. Following Larsen (2000), we used the term ‘affect’ to refer to the experienced, evaluative feeling of moods and emotions, that can be either positive or negative, promoting approach or avoidance tendencies. The term ‘mood’ is used to indicate rather diffuse, low intensity and long-lasting affective states, not elicited by a specific event or object, as opposite to an ‘emotion’ (Beedie, Terry, & Lane, 2005; Gross, 1998; Larsen, 2000; Russell, 2003). Thus, although moods and emotions differ from each other, they can both be described in terms of their affective content. However, given that many more studies have been conducted for emotion than mood in the field, we focus in the next section on the former construct (and theories) to highlight its typical properties and underlying dimensions, which are thought to be shared with mood.

1.1.1. Dimensions of affect

Emotion is often described by positioning it along the dimensions of valence and arousal. In such a framework, valence and arousal are considered independent of each other (though often correlated), and conceived as continuous dimensions, ranging from

positive to negative and from sleepiness to aroused, respectively (Barrett, 1998; Russell, Weiss, & Mendelsohn, 1989). Support for such two-dimensional organization of emotion was found in the categorization of verbal responses (Barrett, 2004; Russell, 1979) and estimates of relatedness of affective words (Barrett & Fossum, 2001) along these dimensions, as well as in peripheral physiological responses and brain activity to emotional information (Anders, Lotze, Erb, Grodd, & Birbaumer, 2004; Colibazzi et al., 2010). Moreover, valence and arousal partly depend on the integrity of different neurotransmitter systems, with variations in positive valence relatively depending on the dopaminergic and the serotonergic system (Ashby, Valentin, & Turken, 2002; Berridge & Kringelbach, 2011; Helie, Paul, & Ashby, 2012; Mitchell & Phillips, 2007; Szily, Bowen, Unoka, Simon, & Kéri, 2008; Young & Leyton, 2002), and in arousal on the norepinephrine system (Aston-Jones & Cohen, 2005; Berridge, 2008; Berridge, Schmeichel, & Espana, 2012).

Alternatively, emotion can also be viewed in terms of approach or avoidance motivational drives (Cacioppo & Gardner, 1999; Lang & Bradley, 2010; Lang, Bradley, & Cuthbert, 1998). In this framework, positive emotions are usually associated with the motivation to approach rewarding stimuli, while negative affect can be paired with either tendency (e.g., anger is usually associated with approach while fear or sadness with avoidance). Moreover, emotions that are highly motivating are typically also arousing (Gable & Harmon-Jones, 2013), and thus stimuli aimed at inducing positive affect high in approach-motivation are often high in arousal too (Gable & Harmon-Jones, 2008, 2010b). Hence, arousal is an important confound in research on positive affect (Ashby et al., 2002; Gable & Harmon-Jones, 2013), although some positive emotions do not elicit the motivation to approach or avoid certain objects or situations, such as 'amusement' (Gable & Harmon-Jones, 2013) and 'contentment' (Fredrickson & Branigan, 2005). Importantly, this framework suggests that reward may be the evolutionary precursor of positive mood, and punishment of negative mood (Nettle & Bateson, 2012). From this perspective, motivation and valence are lumped together, with the activation of the approach-related motivational system primarily eliciting positive affect (or the other way around) whereas a defensive, withdrawal-related motivational reaction is associated with negative affect. The intensity of the activation

within the respective motivational system ultimately determines the level of arousal (Lang & Bradley, 2010).

1.1.2. *Positive mood vs. Reward*

Because emotion and motivation circuits are tightly intertwined, it is difficult to disentangle reward from positive affect as well as their respective underlying mechanisms (Ashby, Isen, & Turken, 1999; Kringelbach & Berridge, 2010). Some researchers previously advocated that they are two sides of the same coin and therefore can simply not be separated from one another. They argued that positive and negative emotions are elicited by rewarding and punishing reinforcing signals, respectively (Burgdorf & Panksepp, 2006; Rolls, 2000), and that the experience of emotions is a result of the activation of brain circuits specialized in coping with such signals (Lang & Bradley, 2010). Mood can be conceptualized as a reward system itself, biasing people to learn new contingencies, perform free associations and broaden their cognition (Bar, 2009), in line with research suggesting that acquiring information is inherently pleasant for humans and the presence of rewarding opioid receptors along sensory pathways (Biederman & Vessel, 2006). On the other hand, positive affect cannot be reduced to reward either, because it also encompasses a conscious subjective experience of emotion (Barrett, Mesquita, Ochsner, & Gross, 2007; Kringelbach, 2005). Moreover, neuroimaging studies showed different neural systems underlying separate aspects of positive affect. More precisely, 'wanting' would reflect the motivational aspect to acquire a reward, and 'liking' the subjective experience of pleasure (Berridge, 1996; Berridge, Kringelbach, & Valentin, 2008; Berridge, Robinson, & Aldridge, 2009). However, this reasoning does not deny the close ties between reward and positive mood, but rather posits that positive mood evolved from reward and therefore partially shares the same brain mechanisms (Funahashi, 2011; Kringelbach, 2010), in line with findings linking reward-sensitivity to positive emotionality (Tellegen, Watson, & Clark, 1999).

This idea also converges with older work and theories in neuropsychology, focusing on positive affect (Ashby et al., 1999). Inspired by research showing a link between positive mood on the one hand and the intake of dopamine (DA) stimulating drugs or naturally occurring endorphins on the other, Ashby and colleagues (1999)

proposed that positive affect is associated with an increased DA release by midbrain reward centra, especially the ventral tegmental area, affecting in turn widespread brain areas receiving DA projections, like the prefrontal cortex (PFC; see also Burgdorf & Panksepp, 2006). Hence, an increase in DA in the midbrain is thought to propagate its effects throughout the brain, evoking the experience of positive emotion, and ultimately affecting specific cognitive functions that share common neurobiological grounds (e.g., executive functions and working memory within the PFC; see Duncan, 2001). However, this theory overlooked the likely implication of other neuromodulator systems, besides DA, in both reward and positive affect (Berridge & Kringelbach, 2013; Berridge et al., 2009; Biederman & Vessel, 2006; Koeppe et al., 2009) and has actually received little empirical support.

Importantly, effects of positive mood on cognitive functions seem to be qualitatively different and dissociable from the influences of reward, suggesting the existence of partly non-overlapping brain systems for positive mood and reward. While interaction effects between these two systems have already been extensively investigated in the past (e.g., Johnson, Ruggero, & Carver, 2005; Martin-Soelch et al., 2009; Shankman, Klein, Tenke, & Bruder, 2007), no study to date directly compared effects of positive mood vs. reward on cognition and internal affective states of participants (Chiew & Braver, 2011). Independent lines of research show important methodological and theoretical differences between studies focusing on mood vs. on reward. For instance, experimental paradigms using reward usually imply the use of goal-directed behavior aimed at attaining specific rewards (see Lang & Bradley, 2010; Roseman, 2011). Hence, in studies assessing effects of reward on cognition, the reward is usually contingent on certain aspects of the task or the behavior of the participant. In contrast, positive mood is not closely associated with a specific goal, but rather reflects the preparation of the organism at a given moment in time for a multitude of actions (Roseman, 2011). Therefore, the modulatory effects of reward on behavior might be more intense and phasic (i.e. tightly bound to the rewarded task aspect), whereas positive mood is usually mild, lasts for several minutes or hours (i.e., tonic) and does not influence the intensity of task-involvement. Even though no study so far assessed the actual commonalities and differences in the propensity of positive mood vs. reward to influence specific cognitive functions, a recent review by Chiew and Braver (2011)

compared independent findings on emotion and reward to disentangle their respective influences on cognitive functions. These authors concluded that reward and positive affect can have similar, different or even opposing effects on various cognitive functions. One of the reasons accounting for this discrepancy might be the lack of specification regarding positive affect. Presumably, different kinds of positive mood are likely to exist (as is the case with negative emotions), some of which relying more than others on reward (Shiota et al., 2014). Other factors explaining this discrepancy are the differential time-course of the emotional response and the activation of additional brain structures in the case of positive mood, when compared to reward processing and its well-circumscribed functional neuro-anatomy (Chiew & Braver, 2011; Schultz, 2006; Wise, 2008).

1.1.3. Specificity of positive mood

The assumption of distinct emotions stems from the evolutionary theory of Darwin (1872), proposing the existence of a universal set of affective states, common to all humans, with specific biological underpinnings. In the early days of research on human emotions, the notion of a set of different basic emotions was based on the observation of so called culturally universal facial expressions (but see Jack, Garrod, Yu, Caldara, & Schyns, 2012 for opposite results), thought to reflect distinct underlying physiological responses (Ekman, Sorenson, & Friesen, 1969). This way, four different negative emotions (e.g. anger, fear, disgust and sadness) were identified, whereas ‘happiness’ was determined as the single generic basic emotion for positive affect. This imbalance between negative and positive emotions accords with findings showing that specific negative emotions are associated with dissociable physiological reactions (Christie & Friedman, 2004; Grillon, Falls, Ameli, & Davis, 1994) and brain circuits (Calder, Lawrence, & Young, 2001; LeDoux, 2000), while such differentiation in (neuro)physiological reactions is usually not found for positive emotions (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Levenson, Ekman, & Friesen, 1990; Lucas, Diener, & Larsen, 2009; Mauss & Robinson, 2009).

However, just as one can feel bad or uncomfortable in a variety of ways, it is likely that we can also experience several kinds of positive affect. In line with this idea, several researchers already suggested the existence of different discrete emotions

under the overarching term ‘positive’ affect (Griskevicius, Shiota, & Nowlis, 2010; Shiota et al., 2014). For example, Burgdorf and Panksepp (2006) proposed that the general construct of positive affect can be decomposed in more specific emotions, depending on how they facilitate adaptive responses in different environments (Griskevicius et al., 2010), such as gratitude (Bartlett & DeSteno, 2006), pride (Tracy & Robins, 2007), hope (Horton & Wallander, 2001) and joy (Panksepp, 2007). Others have proposed that positive affect can be subdivided into joy and love (Diener, Smith, & Fujita, 1995), in addition to interest and contentment (Fredrickson & Levenson, 1998), although these different positive emotions strongly correlate with each other (Lucas et al., 2009). In addition, humans can distinguish different positive emotions in non-verbal vocalizations (and not facial expressions as in Ekman et al., 1969), such as pride, amusement, contentment, sensual pleasures and relief (Sauter & Scott, 2007). Finally, given that the induction of a general positive mood influences various measures of emotion, positive mood might contain many variables (Westermann, Spies, Stahl, & Hesse, 1996).

Therefore, in our studies, we aimed at inducing a more specific positive mood in healthy adult participants, which was mainly characterized by joy and happiness, and being relatively low in approach-motivation (such as to differentiate it clearly from reward for example). We also wanted to induce and sustain positive affect that was not contingent on task performance in order to overcome changes in motivation, besides positive mood. In the following part, we describe how positive mood is usually induced in standard laboratory conditions, when the goal is to explore how this affective state dynamically influences cognition.

1.2. Inducing positive mood in the lab

MIPs are used to experimentally induce a transient change in the actual mood state of the participant, comparable with fluctuations in mood we naturally experience in everyday life (Jallais & Gilet, 2010). Many different types of MIP were devised and described in earlier studies, including listening to music or watching video clips, mimicking emotional facial expressions, receiving feedback on task performance or social behavior, recalling emotional memories and mental imagery (Martin, 1990; Mayer, Allen, & Beauregard, 1995; Westermann et al., 1996). Negative MIPs have generally been found to be more effective than positive ones (Mayer et al., 1995;

Westermann et al., 1996), probably because healthy participants tend to have a positive baseline mood (Diener & Diener, 1996) that might be difficult to elevate even more. However, most of these MIPs were only used to induce negative moods, and MIPs used for positive mood were primarily based on reward processing, such as unexpectedly receiving candy or other gifts (Ashby et al., 1999; Isen & Daubman, 1984; Isen, Daubman, & Nowicki, 1987; Isen, Rosenzweig, & Young, 1991). Nowadays, thanks to an increased scientific interest in positive mood, a wide range of MIPs is also used for the induction of positive moods. Hereafter, we present some recent studies using positive MIPs, emphasizing their respective strengths or weaknesses in order to induce this specific affective state.

A majority of positive MIPs relies directly on the use of reward (processing). These MIPs can consist of receiving gifts (Carpenter, Peters, Vastfjall, & Isen, 2013; Yang, Yang, & Isen, 2013), winning money in games (Gable & Harmon-Jones, 2010a, 2011) or the presentation of biologically relevant approach-related motivational stimuli, such as (tasty) food (Gable & Harmon-Jones, 2008, 2010b). However, while these MIPs are shown to be effective in changing the affective state of participants towards positive affect, they are also somewhat problematic because not only positive affect but also (approach) motivation is eventually changed. A second class of MIPs aims at inducing a more subtle and longer-lasting positive mood, manipulated independently of the task. Here, funny video clips (e.g. Franklin & Adams, 2011; Johnson, Waugh, & Fredrickson, 2010; Martin & Kerns, 2011; Van der Stigchel, Imants, & Ridderinkhof, 2011; van Wouwe, Band, & Ridderinkhof, 2011), reading positive stories or imagery of positive scripts are often used (e.g., Bruyneel et al., 2013; Goritz & Moser, 2003; Huntsinger, 2012; Jallais & Gilet, 2010; Mayer et al., 1995). Other MIPs make use of the recall of *personal* memories with a specific emotional valence (e.g., Bruyneel et al., 2013; Chermahini & Hommel, 2010; Holmes, Coughtrey, & Connor, 2008; Holmes & Mathews, 2005; Jallais & Gilet, 2010; Katzir, Eyal, Meiran, & Kessler, 2010; Phillips, Bull, Adams, & Fraser, 2002; Schwager & Rothermund, 2013). While watching video clips and reading stories are effective methods to induce positive mood (Gerrards-Hesse, Spies, & Hesse, 1994; Westermann et al., 1996), writing down, thinking about or imagining positive personal memories might lead to a stronger change in positive affect, given that it is based on person-specific information and thus ‘customized’ for each and every

participant. This element is especially important to consider in light of earlier research showing large inter-individual differences in the susceptibility to positive mood states (Gomez, Cooper, & Gomez, 2000).

1.2.1. Inducing positive mood with guided imagery

Imagery and emotion seem to be tightly linked together (Conway & Pleydell-Pearce, 2000; Holmes, 2006), as reflected in the finding that emotional experiences are often stored as mental images in autobiographical memory (Holmes & Mathews, 2005). In accordance with this framework, recent research directly comparing the impact of verbal information vs. (mental) imagery on affective states actually showed a stronger effect of the latter compared to the former method (Holmes, 2006). Moreover, the ability to imagine oneself in past situations characterized by positive affect is crucial for our well-being, and dysphoric individuals lack this capacity (Holmes, Lang, Moulds, & Steele, 2008; Joormann & Siemer, 2004). For all these reasons, mental imagery is often used in psychotherapy (Holmes, Arntz, & Smucker, 2007), and can also serve specific research purposes.

The MIP validated and used across our studies directly capitalizes on this prior knowledge and uses the fantastic capacity of humans to mentally travel back in time and vividly re-live former experiences (see Slotnick, Thompson, & Kosslyn, 2012). For example, when you think back of that particular sunset on the beach, it might ‘automatically’ bring back a smile on your face and you might be filled with the same joy you experienced when you witnessed this sunset. Mental imagery involving visual and other sensory modalities can influence the affective state, especially when situations are imagined from one’s own perspective (‘field perspective’), as compared to an external observer’s perspective (Holmes, Coughtrey, et al., 2008; Holmes & Mathews, 2005, 2010). When imagining a specific, personal event from a field perspective, participants tend to report more affective reactions, physical sensations and psychological states in the descriptions of what they imagine, compared to an observer perspective (McIsaac & Eich, 2002). Compared to other techniques, a MIP using personal memories can elicit stronger bodily sensations associated with affective states (Kosslyn, Ganis, & Thompson, 2001) and engages cognitive functions to a larger

extent (e.g. for recall from episodic memory, selection of a suitable memory), two fundamental components of an emotional experience (Kucera & Haviger, 2012).

Based on these earlier findings, we devised, validated and used a specific MIP consisting of two consecutive phases in this dissertation. First, we trained participants to use a field perspective by giving them precise instructions and imagery exercises. We then instructed them to recall a very positive (or neutral, depending on the group they were allocated to) event from their episodic memory, and describe their experience to the experimenter. Importantly, merely disclosing subjective experiences to others is already intrinsically rewarding for people (Tamir & Mitchell, 2012), and it is easily conceivable that this is even more the case for positive events, for which one likely felt good about oneself. Next, participants were instructed to imagine re-experiencing the recalled event and were asked about the nature of the sensory experiences during imagery, in order to facilitate field perspective and affective experience. Mental imagery was combined with music that played in the background throughout the experimental session. This way, the music served to facilitate the maintenance of the induced mood when the participants performed the task after the MIP. Importantly, this MIP did not reward or encourage any specific behavior, nor was it relevant in terms of task goals or demands. Accordingly, a rather general, diffuse and mild positive mood was elicited with this MIP, sharing many similarities with changes in mood naturally occurring in daily-life situations, reinforcing the ecological validity of this manipulation.

1.3. Interim Conclusions

“Everyone knows what an emotion is until asked to give a definition. Then it seems that no one knows” (Fehr & Russell, 1984). This citation nicely emphasizes the difficulty to grasp and later operationalize emotion or mood in the field of affective neuroscience (Pessoa, 2008). Because this debate clearly goes beyond the scope of this dissertation, we have tried to delineate instead, in light of existing models and data available in the corresponding literature, how we defined positive mood in this dissertation and how it differs from phasic emotional reactions or reward processing. In accordance with these earlier models and findings reviewed above, we conceived positive mood as a diffuse affective state that is low in approach motivation and has longer-lasting effects compared to reward. Besides a clear positive valence, positive mood can also be

associated with an increase in arousal, as emotions usually comprise a compound of these two components. In line with the model put forward by Ashby et al. (1999), positive mood is conceived as a general, mild positive state, presumably originating from (tonic) dopaminergic activations in a distributed network comprising reward-related brain areas, both at the cortical and subcortical levels. To induce this specific affective state in our studies, we used guided imagery and music, bearing in mind that the mood change was always orthogonal to the task participants had to complete such as to avoid a concurrent and uncontrolled change in motivation, besides mood. In the next section, we outline several theories available in the affective sciences literature that made predictions regarding the interplay of emotion and cognition, focusing on mood in the former case and selective attention in the latter, given the specific aims and scope of the present dissertation.

2. INFLUENCE OF MOOD ON COGNITION

With regard to effects of positive mood on cognition, the most influential framework is the broaden-and-build theory (Fredrickson, 2001, 2004). Therefore, we mostly refer to this theory throughout the empirical chapters presented in this dissertation, as well as interpret our new findings against this specific theoretical framework. However, other theories describing the relationship between positive mood and cognition have also been proposed in the literature. Below, we present first the broaden-and-build theory extensively, before turning to these few alternative models.

2.1. The broaden hypothesis of the broaden-and-build theory

The broaden hypothesis posits that positive emotions can generate a broadened cognitive processing and thinking style (Fredrickson & Levenson, 1998). A 'broad cognitive style' can be understood as 'zooming out' and paying attention to the globality of concepts, situations or objects. According to this theory, such broadening effect can occur at all levels of cognitive functioning. At the level of attention, broadening is defined as an attentional focus encompassing a large portion of the visual field and the encoding of global rather than local features of an object. In higher-order cognitive tasks (thinking, reasoning or language-related processing), a broad cognitive style can be conceptualized as more inclusive and flexible thinking styles, the use of

broader semantic categories and enhanced creativity. Earlier studies investigating cognitive broadening showed that experiencing positive mood can stimulate a thinking style that is open (Estrada, Isen, & Young, 1997), creative (Chermahini & Hommel, 2012b; Isen et al., 1987), integrative (Isen et al., 1991) and flexible (Isen & Daubman, 1984). Similarly, positive mood can influence cognitive control, suggested by findings showing faster conflict processing (Kanske & Kotz, 2011) but reduced conflict adaptation (Van Steenbergen, Band, & Hommel, 2009, 2010), both increased (Yang et al., 2013) and decreased working memory capacity (Martin & Kerns, 2011), increased flexibility and higher distractibility (Dreisbach, 2006; Dreisbach & Goschke, 2004). Finally, other studies have investigated modulation of attention by positive mood, showing a broadening of attention (e.g. Derryberry & Tucker, 1994; Moriya & Nittono, 2011; Rowe, Hirsh, & Anderson, 2007; Schmitz et al., 2009) and a global processing style (Basso, Schefft, Ris, & Dember, 1996). These latter studies are discussed more extensively here below (see section 1.3.2.).

While the broaden-and-build theory is encompassing many, if not all aspects of cognitive functioning and behavior, it does not provide however specific hypotheses, and the definition of what is a 'broad cognition' remains vague. Moreover, while several studies yielded support for a broader cognition and attention with positive mood or affect, many others failed to replicate these findings (e.g. Bruyneel et al., 2013; Gable & Harmon-Jones, 2008; Huntsinger, Clore, & Bar-Anan, 2010; Kaufmann & Vosburg, 1997). These inconsistencies might stem from the poorly defined and operationalized broadening effect on cognition attributed to positive mood within broaden-and-build theory. To overcome these limitations, other models have been put forward in the affective sciences literature in order to explain how (positive) mood might influence specific cognitive functions.

2.2. Alternative theories predicting effects of positive emotion on cognition

Another theoretical account is the affect-as-information hypothesis, proposing that a specific mood 'tunes' a specific context for cognitive processing (Schwarz, 1990). In this model, positive mood informs a person that the environment is safe, leading to a less effortful and more heuristic information processing style. An extension of this model is the mood-as-input hypothesis (Clore, Schwarz, & Conway, 1994), proposing that people

in a positive mood tend to find tasks more enjoyable and feel more easily satisfied with their performance, cueing them to diminish their efforts or involvement in the task. One way such 'laziness' effect could be expressed, is by a diminished adjustment of the processing style across different and changing task contexts. For instance, after a positive mood induction, people spend less efforts on the evaluation (Schwarz, 1990) or categorization of stimuli (Park & Banaji, 2000). Interestingly, healthy people are naturally biased towards a global (as opposed to local) processing style (Navon, 1977). Based on this finding, Huntsinger (2012, 2013) proposed that positive feelings influence the attentional focus in a flexible manner, as opposed to a fixed association between a certain internal state (e.g., positive) and a specific attentional bias (e.g., broad). More specifically, he argued that positive affect acts as a 'go-signal' to proceed using the most accessible attentional tendency, whether this involves a broad or a narrow attentional focus. Thus, the findings showing that positive mood can broaden attention and cognition might be explained by a reinforcement of the default or dominant processing style towards global information after the induction of positive mood (Huntsinger, 2012, 2013; Huntsinger et al., 2010).

Alternatively, the hedonic contingency theory proposes that in a positive mood, people carefully assess the affective consequences of a task, in order to make decisions that do not jeopardize their pleasant mood (Hirt, Devers, & McCrea, 2008). Hence, when feeling happy, people make efforts to protect or even improve their mood. Interestingly, a broad (as opposed to narrow) processing style might be congruent with the experience of positive mood (see Bar, 2009; Brunye et al., 2013; Chermahini & Hommel, 2012a), explaining thereby why it is usually associated with positive affect.

More recently, the systems account of the global and local processing model (Forster, 2012; Forster & Dannenberg, 2010) proposed the existence of separate systems for global and local information processing. According to this more recent model, these systems manage both perceptual and conceptual processes, and a wide range of factors including familiarity, colors and feelings can determine which system takes over (Forster & Dannenberg, 2010). Crucial in eliciting the activation of one or the other processing system is uncertainty. When a situation is novel, ambiguous, unfamiliar, complex, or for other reasons unclear, a global processing style is adopted in such a way to swiftly increase our understanding of the situation, given that it is

supposedly faster, easier and thus adaptive in such situations (Förster, Liberman, & Shapira, 2009), supporting creative and inclusive thinking styles (Forster & Dannenberg, 2010). By comparison, when an event is familiar, the local system is activated for an in-depth analysis of detailed information, prompting analytic thinking. Importantly, this pattern of activations can be influenced by mood. For example, when participants feel unsafe, the local system becomes active and the attentional scope narrows to favor a detailed analysis of the situation or stimulus. On the other hand, when the environment is safe, the experience of positive affective states is more plausible and the preferred mode of processing is biased towards global information (Forster & Dannenberg, 2010).

While most theories and research focusing on the influence of affect on attention and cognition have usually contrasted positive to negative affective states, other emotion dimensions have also been considered. Orthogonally to the (positive or negative) valence, an emotion can be either high or low in approach motivation, as discussed above (see section 1.1.1.). Recently, Gable and Harmon-Jones (2010a, 2010c) proposed that emotions high in approach motivation elicit a narrowing and emotions low in approach motivation a relative broadening of attention. Importantly, different positive moods can be characterized by different levels of approach motivation. Research supporting this hypothesis has shown that positive emotions low in approach motivation (e.g., joy) elicit a broadening of attention and a better memory for information presented in the periphery of the visual field, while the opposite effects were found for positive emotions high in approach motivation (e.g., desire or urge to eat a bar of chocolate; Gable & Harmon-Jones, 2008, 2010a, 2010c). However, inconsistent findings suggest that while the motivational dimension of emotions is important in predicting the direction of the change in the attentional scope and cognitive style, it likely disregards other significant factors (Finucane, Whiteman, & Power, 2010; Gasper & Clore, 2002; Johnson et al., 2010; Rowe et al., 2007).

Finally, the facial feedback theory hypothesizes that the effects of positive vs. negative affect or approach vs. withdrawal motivation on cognitive functions do not stem from complex affective-cognitive interaction effects, but rather from the facial expression (Johnson et al., 2010; Strack, Martin, & Stepper, 1988) and by extension also bodily postures associated with affective states (Price & Harmon-Jones, 2010). For example, a face expressing happiness has typically wide open eyes, while a face

expressing disgust has smaller eyes, possibly accounting for the relative broader and narrow scope of attention, respectively (Susskind et al., 2008). However, because little research has been carried out in the past to corroborate this theory, it remains difficult to appraise its validity in order to account for mood-related change of the attentional focus or thinking style.

2.3. Interim conclusions

While the different theories outlined here above differ regarding the proposed underlying mechanisms accounting for a change in the attentional focus and cognitive style as a function of mood, they share in common the assumption that mood reliably influences them. An important difference across them lies in the mediation by motivation in order to explain these effects. In this dissertation, we focused on positive mood defined as low in approach motivation (such as joy and happiness), for which all the described theories concur and predict a broad attentional focus. In the next section, we focus on attention and more specifically the different components of attention control that are likely influenced by positive mood. Because positive mood could broaden attention, it is relevant to outline first the likely functions and neural mechanisms of attention. This is the goal of the next section, reviewing not only behavioral data and models, but also important neurophysiological findings that shed light on the time-course of attention control brain mechanisms and their compelling influences on early sensory processing where ubiquitous gain-control effects take place (Hillyard, Vogel, & Luck, 1998), with a focus on the visual modality.

3. ATTENTION

The amount of information that we are confronted with largely exceeds our brain processing capacities, requiring some selection and pruning in this constant flow of information. Attention control processes ensure a timely and efficient selection of incoming relevant information during sensory processing, while filtering out irrelevant or distracting elements (Marois & Ivanoff, 2005). This selection is required because of structural constraints, such as a 'limited processing capacity' (Buschman, Siegel, Roy, & Miller, 2011) and the high cost of cortical processing (Alvarez & Franconeri, 2007; or due to competition between stimuli for representation, see Scalf, Torralbo, Tapia, &

Beck, 2013). Accordingly, attention selection is characterized by trade-offs (Carrasco, 2011), assigning more weight to certain information or stimuli at the cost of other ones, depending on their behavioral relevance, in order to bias competition (Desimone & Duncan, 1995). For example, fMRI studies have shown that the cortical response to specific stimuli decreases when multiple stimuli are presented simultaneously, unless attention is directed to one of them (Kastner, De Weerd, Desimone, & Ungerleider, 1998). In addition, when the attentional focus is broad, a larger part of visual cortex is activated, however, to a lower extent (Müller, Bartelt, Donner, Villringer, & Brandt, 2003). In the next section, we review the dominant models available in the existing literature that account for this selection and biased competition during sensory processing.

3.1. Selecting a model of attention

Attention is a widely used term, covering a myriad of mental processes, and is usually subdivided into dissociable components or mechanisms, depending on the kind of information that is selected and processed. Our goal is not to provide an exhaustive overview of these components and mechanisms, but rather to present the divisions and taxonomies used to explain attention selection that appear relevant in light of the empirical studies reported in this dissertation.

Several metaphors have been introduced to explain selective attention, including the spotlight (Broadbent, 1982), zoom lens (Eriksen & St-James, 1986) or gradient of attention (Mangun & Hillyard, 1988). These metaphors all emphasize space as an important feature of attention or property on which attention operates. Spatial attention can be conceptualized as the selection of and focus on a specific location in the visual field that can occur either overtly or covertly (i.e., without moving the eyes; see Corbetta, 1998; Posner, 1980). At the neurophysiological level, this process is reflected in enhanced processing of stimuli falling into the attended part of the visual field, while the processing of stimuli falling outside the attentional focus (i.e., at an unattended location) is suppressed (Hillyard et al., 1998; Kastner & Ungerleider, 2000). Moreover, when attention is directed to a specific location, baseline activity in visual cortex accounting for the unattended part of the visual field is decreased (Smith, Singh, & Greenlee, 2000). Hence, spatial attention operates by selecting a circumscribed part

of the visual field in which visual stimuli receive priority in the competition for further processing, as opposed to stimuli shown at an unattended spatial location.

3.1.1. Flexible timing of selection

A long-standing debate in research on attention concerns the exact locus of attentional filters in the stream of information processing, with one camp defending an early (perceptual; Broadbent, 1958) and the other camp a late (post-perceptual) selection process (Deutsch & Deutsch, 1963). Each position is supported by a vast amount of empirical evidence, suggesting that selection may actually be a dynamic and flexible process that can occur either early or late following stimulus onset, depending on specific factors. This position is defended by hybrid models, such as Lavie's load theory (1995, 2001, 2005), predicting that the extent to which unattended stimuli are suppressed actually depends on the amount of resources currently available and not consumed by the task at hand. This filtering of irrelevant information can occur at all levels of visual cortex, from primary visual cortex onwards (Rauss, Schwartz, & Pourtois, 2011). If the primary task is characterized by high perceptual load (i.e., many resources are used to resolve this task), an early filtering of distracting information can occur. By contrast, if the primary task is characterized by low perceptual load (i.e., only a small amount of resources is necessary to resolve the task), distractors are processed by the resources spilled over from the primary task, consistent with a late selection. Hence, the amount of resources available at a given moment in time dynamically determines the locus of the attention selection or filtering. Moreover, the efficiency of late selection depends on the extent to which cognitive control processes are active, in such a way that increased cognitive load (e.g., by a working memory task or demand) results in a decreased filtering of distractors, unlike effects of perceptual load (de Fockert, Rees, & Lavie, 2001; Lavie, 2010).

This theory was recently extended by Linnell and Caparos (2011, 2013), who showed that this suboptimal filtering of distractors in conditions of low perceptual load was not merely a result of spillover of spare resources. Rather, they showed that prefrontal cognitive control mechanisms are actively recruited to coordinate perceptual processing only when perceptual load is high and the task challenging. On the other

hand, when perceptual load is low, there is no need for extra cognitive control to manage perceptual processing, and thus distractors are not filtered out efficiently.

Together, these models provide elegant accounts to explain tradeoff effects in attention selection, between the need to efficiently process task-relevant processing on the one hand, and the requirement to filter out irrelevant information on the other. While these models aimed at formulating an answer to the question *when* attention selection occurs, we now briefly discuss the issue of *what* is selected.

3.1.2. Top-down vs. bottom-up attention control

Attention selection is governed either by external stimuli (such as an abrupt light flash or sudden change in our environment) or internal processes (such as specific goals or intentions; Corbetta & Shulman, 2002; Desimone & Duncan, 1995). For example, when reading, we choose to direct our attention to the article and we aim at understanding its semantic content. This type of attention involves voluntarily directing attention to information that is relevant in terms of our intentions and goals, and is usually referred to as top-down or endogenous attention (e.g. Hopfinger, Buonocore, & Mangun, 2000; Müller, Geyer, Zehetleitner, & Krummenacher, 2009). In the lab, this type of attention is classically explored using the Posner cueing task (Posner, 1980). In this task, a symbolic cue (e.g., a vertical arrow) is first presented at fixation indicating where to attend, before a visual target is presented at this location (valid location) in a majority of trials or in the opposite hemifield (invalid location) in a minority of cases. Performance is typically faster for valid compared to invalid locations, suggesting that attention was voluntarily oriented towards the cued hemifield, eventually leading to a facilitated processing of this specific location (Posner, 1980). This process is thought to depend on the PFC, which maintains and updates online the attentional set in working memory (Miller & Cohen, 2001).

However, although you decided to be concentrated on a paper, the sound of an email alert is likely to ‘automatically’ distract you away from your reading. This type of attention orienting is called bottom-up or reflexive and it is classically assessed by using a similar cueing paradigm, with exogenous (non-predictive) salient cues shown at peripheral locations (Posner, 1980). Thus, bottom-up attention refers to the attentional capture by new, moving, unexpected or otherwise salient sensory stimuli, even though

they remain task-irrelevant (e.g. Hickey, McDonald, & Theeuwes, 2006; Ranganath & Rainer, 2003; Wolfe & Horowitz, 2004). Such stimulus-driven attention capture acts in a rapid and automatic way and is thought to precede top-down attentional influences (Theeuwes, 2004; Theeuwes, Atchley, & Kramer, 2000). Importantly, these two processes do not operate independently from each other. For instance, salient stimuli capture attention more easily when they match with specific goals (Folk, Remington, & Johnston, 1992; Vogt, De Houwer, Moors, Van Damme, & Crombez, 2010; Vogt, Lozo, Koster, & De Houwer, 2011) or stimuli maintained in working memory (Olivers, Meijer, & Theeuwes, 2006). Hence, the selection of information for further processing is a result of a dynamic interaction between bottom-up and top-down factors (Connor, Egeth, & Yantis, 2004; Egeth & Yantis, 1997; Schneider, Beste, & Wascher, 2012).

This interplay is also reflected in the partial overlap of and interactions between the neural mechanisms underlying these two types of attention control (Peelen, Heslenfeld, & Theeuwes, 2004). Evidence from both animal and human electrophysiological as well as imaging studies suggests that attention is controlled by a fronto-parietal network gating sensory processing 'remotely' in the visual cortex. However, partially separate brain structures within this fronto-parietal network are thought to be responsible for top-down and bottom-up selection mechanisms, respectively : a ventral fronto-parietal network is involved in stimulus-driven attention while a more dorsal fronto-parietal network is involved in goal-directed selection of sensory information (Corbetta & Shulman, 2002). The ventral fronto-parietal network includes the temporo-parietal junction, and is largely right-lateralized. This system would play the role of a 'circuit breaker', alerting the dorsal system upon detection of behaviorally relevant, salient or unexpected stimuli, in a genuine bottom-up manner. The dorsal network comprises the parietal cortex along the intra-parietal sulcus and extends into the superior parietal lobe and frontal cortex, more precisely, the frontal eye fields. Earlier fMRI studies aimed at isolating top-down brain activity found that the expectancy of a stimulus before its actual presentation (i.e., in the absence of any stimulation) was associated with increased activity in the visual cortex, suggesting that attention could gate sensory cortex in the absence of any external visual stimulus, in line with an endogenous component. Interestingly, dorsal fronto-parietal regions were activated in this condition (Hopfinger et al., 2000; Kastner, Pinsk, De Weerd, Desimone,

& Ungerleider, 1999), consistent with the assumption of a preferential involvement of these regions in the top-down biasing of sensory processing. The posterior part of the parietal cortex and the frontal eye fields were proposed as important loci of interaction between top-down and bottom-up networks (Corbetta & Shulman, 2002; McMains & Kastner, 2011). Such neuro-anatomical model comprising frontal and parietal brain areas has been confirmed by a large number of studies (Grent-'t-Jong & Woldorff, 2007; Miller & Buschman, 2013; Nelissen, Stokes, Nobre, & Rushworth, 2013; Shulman et al., 2009; Woldorff et al., 2004). Miller and Buschman (2007) proposed that bottom-up attention shifts 'flow' from parietal to frontal cortex in a cascade-wise fashion (using higher-frequency band, such as Gamma), while top-down control originates in frontal cortical areas and propagates, via lower-frequency band (i.e., Beta) to the posterior-parietal cortex, and in turn into lower tier visual areas. Moreover, they suggested synchronized oscillations as a mechanism for the interaction between these non-overlapping networks (Miller & Buschman, 2013).

Altogether, the division into bottom-up and top-down mechanisms (with partly dissociable underlying brain networks) has proved extremely useful to account for a wide range of modulations by attention during (early) sensory processing. However, as it is the case for almost all theoretical concepts, not all attention processes easily fit into this taxonomy (Awh, Belopolsky, & Theeuwes, 2012). In the following section, we briefly overview other categorizations of attentional control processes put forward in the literature recently, going beyond the mere distinction between 'bottom-up' vs. 'top-down' processes.

3.1.3. Other divisions

Recently, Chun and colleagues (2011) proposed an alternative taxonomy in which selective attention is inherent to various systems, such as perception, memory and response selection. They differentiated attentional processes involved in the selection of (external) information from perception on the one hand, from (internal) information that is already present in the mind, such as memories, on the other. The example of being distracted by an email alert while reading a paper belongs to the first category of external or perceptual attention. A shift to internal attention would occur if attention would rather be drawn to internal mental representations, such as trying to remember

the author's name of a related study or making a mental grocery list. Internal attention is characterized by cognitive control mechanisms, for selecting responses, options or memories (see Miller & Cohen, 2001; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004), with a special role for working memory as the interface between internal and external attention (see also Chun, 2011; Gazzaley & Nobre, 2012; Kuo, Stokes, & Nobre, 2012). Other concurrent models of selective attention support such division implicitly, such as the load theory of selective attention, predicting opposing effects of perceptual vs. cognitive (load) manipulations on the suppression of distracting information (de Fockert et al., 2001).

Importantly, the proposed taxonomy (Chun et al., 2011) encompasses previous classifications that were based on mechanisms and features of attention. For example, top-down attention control can act on any level throughout internal and external attention, whereas bottom-up processes only occur in the latter (Corbetta & Shulman, 2002). This taxonomy also reflects the way a 'broadening of attention' has been conceptualized in research on the cognitive effects of positive mood, ranging from a large attentional scope in perceptual processing to a broad attentional set in the generation of associative thoughts and creative ideas. Importantly, Chun and colleagues (2011) acknowledged that emotion is also an important factor in the control of both perceptual and internal attention. However, they did not specify the place of emotion within their taxonomy, nor did they propose mechanisms by which emotion could exert such influence on attention (and in turn perception).

Other authors, on the other hand, have put more emphasis on emotional influences on perception, and introduced the concept of 'emotional attention' (Vuilleumier, 2005). Here, emotion is proposed as a modulatory system biasing perceptual processing in addition to top-down and bottom-up attention control mechanisms (Brosch, Pourtois, Sander, & Vuilleumier, 2011; Markovic, Anderson, & Todd, 2014; Pourtois, Schettino, & Vuilleumier, 2013). This proposition was largely based on studies showing a preferential selection of (mostly negative) emotional information and the amplification of neural responses to threat-related emotional relevant stimuli (e.g. Keil et al., 2010; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Stolarova, Keil, & Moratti, 2006; Weymar, Keil, & Hamm, 2013). These observations suggest that emotional information is processed more efficiently,

resembling the gain control mechanism of attention usually observed with neutral stimuli during endogenous selection (Hillyard & Anllo-Vento, 1998). In addition, a difference in the time-course for the processing of emotional compared to neutral stimuli was found (Pourtois, Thut, de Peralta, Michel, & Vuilleumier, 2005), with early activation in limbic regions regardless of top-down attention control mechanisms (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010).

Hence, while the effects of emotion and attention on information processing are similar in that they enhance information processing and possibly act via the same sensory pathways, different neural sources and brain systems might be involved (Pourtois et al., 2013). More precisely, given its tight anatomical connection with the visual system, the amygdala might play a key role in biasing sensory processing in favor of emotional relative to neutral visual information (Amaral, Behniea, & Kelly, 2003; Brosch et al., 2011; Pessoa, 2010; Vuilleumier, Armony, Driver, & Dolan, 2001; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004). Given its specific position in the human brain and reciprocal anatomical connections with many other brain regions, the amygdala might orchestrate the modulation of sensory processing in response to emotional stimuli, thereby fostering a preferential processing and encoding of these stimuli (Pessoa & Adolphs, 2010). Importantly, also the current affective internal state of the participant (e.g., state anxiety) can influence emotional attention, possibly via similar pathways and neural routes (e.g. Rossi & Pourtois, 2012; Shackman, Maxwell, McMenemy, Greischar, & Davidson, 2011). However, the proposed neural mechanisms underlying emotional attention are based almost exclusively on research focusing on the processing of negative (threat-related) emotional information, and in a lesser degree attention modulations by negative affective states, while it remains unclear if positive mood might have similar effects on visual processing and operate via similar mechanisms. In the following section, we review a large body of (behavioral) studies that directly addressed this question, i.e., effects of positive affect on attention. Based on these studies, it appears that emotional attention effects triggered by positive mood might be qualitatively dissociable compared to typical emotional attention effects induced by negative stimuli or affect.

3.2. The influence of positive mood on attention

Several paradigms have been used to investigate influences of positive mood on selective attention. One prevailing strategy to capture these effects is the use of interference paradigms, such as flanker tasks (Eriksen & Eriksen, 1974). In this task, participants are instructed to respond to a centrally presented target, that is surrounded by distractors, or ‘flankers’ (see Fig. 2A). When flankers are mapped to a different response compared to the target (‘incompatible flankers’), they cause more interference than compatible flankers, resulting in increased RTs to the target. The reasoning behind the usage of flanker tasks to investigate mood effects on selective attention is that if the attentional focus is broad enough to encompass the flankers in addition to the centrally presented target, the interference of these flankers will be greater compared to a narrow scope of attention. Two studies found increased interference effects of flankers on central target processing compared to a neutral or negative mood, even when the spacing between the target and the flankers was increased (Moriya & Nittono, 2011; Rowe et al., 2007). However, other studies did not find any modulation by mood using flanker tasks (Bruyneel et al., 2013; Finucane et al., 2010; Martin & Kerns, 2011).

The global-local processing paradigm is another often used task in this field, measuring the extent to which information is processed globally, in its entirety, or locally, with a focus on the details. For example, in one such task, a geometric shape (e.g. a square) is build up from smaller figures (e.g. triangles) and participants are asked to make a similarity judgment between this geometric figure and two other figures, that match either its global form (e.g. a square), or its local element (e.g. a triangle; Kimchi & Palmer, 1982; see Fig. 2B). A global mode of processing would facilitate the recognition of the overall shape, compared to a local processing mode. Studies using these figures to study the influence of mood on global-local information processing showed that people transiently experiencing positive mood were more inclined to process the figures globally compared to both neutral (Fredrickson & Branigan, 2005) and sad moods (Gasper & Clore, 2002). In accordance, trait positive mood and optimism correlate positively with a global processing bias, and negatively with a local processing bias (Basso et al., 1996).

These findings were refined by studies showing that the context should be taken into account when predicting mood effects on attention. For instance, one study comparing positive to sad moods found a global processing bias for positive mood, but only when participants perceived their feelings as relevant to the task and when the stimuli were ambiguous (Gasper, 2004). However, no difference was found between moods when the feelings were irrelevant for the task or the response criteria clear. Moreover, Huntsinger and colleagues found that positive mood does not induce a global (using a global-local task; Huntsinger et al., 2010) or a broad (using a flanker task; Huntsinger, 2012) processing style per se, but rather enhances the dominant attentional focus, whether it is broad or narrow, providing a possible explanation for previous discrepant findings.

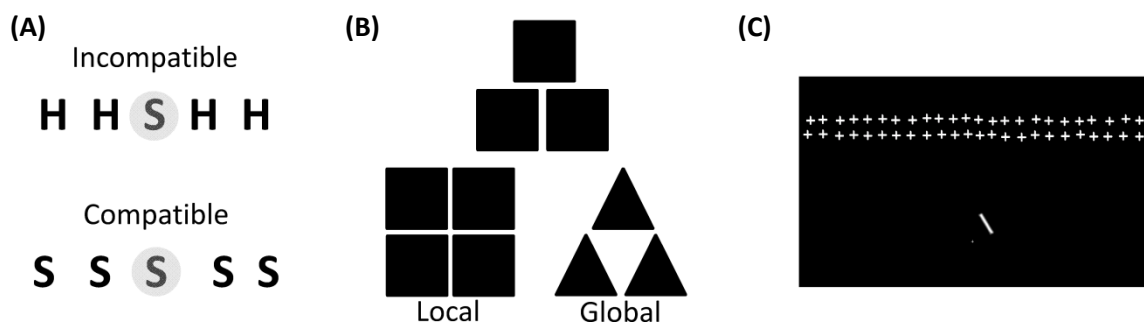


Figure 2. Classical experimental paradigms used for assessing influences of positive mood on attentional breadth. (A) Flanker task. Participants have to respond to the central letter (e.g., S, gray circle), either when it is flanked with incompatible (e.g., H, upper array) or compatible flankers (e.g., S, lower array). (B) Kimchi figures. Participants are instructed to match the upper figure (e.g., triangle made up out of squares) with one of the figures below, resulting in a match either with its local (e.g., left figure, square) or its global feature (e.g., right figure, triangle). (C) Load like paradigm. Participants perform a task at fixation requiring foveal vision (tilted line) while stimuli are presented in the peripheral visual field. The extent to which these stimuli are processed or rather filtered out is established, using both behavioral and electrophysiological measures.

Other studies investigating the positive mood-attention link have focused on attentional biases in positive mood. For example, Tamir and Robinson (2007) used a dot-probe paradigm with reward-related and neutral word stimuli, and showed that daily positive mood was associated with a greater tendency to attend to reward-related words. In an eye-tracking study, attentional preferences were assessed by the presentation of emotional pictures at different peripheral locations, showing that

participants in a positive mood fixated positively valenced peripheral stimuli more than neutral stimuli, compared to a neutral mood (Wadlinger & Isaacowitz, 2006). However, these studies focus on the content of the attended information, rather than changes in the attentional scope.

In summary, the broadening effects of positive mood on attention have been investigated with various paradigms, however, with a great inconsistency of results. Moreover, the used tasks were not really designed to measure modulations of the size of the attentional focus and covert spatial attention. For instance, flanker tasks are typically used to measure other processes besides selective attention, due to their heavy reliance on executive functions and cognitive control (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Moreover, research suggested that a preference for local or global processing differs from local or global selective attention (Caparos, Linnell, Bremner, de Fockert, & Davidoff, 2013). To reliably assess correlates of covert attention, overt attention should be fixated at one location in the visual field (Carrasco, 2011), as is often the case in tasks measuring the effects of load on processing of peripheral stimuli (see Lavie, 1995; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rossi & Pourtois, 2012; Schwartz et al., 2005). The tasks we used in the studies described in **chapters 2-4** were therefore inspired by these load-related experimental paradigms (see Fig. 2C). By blocking overt attention at fixation and presenting peripheral stimuli at different eccentricities in the upper visual field, the extent to which these peripheral stimuli would fall into the attentional scope could be inferred from the extent to which they were processed or rather filtered out, by means of systematic changes in their electrophysiological responses.

3.3. Neurophysiological correlates of attention and perception

A precise assessment and characterization of the temporal structure of attentional influences on different stages of visual processing are possible thanks to the high temporal resolution provided by scalp EEG recordings. Following stimulus onset, several sequential electrical field potentials are generated in the visual cortex (and beyond), called visual event-related brain potentials (ERPs), reflecting the time course of visual information processing, with a millisecond time resolution. These visual ERP components can be characterized in terms of amplitude and latency when measured at

few isolated scalp positions (Picton et al., 2000), as well as topographies when considering the actual distribution of the entire electric field, including all channels (see Pourtois, Dan, et al., 2005). Modeling algorithms have been developed to make the estimation of the underlying intracerebral sources of these ERP components or topographies relatively accurate and reliable (see Pascual-Marqui, 2002). Hence, EEG is an excellent neurophysiological tool to investigate the time course of visual information processing and how attentional and mood-related effects influence it.

3.3.1. Attention modulations of P1 and N1

Spatial attentional mechanisms can modulate stimulus processing in visual cortex, affecting several visually evoked potentials (VEPs) rapidly following stimulus onset. Classically, the P1 was considered to be the first VEP influenced by manipulations of spatial attention, followed by the N1. The P1 is a positive deflection, peaking between 80 to 130 ms post-stimulus onset at occipital leads, and presumably generated in the extrastriate visual cortex (Clark, Fan, & Hillyard, 1995; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Gomez, Clark, Fan, Luck, & Hillyard, 1994). The N1 is a negative component peaking between 120 and 180 ms, hence after the P1 and with a different scalp topography. The N1 is thought to be constituted by several subcomponents with multiple sources, presumably located in occipito-parietal, temporo-parietal and deeper parietal lobe, as well as frontal cortices (Clark et al., 1995; Di Russo et al., 2002). The P1 and N1 are typically increased contralaterally to the attended hemifield and are sensitive to the content of stimuli. Typically, increased P1 and N1 amplitudes are found for attended compared to unattended stimuli, providing electrophysiological evidence for a gating of sensory cortices with selective attention (Hillyard & Anllo-Vento, 1998; Luck, Woodman, & Vogel, 2000), as further supported by evidence from studies combining ERP and fMRI methods (Heinze et al., 1994; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997). However, while the P1 is also suppressed for unattended stimuli, no such suppression has been observed for the N1 (see Hillyard & Anllo-Vento, 1998), indicating that the N1 likely reflects different attentional processes compared to the P1 (Luck, Heinze, Mangun, & Hillyard, 1990). Indeed, the N1 is thought to reflect discriminative processes, based on evidence showing increased N1 amplitudes when stimuli had to be discriminated, for both form

and color properties, compared to mere stimulus detection (Vogel & Luck, 2000). Interestingly, it has been shown that the P1 and N1 components can be boosted by (mostly negative) emotional stimuli, in the same way as by attention (Olofsson, Nordin, Sequeira, & Polich, 2008; Pourtois, Dan, et al., 2005; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Shackman et al., 2011). In addition, one study used VEPs to investigate the influence of a positive affective state on stimulus processing in a flanker task, showing larger probe-evoked P1 amplitudes in positive compared to neutral and negative moods and a diminished lateralization of the N1 (Moriya & Nittono, 2011).

Altogether, while it has been established that the amplitude of both the P1 and the N1 components is sensitive to effects of selective attention and the emotional content of stimuli, it remains unclear whether a positive affective state might influence these components in a similar way. Moreover, recent evidence reviewed in the next section actually showed that top-down attention modulations might influence earlier stages of processing, preceding the P1 and N1. More specifically, several studies reported that the amplitude of the C1 component, which is the first VEP component following stimulus onset generated in V1, was influenced by manipulations of attention (load), unlocking a debate in the psychophysiology literature on what stages of processing following stimulus onset are actually reliably influenced by attention (see Ales, Yates, & Norcia, 2013 vs. Kelly, Vanegas, Schroeder, & Lalor, 2013 and Ding, Martinez, Qu, & Hillyard, 2013 vs. Rauss et al., 2009).

3.3.2. *(Im)permeability of the C1 to top-down modulations*

The C1, or 'Component 1', peaks between 60 and 100 ms following stimulus-onset. Unlike the subsequent P1 and N1, the C1 is a retinotopic component, and its polarity varies with the position (rather than the content) of the stimulus in the visual field. It gets a negative polarity for stimuli shown in the upper part of the visual field but positive for the same stimuli shown in the lower hemifield. In their seminal study, Jeffreys and Axford (1972) proposed that this polarity reversal is consistent with the cruciform organization of the calcarine fissure and a V1 generator for this striate component (see also Clark et al., 1995; Di Russo et al., 2002; Rauss et al., 2011, see Fig. 3). More precisely, because the pyramidal neurons in the upper and lower bank of the calcarine fissure are oriented in opposite directions, stimulation of the upper visual field

gives rise to a negative component measured at occipito-parietal scalp electrodes, but positive for stimulation in the lower visual field (Clark et al., 1995). However, some researchers have questioned V1 as the main and exclusive neural generator of the C1 (e.g. Ales, Yates, & Norcia, 2010), although the objections do not challenge the C1 as the earliest VEP measured at scalp, nor do they contradict that V1 as an important neural source of C1 (see Kelly et al., 2013).

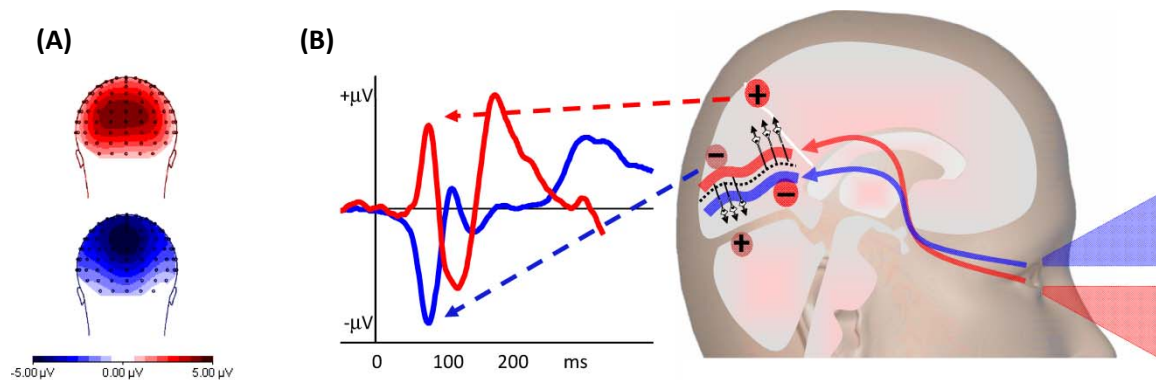


Figure 3. V1 as generator of C1. (A) C1 electrical distribution at scalp, with a positive polarity for stimuli presented below fixation (upper map) and a negative polarity for the exact same stimuli presented above fixation (lower map). (B) Illustration of the cruciform model put forward by Jeffreys and Axford (1972), adapted from Rauss, 2011.

A second ongoing debate concerns the sensitivity of the C1 to top-down cognitive influences, such as attention or learning (see Rauss et al., 2011 for an overview of studies from both camps). Many earlier ERP studies found evidence for effects of selective attention taking place after the C1, at the level of the P1 or N1 or both (see section 3.3.1.), casting doubt on the assumption that V1 can be modulated by this factor at this early stage following stimulus onset (Ding et al., 2013; Fu, Fedota, Pamela, & Parasuraman, 2010; Hillyard & Anllo-Vento, 1998). In this framework, effects of attention in V1 shown by fMRI data are usually interpreted as reflecting a re-entrant feedback effect of attention in V1, as opposed to a genuine ('feedforward') modulation of V1 rapidly following stimulus onset (Di Russo, Martínez, & Hillyard, 2003; Noesselt et al., 2002). According to these authors, top-down 'gain-control' modulations of attention are surmised to influence stimulus processing starting from V2 or V3 in the extrastriate visual cortex (Martínez et al., 1999; Woldorff et al., 2002). However, several

methodological reasons have been brought forward in the literature to explain these null-findings for the C1 (see Clark et al., 1995; Foxe et al., 2008; Poghosyan & Ioannides, 2008). Moreover, other authors have argued that there is no theoretical reason to assume that all levels of processing could be subject to amplitude modulations by selective attention, except the very first (Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss et al., 2011).

Accordingly, neurophysiological studies questioning that V1 is impermeable to top-down influences of attention at an early stage following stimulus onset have flourished over the last years. Neurophysiological studies performed in non-human primates showed modulations of the V1 by top-down processes, lending support to the assumption that V1 is not an encapsulated module, but can be flexibly and dynamically influenced (e.g. Gilbert, Ito, Kapadia, & Westheimer, 2000; Mehta, Ulbert, & Schroeder, 2000). However, based on these studies, it remained unclear whether these modulations occurred during the early wave of activation in V1 or later phases of processing corresponding to re-entrant processes (see Lamme & Roelfsema, 2000; Rauss et al., 2011). This flexibility is also reflected in ERP studies assessing effects of spatial attention on human primary visual cortex and hence the C1. In one study, after controlling for the large inter-individual variability in V1 anatomy, the authors reported a clear amplitude modulation of the C1 by visuo-spatial attention; this component being larger for attended relative to unattended spatial locations (Kelly et al., 2008). Another study, using magnetoencephalography (MEG), also reported increased activity in V1 when attention was directed to the stimulated visual field, and, importantly, using a highly precise localization technique, this modulation was found to occur during the initial sweep of activation in V1 (Poghosyan & Ioannides, 2008). Further evidence comes from Rauss and colleagues (2009), who manipulated perceptual load at fixation instead of visuo-spatial attention per se, while measuring the C1 to unattended peripheral distractors shown asynchronously relative to the central stimuli. When load was high, the amplitude of the C1 to the distractors was smaller than when the task at fixation was easy (see also Rossi & Pourtois, 2012). Interestingly, this load-dependent pattern for the amplitude of the C1 was reversed when these central and peripheral stimuli were presented simultaneously (Rauss, Pourtois, Vuilleumier, & Schwartz, 2012, but see Ding et al., 2013 for opposite results), suggesting that V1 can be flexibly modulated by

gain-control mechanisms of selective attention likely operating higher-up in the hierarchy, within the fronto-parietal network.

3.3.3. *Affective modulation of the C1*

Although less studies have been dedicated to this issue, early visual processing (and the C1) can also be influenced by emotion. One study using a Posner cueing paradigm to assess the influence of emotional threat-related face stimuli on the C1, showed an increased C1 component to fearful compared to neutral or happy faces (Pourtois et al., 2004), while a MEG study showed a differentiation between happy and sad faces in midline occipital activation generated in V1/V2 (Halgren, Raji, Marinkovic, Jousmäki, & Hari, 2000). In a conditioning study, negative pictures were coupled to gratings (Stolarova et al., 2006). These conditioned, threat-related stimuli elicited increased C1 amplitudes compared to the neutral stimuli, while the low-level features of these stimuli were identical. In another study, the authors investigated contextual emotional effects on the C1 in spider phobics, and found that in a threat-related (as opposed to safe) context where images of spiders could appear on the screen, the amplitude of the C1 was enhanced for all (threat and non-threat-related) stimuli (Weymar et al., 2013). Finally, in one study, the authors assessed how the internal affective state of the participants could influence the C1 to peripheral neutral stimuli, showing that, under conditions of state anxiety, the normal gating of this striate component by attentional load (see Rauss et al., 2009) was no longer visible, relative to a control condition without state anxiety (Rossi & Pourtois, 2012). Together, these ERP studies suggest that the C1 component might capture early attention-related effects taking place in V1 and being related either to the motivational significance of the visual stimuli used, or the current internal (negative) affective state of the observer.

3.3.4. *Summary*

Although still highly debated currently in the psychophysiology literature (see Ding et al., 2013), accumulating evidence suggests that, in addition to the P1 and N1 components, the C1 component is modulated in amplitude by attention-related factors, in addition to emotional factors presumably creating 'emotional attention' effects in the primary visual cortex. Recent ERP studies showed that the first sweep of activation

within the primary visual cortex (C1) is reliably influenced by higher-level factors, such as perceptual load or emotional attention. In **chapters 2-4** of this dissertation, we adhered to this logic and focused on the C1 as a marker of the early, position-specific visual sensory processing of a peripheral stimulus in V1 being presumably modulated by attention and/or positive mood. We addressed the question whether positive mood could influence and gate this early stage of visual processing in V1, in line with an early broadening effect, and whether such an effect was component-specific or instead influencing the subsequent P1 and N1 components alike.

3.4. RESEARCH GOALS AND OVERVIEW OF THE EMPIRICAL CHAPTERS

This dissertation is inspired by the increasing interest in the functions and mechanisms of positive mood, that has been revitalized since the publication of the influential broaden-and-build theory (Fredrickson, 2001, 2004). One of the basic assumptions of this theory is that a broadening of attention lies at the foundation of the beneficial effects of positive mood on wellbeing and health. Consistent with this proposition, previous research has shown that positive mood can influence selective attention, both at the behavioral (e.g., Rowe et al., 2007) and electrophysiological levels (Moriya & Nittono, 2011). However, evidence for a genuine broadening of attention by positive mood is rather scant in the existing literature, and the findings currently available remain vague and inconclusive (see Bruyneel et al., 2013; Huntsinger, 2013). Hence, the main goal of this dissertation was to investigate whether positive mood could bias attention and more specifically broaden it.

We put this prediction to the test in a series of studies, investigating systematically, both at the behavioral and electrophysiological levels, the influence of positive mood on the processing of (peripheral) stimuli that were either fully unattended distractors (**chapter 2**), or attended task-related stimuli (**chapter 3**), or shown in different experimental contexts differing in the amount of attentional demands required to resolve the task (**chapter 4**). In addition, we tested the assumption often put forward -but rarely tested- in the literature, that a decreased inhibitory control under positive mood might explain or underlie the broadening of attention typically observed with this specific mood state (**chapter 5**). In all these chapters, continuous EEG was recorded from 128 channels during task performance.

These neurophysiological data were analyzed offline using standard peak analyses, assessing amplitude changes of the different ERP components of interest as a function of mood and attention or inhibition (Picton et al., 2000). We also used complementary data-driven topographical mapping analyses to gain insight into the configuration of the intra-cranial generators giving rise to these scalp ERP components and their modulation by attention and positive mood (Pourtois, Delplanque, Michel, & Vuilleumier, 2008). First, however, we attempted to validate our MIP and assess its effectiveness to induce positive mood in adult healthy participants (**chapter 1**). Importantly, across all studies and chapters reported in this dissertation, we always used the same structure for the experimental design: positive mood was induced and sustained in a group of adult healthy participants while they performed a specific task (targeting attention, inhibition or creative thinking depending on the specific research question). Crucially, we then compared their behavioral and/or EEG data to a matched group of participants receiving an active MIP alike, but with a neutral content.

Earlier in this Introduction, we argued that many previous studies looking into the positive mood-selective attention link used MIPs that largely relied on reward, while effects of positive mood ‘mimicking’ every-day life positive affective states were actually rarely assessed, possibly introducing a confound between positive mood and approach motivation in these earlier studies. Therefore, in our studies, we wanted to depart from reward and set out a MIP providing enhanced ecological validity. For this purpose, we used guided imagery of personal past experiences, freely chosen by each and every participant from episodic memory, tailoring our MIP to the specific affective history and background of the participant, thereby individualizing our MIP (based on Holmes, 2006). The **first chapter** was aimed at validating the efficiency of this procedure in the elicitation of a positive mood, using both self-report questionnaires and psychophysiological measures (blink rate and facial EMG). In addition, we tested if positive mood induced with this MIP would give rise to an enhanced creative thinking potential (when measured using standard tasks available in the field), given that this has often been reported in early studies (Ashby et al., 1999; Estrada, Isen, & Young, 1994; Isen & Daubman, 1984; Isen et al., 1987; Isen et al., 1991) and lies at the foundation of the conceptualization of the broaden-and-build theory (Ashby et al., 1999; Fredrickson, 2001, 2004; Isen, 2000).

Our main line of research consists of a set of experiments reported in **chapters 2 to 4**, each aimed at delineating effects of positive mood on the breadth of attention, with a focus on early VEPs and hence the electrophysiological time-course of these effects, including the striate-dependent C1 component. Assessing effects of positive mood on the C1 is not an easy job, given that this striate component is elicited only by peripheral stimuli. Therefore, we developed a task enabling us to titrate a putative broadening of attention by positive mood, with corresponding effects measurable at the level of the C1 amplitude and/or topography. To achieve this, we systematically manipulated the actual position of the peripheral stimuli shown in the upper visual field. In these studies, we operationalized a ‘broad attentional focus’ as the amplified neural processing of peripheral stimuli. Hence, we reasoned that if the attentional scope is broad after the induction of positive affect, peripheral stimuli presented far away from fixation should benefit from an enhanced early sensory processing (if central processing capacities are not depleted by a high load/demanding task, see **chapter 4**), visible at the level of the C1 already, relative to a neutral mood condition.

Whereas studies reported in **chapters 2-4** informed about the locus and expression of a broadened attentional focus in positive mood, they did not address the question what mechanisms might underlie such effect. Therefore, in **chapter 5**, we aimed at investigating if a drop in inhibitory control might underlie positive mood influences on cognition and selective attention. This proposition was inspired by earlier research suggesting that a broader, and thus less constrained, attentional focus might be enabled by a decreased inhibitory control on visual processing, resulting in a greater openness to non-foveal information and a greater proneness to distractibility, relative to neutral or negative mood (Biss & Hasher, 2011; Dreisbach & Goschke, 2004; Rowe et al., 2007). To investigate if positive mood was associated with such lower inhibitory control, we used a standard task, suited to measure response inhibition (i.e., the anti-saccade task, see Hallett, 1978), one of the best understood inhibitory mechanisms in the human brain.

In the general discussion, we integrate our novel scientific findings with the existing models and data available in the affective sciences literature. We also propose a new framework against which these new findings may be understood. There, we also

discuss the actual place occupied by positive mood in the classical taxonomy of attentional components.

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No evidence for dissociable effects of positive affect on convergent vs. divergent creative thinking using guided imagery as mood induction procedure

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ABSTRACT

Positive mood can broaden attention, enhance flexibility and foster creative thinking. In this study, we devised a new mood induction procedure (MIP) consisting of guided imagery and music to assess (i) whether it might enhance positive affect, when assessed using both subjective and psychophysiological measures, as well as (ii) influence creative thinking, when contrasting convergent to divergent thinking. The results showed that the MIP was successful to increase positive affect in the positive compared to the neutral mood group. However, we did not find evidence for concurrent mood-related changes in facial electromyogram (EMG) activity, nor the eye-blink rate. Likewise, positive mood did not influence convergent or divergent creative thinking. We discuss these findings in terms of a limited transfer of the beneficial effects brought about by the MIP to complex cognitive processes, such as creative thinking or reasoning.

INTRODUCTION

Positive affect and its influence on psychological wellbeing and cognition have received increasing interest during the last two decades. Instrumental to this shift away from negative affect in the affective sciences literature, is the broaden-and-build theory (Fredrickson, 2001, 2004; Fredrickson & Levenson, 1998), positing that positive emotions are associated with a larger attentional focus and expansion of the thought-action repertoire (Ashby, Isen, & Turken, 1999; Fredrickson, 2001, 2004; Fredrickson & Levenson, 1998). This theory is largely based on evidence suggesting that positive affect is associated with a flexible, integrative, open and creative cognitive style (see Estrada, Isen, & Young, 1997; Isen, 2000; Isen & Daubman, 1984; Isen, Daubman, & Nowicki, 1987; Isen, Rosenzweig, & Young, 1991), all cognitive functions important for creative thinking (see Baas, De Dreu, & Nijstad, 2011). In these older studies, positive mood was mostly induced by giving participants candy or gifts, or showing them funny movie clips. Hence, these MIPs use rewards to induce a positive feeling in participants and might elicit a rather brief increase in positive affect high in approach motivation. However, we were interested in testing how a more durable affective state, closely related to naturally occurring mild positive moods, could be triggered with an experimental MIP. Therefore, we developed a MIP based on guided imagery of personal experiences, selected by each participant individually. In the presented experiments, we aimed at putting this MIP to the test, both using self-reports, facial EMG and eye blink rate, as well as by trying to replicate previous findings of enhanced creative performance in positive mood.

Creative thinking and happiness: a positive relation?

Creativity is often regarded as a special talent of ingenious individuals. While early research focused mainly on trait-characteristics accounting for creativity, it is nowadays also aimed at delineating state-dependent factors that enable people to be creative, implicitly assuming that we are all capable of producing creative work or ideas to some degree (Byron & Khazanchi, 2012; Desseilles, Chang, Piguet, Bertschy, & Dayer, 2012; Hennessey & Amabile, 2010). In that sense, creativity can be defined as the production of ideas that are both novel and useful regarding the achievement of specific goals (Amabile, 1983; Byron, Khazanchi, & Nazarian, 2010; Shalley & Perry-Smith, 2001).

One of the most extensively assessed topics within this field of research is the link between positive affect and creativity. Research has suggested that positive mood and reward can enhance the capacity to adopt alternative cognitive perspectives and to organize ideas in a flexible manner (Isen & Daubman, 1984; Isen et al., 1987; Isen et al., 1991, see Ashby et al., 1999; Byron & Khazanchi, 2012 for review). However, other studies showed effects of positive mood only on specific components of creativity (Bartolic, Basso, Schefft, Glauser, & Titanic-Schefft, 1999; Vosburg, 1998), similar effects obtained with negative mood (Desseilles et al., 2012), and sometimes even costs associated with positive compared to negative mood (Kaufmann & Vosburg, 1997; George & Zhou, 2002).

One account, linking dopaminergic activation in the brain with cognitive flexibility and creative thought processes, might partly explain these discrepant findings (Chermahini & Hommel, 2010, 2012b). More specifically, the induction of positive mood would activate midbrain dopaminergic centra that modulate in turn neural activity in prefrontal cortical areas (Ashby et al., 1999), influencing cognitive functions such as working memory and task-switching. These two specific cognitive processes are presumably crucial for allowing creative thinking (Dreisbach, 2006; Floresco & Phillips, 2001; Kimberg, D'Esposito, & Farah, 1997). In line with this assumption, Chermahini and Hommel (2010, 2012b) found a relationship between positive mood, creativity and dopamine (DA). These authors used the spontaneous blink rate of participants as an indirect neurophysiological marker of DA levels, and found that the blink rate increased after the induction of positive mood. Furthermore, they found an inverted U-shaped relationship between blink rate and cognitive flexibility, showing that only when the baseline blink rate (and thus DA levels) was low, positive mood improved performance on creative thinking tasks (presumably by increasing brain DA), whereas performance dropped after the induction of positive mood when the baseline blink rate was already elevated.

In another, more complete attempt to reconcile the discrepant findings reported in literature, DeDreu and colleagues (De Dreu, Baas, & Nijstad, 2008) proposed in their dual pathway model that not valence alone, but rather the interaction of valence and arousal plays a key role in the link between mood and creativity. These authors suggest that arousal provides the necessary activation to engage in creative thinking, and that

different mood valences in combination with arousal can result in enhanced creativity via different routes: while positive mood leads to a greater cognitive flexibility and inclusiveness when categorizing information, negative mood will improve creative performance by enhancing cognitive perseverance and persistence. In the same line, the authors showed in a later study that activating motivational states will enhance creativity, independently of their focus on attaining desired outcomes or on preventing negative outcomes (Baas et al., 2011). Based on this reasoning, the induction of a specific mood can elicit both gains and costs for creative thinking, depending on the task used to measure it, through the enhancement of specific aspects of cognitive processing.

Hence, these findings and models might explain why earlier studies in the literature found either beneficial or detrimental effects of positive mood on creative thinking. Importantly, as already emphasized in De Dreu et al. (2008), creative thinking is not a monolithic construct, but it encompasses different components, including the dissociation between divergent vs. convergent thinking, as outlined in the next section.

Two complementary aspects of creativity: divergent vs. convergent thinking

Creativity has been tested using various methods, including free association, insight and problem solving tasks. These tasks mostly assess only a single component of creativity, either divergent or convergent thinking (Arden, Chavez, Grazioplene, & Jung, 2010; Baas et al., 2011). Tasks assessing divergent thinking are mostly open-ended and participants are instructed to generate as many solutions as possible to a given problem, reflecting the ability to come up with multiple alternative ideas (Arden et al., 2010; Dietrich & Kanso, 2010). The Alternate Uses Test (AUT; Guilford, 1967) assesses divergent thinking, and more specifically fluency, originality and flexibility of responses. In the AUT, participants are presented with three object words and are instructed to generate as many possible uses of the objects as possible, putting few constraints on their thinking process. However, a main critique of divergent thinking tests is that they are strongly focused on the novelty criterion, while the usefulness of responses is not properly evaluated (Davis, 2009). To address this concern, problem solving tasks with only one correct solution (Arden et al., 2010) can be used, such as the Remote Associates Task (RAT; Mednick, 1962) that measures convergent thinking.

The Dutch version of the RAT (Chermahini, Hickendorff, & Hommel, 2012) consists of several triads of words and the goal is to find, for each of them, the word that can form a common composed word or word combination (anagram). In order to find the solution, participants have to break down the three provided words into small entities/syllables and restructure them in order to make new, uncommon associations between these attributes. Since there is only one correct solution possible, cognitive control processes are probably necessary to find the single correct solution amongst all the possible options the participant might generate.

Hence, the RAT and the AUT are complementary to each other in the sense that they each measure a different component or facet of creative thinking (convergent and divergent thinking, respectively).

Because positive mood is thought to weaken inhibitory control and loosen cognitive control processes, resulting in a more flexible mindset and broader attention focus (Biss & Hasher, 2011; Biss, Hasher, & Thomas, 2010; Dreisbach, 2006; Rowe, Hirsh, & Anderson, 2007), this specific affective state might influence creative thinking, with dissociable effects for divergent (AUT) and convergent thinking (RAT).

Rationale for this study

In this study, we sought to test this prediction using a more stringent and better controlled MIP consisting of guided imagery (based on Holmes, 2006; Holmes, Coughtrey, & Connor, 2008; Holmes & Mathews, 2005, 2010) and music. Based on studies showing a special link between imagery and emotion (Conway & Pleydell-Pearce, 2000; Holmes & Mathews, 2005) and individual differences in susceptibility for mood states (Gomez, Cooper, & Gomez, 2000), participants personally selected and imagined to relive one of their most happy memories (or a neutral event in the neutral mood group) from autobiographic memory in our MIP. Moreover, attention was paid to bodily sensations (Kosslyn, Ganis, & Thompson, 2001), an important aspect of affective experiences (Kucera & Haviger, 2012).

We conducted two separate experiments. Before examining possible beneficial effects of positive mood on creative thinking using this specific MIP, we first aimed at validating it in a first experiment. More specifically, we assessed its effectiveness to induce and sustain moods in healthy adult participants by comparing the induction of a

positive mood with an active control condition using the same MIP with neutral content and affect, in a between-subjects design. We randomly allocated participants either to a positive or a neutral MIP, followed by mood-related questionnaires (i.e., subjective ratings) and an attention task (which will not be discussed here). Additionally, we recorded facial electro-myographic activity from the zygomaticus major (ZM; activated when smiling), and the corrugator supercilii (CS; activated when frowning), to investigate if the MIP might influence these facial EMG measures. Previous research showed that processing negative information or experiencing negative affect increased CS activation during passive viewing, while processing positive stimuli or experiencing feelings of happiness enhanced activity of the ZM (Achaibou, Pourtois, Schwartz, & Vuilleumier, 2008; Hess, Kappas, McHugo, Kleck, & Lanzetta, 1989; Larsen, Norris, & Cacioppo, 2003). Furthermore, there is also evidence showing that increases in positive affect can inhibit activation of the CS (Larsen et al., 2003).

In the second experiment, we used the same MIP as in the first experiment, but additionally asked participants to complete the RAT (convergent thinking) and the AUT (divergent thinking). Given that previous research suggested a link between positive mood and the spontaneous blink rate (indirectly reflecting DA brain activation, see Chermahini & Hommel, 2010), we compared the number of blinks participants made at baseline vs. after the MIP, when they performed either the RAT or the AUT.

We formulated several predictions. First, in both experiments, we expected an increase in positive affect (when measured using subjective reports) after the MIP compared to baseline, in the positive (and not the neutral) mood group. Moreover, we predicted that this increase would be specific to positive valence, in such a way that concurrent measures of negative affect would not be influenced by the MIP. Second, at the psychophysiological level, we tested if positive mood can increase ZM activation and/or lower CS activation compared to a neutral mood (Experiment 1), as well as increase the eye blink rate relative to baseline (Experiment 2). Regarding creative thinking (Experiment 2), we predicted that positive mood could facilitate performance on the AUT (when compared to a neutral mood control condition), given that this affective state might weaken inhibition and eventually facilitate divergent thinking. Our prediction regarding possible modulatory effects of positive mood on convergent thinking, and hence performance on the RAT, was less clear, and hence we will use a

more exploratory approach. The RAT contains an important additional component compared to the AUT, namely the pruning of different alternative options and the selection of a single correct one, presumably playing a role after a first phase of associative thinking. Hence, positive mood might actually exert different effects on these two sub-components and finally result in a null or even negative effect on performance in this task. Thus, depending on the outcome for the AUT, we will be able to deduce the influence of positive mood on convergent thinking. Accordingly, we did not formulate a clear directional effect for influences of positive mood on the RAT.

METHODS

Participants

Eighty undergraduate psychology students from Ghent University were recruited and participated either in Experiment 1 or 2. The 40 participants from Experiment 1 (age: $M = 23$; $SD = 5$; 9 males) received financial compensation for their participation. From the 40 participants (age: $M = 22$; $SD = 2$; 2 males) of Experiment 2, three participants received course credits and the others financial compensation. All participants gave written informed consent prior to participation and reported to be right-handed, to have normal or corrected-to-normal vision and no history of psychiatric or neurologic disorder. The study protocol was approved by the local ethics committee.

Materials

Mood Induction. Participants were allocated to either a positive or a neutral mood condition. A between-subjects design was used in both experiments to avoid possible carry-over effects between mood conditions. The MIP consisted of a guided imagery procedure in which participants were instructed to vividly imagine to re-experience an autobiographical/episodic memory (Holmes, 2006; Holmes et al., 2008). The MIP was preceded by a training phase, during which participants were instructed to imagine manipulating a lemon in order to train them in mental imagery from their own perspective (i.e. field perspective; Holmes, 2006; Holmes et al., 2008). During the MIP, participants were asked to recall and report a specific experience they had at least one week prior to the test session that made them feel either very happy (positive mood condition) or did not influence their mood (neutral mood condition). Next, participants

closed their eyes and tried to vividly imagine reliving the reported experience. After 30 seconds of imagining, the experimenter asked the participants questions about sensory sensations they experienced during mental imagery, in order to encourage concrete imaginations from the requested field perspective (Watkins & Moberly, 2009; based on Holmes et al., 2008). Then, participants imagined the recalled experience for another 30 seconds. During the memory recall, classical music was played in the background (Bower & Mayer, 1989; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007). During the task, the same music excerpt continued playing in order to trigger the corresponding mood. Participants were instructed to pay no attention to the music. Using a cover story making participants believe that the experiment concerned the relationship between the use of imagination and the processing of visual information (Experiment 1) or specific thinking styles (Experiment 2), we ensured participants remained naïve regarding the actual purpose of the MIP (see also Vanlessen, Rossi, De Raedt, & Pourtois, 2013, 2014 for a similar procedure).

Mood questionnaires. Changes in subjective levels of mood were measured by means of three 10 centimeters, horizontal Visual Analogue Scales (VAS) for feelings of happiness, pleasantness and sadness, the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988), and the Self-Assessment Manikin for Arousal (SAM; Bradley & Lang, 1994). The VASs were anchored with the labels 'Neutral' on the left end, and 'As happy/pleasant/sad as you can imagine' on the right end.

Facial electromyographic activity (Experiment 1). We recorded activity from the ZM and the CS in Experiment 1, during the attention task after the MIP, to assess whether positive mood could increase the activity of the ZM and/or decrease activity from the CS (in line with Achaibou et al., 2008; Larsen et al., 2003), compared to neutral mood. Participants were told that the electrodes were placed on the face in order to measure eye movements (CS) and tension (ZM). Hence, they remained naïve regarding the actual goal of these facial EMG measurements.

Eye blinks (Experiment 2). Spontaneous blinks were recorded in order to assess whether the blink rate increased after the positive mood induction, in line with a change in

activation of the underlying dopaminergic brain networks (Ashby et al., 1999; Colzato, Slagter, Spapé, & Hommel, 2008). For this purpose, we recorded the spontaneous eye blinks during a five minutes passive viewing task at the beginning of the experiment (e.g. baseline), where participants were instructed to look at a white fixation cross on a black screen. A second measurement period was implemented right after the MIP, during the first five minutes of the RAT or the AUT.

Computer version of the AUT. Three object words were presented: 'brick', 'newspaper' and 'shoe'. The words were written in black font against a homogenous white background. Participants were instructed to name as many uses they could think of for those three objects during a ten minutes period. When participants generated a solution (i.e., usage), they made a key press followed by a screen prompting them to name it out loud. Next, they pressed 'Enter' and the same three object words appeared again on the screen.

Computer version of the RAT. A validated Dutch version of the RAT was used (Chermahini et al., 2012). This version of the RAT consists of 22 combinations of three words and participants are instructed to generate a fourth word that can be combined with each of the three given words to form common compound words or phrases (e.g. AGE / MILE / SAND from the compound words STONEAGE, MILESTONE, and SANDSTONE, with the solution word STONE). Per word triad, only one solution was expected. In order to find the solutions, participants have to break down the information of the three given words into smaller entities and recombine these pieces of information using unconventional associations. The 22 word triads were displayed in a list in black font against a white background and were numbered from 1 to 22. When participants found the answer to one of the word triads, they were asked to make a key press and indicate the number of the word triad to which they provided an answer and their response. Next, participants pressed another key and the display comprising the 22 word triads was presented again.

Questionnaires. Participants were administered three trait-related questionnaires: the Beck Depression Inventory (BDI; Beck, Steer, Ball, & Ranieri, 1996), the BIS/BAS scales

(Carver & White, 1994) and the Dutch version of the Resilience scale (Rs; Portzky, Wagnild, De Bacquer, & Audenaert, 2010).

Procedure

First, participants were prepared for the EMG (Experiment 1) or eye blink (Experiment 2) recording. Participants in Experiment 2 were then instructed to attend a fixation cross during five minutes under fully passive viewing conditions, in order to record the baseline blink rate. Next, a positive or neutral MIP was administered, which was shortly (5 min) repeated after about seven minutes of task performance in Experiment 1, and between the RAT and AUT in Experiment 2, in order to preserve the targeted mood change throughout the entire experimental session. All participants in Experiment 2 performed both the RAT and AUT, each during ten minutes. The order of these two tasks was counterbalanced across participants, such that ten participants of each mood group first completed the RAT followed by the AUT, with a reverse order for the remaining ten participants. Instructions in both tasks emphasized to provide as many solutions as possible. Methodological differences between Experiment 1 and Experiment 2 are summarized in Figure 1.

VASs, PANAS and the SAM were administered at the beginning of both experiments (baseline measure), after each MIP, and at the end of the experiment, in order to detect possible changes in mood before, during and after the MIP.

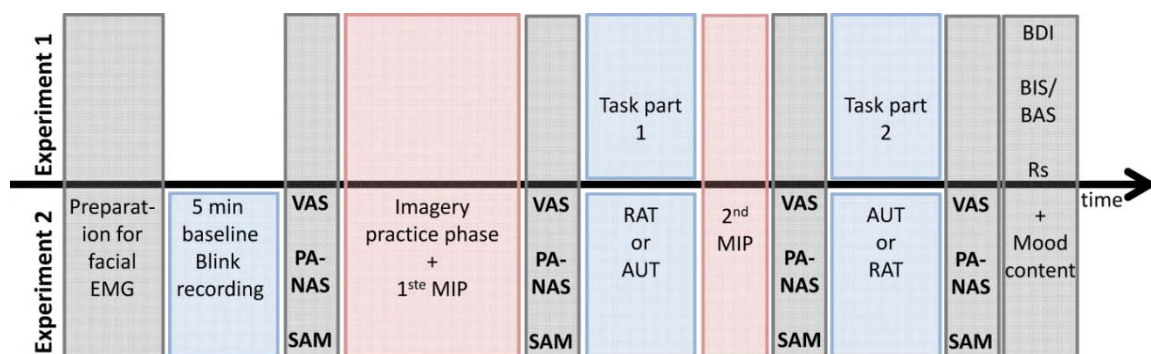


Figure 1. Illustration of the procedure used in Experiment 1 and in Experiment 2.

Once the experimental session was completed, participants filled out the three trait-related questionnaires. In addition, in Experiment 2, a questionnaire assessing the affective content of the memory participants used during the MIP was also

administered. In this questionnaire, participants were instructed to indicate which positive emotion best described their recalled experience, choosing from the ten presumably most common positive emotion nouns (amusement, awe, gratitude, hope, inspiration, interest, joy, love, pride and serenity; Fredrickson, 2009), plus two additional ones (euphoria and relief).

Analyses of behavioral data

To assess changes in mood, we first computed average post-MIP scores for each of the VASs, the PANAS and the SAM separately (average of the scores after the first MIP and the MIP repetition). Next, we performed a 2(Time: baseline vs. post-MIP) x 2(Mood: neutral vs. positive) mixed ANOVA, followed by independent T-tests. Three participants in Experiment 1 did not complete the SAM properly (two participants from the positive and one from the neutral mood group), and their data were therefore not included in the statistical analyses for this questionnaire.

In Experiment 2, three dependent variables were assessed for the AUT: fluency, originality, and flexibility (Chermahini et al., 2012). Following standard practice, *fluency* was defined as the numbers of different responses given by the participant, after possible repetitions of a given response were removed from the analysis. The *originality* of the responses was scored relative to the responses of all other participants. We first computed the probability to come up with a certain response. Based on these values, we assigned an originality score of 2 to responses that were given by only one participant and a score of 1 to responses that were given by two participants. Responses given by more than two participants received 0 points. Next, we calculated the originality score per participant by summing up the individual scores for all given responses. *Flexibility* was operationalized as the number of semantic categories the responses of a participant belonged to. First, we isolated several semantic categories. Next, two independent raters counted how many of these categories were used by each participant. Inter-rater agreement was satisfactory ($r = .89$)¹ after discrepancies between the two raters were reconciled through discussion.

¹ When raters use continuous scales to score responses, as is the case in this study, a correlation can indicate inter-rater reliability, while Cohen's kappa is rather used when categorical ratings are made by the raters (DeCoster & Claypool, 2004).

For the RAT, the number of correct responses was calculated. In line with previous research (Isen et al., 1987), we also compared accuracy scores for items of low, moderate and high difficulty between groups. We classified 21 of the 22 items RAT using these categories, based on the Item Response Theory item parameter estimations for difficulty and discrimination levels (Chermahini et al., 2012). In order to keep the number of items equal between categories (7), we excluded responses on one item, and separate scores were computed for the easy, moderate and difficult conditions. A mixed ANOVA was eventually performed with Mood (positive vs. neutral) and Difficulty (easy, moderate and difficult) on these scores.

Mean scores were calculated for the trait-related questionnaires and compared between groups using independent t-tests. Possible differences between groups in the affective content of the MIP (Experiment 2) were analyzed using non-parametric independent-samples Mann-Whitney U-Tests.

Psychophysiological data acquisition and reduction

ZM and CS (Experiment 1). Facial EMG was recorded from two pairs of external active Ag/Ag-Cl electrodes (Biosemi Active Two System) referenced online to the CMS-DRL ground and continuously sampled at 512 Hz. One electrode pair was placed on the zygomaticus major (smile) muscle and one pair on the corrugator supercilii (frown) muscle, on the left side of the face. Next, two channels were created, one for the CS and one for the ZM, by subtracting the activity of the lateral electrode from the medial one (i.e., closest to the nose). Next, a low cutoff filter of 20 Hz was applied, and a Root Mean Square transformation was applied to each channel separately. Mean activity was computed for a time period of two minutes after the first MIP and after the subsequent MIP repetition, for each muscle separately. These average values were compared between groups using independent sample t-tests.

Eye blinks (Experiment 2). Blink data were recorded from two active electrodes placed above and below the left eye (Biosemi Active Two System). Signals were referenced online to the CMS-DRL ground and continuously sampled at 512 Hz. The signal was referenced offline to the linked mastoids, using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). Next, a single vertical electro-ocular channel

(VEOG) was created by subtracting the activity of the lower from the upper left eye channel. Differences in amplitude exceeding 100 μV for this VEOG channel were semi-automatically detected and considered as blinks. Amplitude differences exceeding 100 μV and not corresponding to blinks (i.e., not showing the typical large, phasic, monopolar deflection) were discarded manually. Blinks were manually counted during baseline and during the first five minutes after the first and the second MIP. Next, we calculated a post-MIP average (after MIP1 and MIP2) and performed a mixed ANOVA with Time (baseline vs. post-MIP) and Mood (positive vs. neutral) as factors.

RESULTS

Changes in mood: manipulation check

The ANOVA on the VAS scores in Experiment 1 showed a significant interaction effect between Time and Mood for feelings of happiness (baseline: positive: $M = 5.86$, $SD = 2.50$, neutral: $M = 4.99$, $SD = 2.67$; post-MIP: positive: $M = 7.17$, $SD = 2.19$, neutral: $M = 4.22$, $SD = 2.31$; $F(1,38) = 18.40$, $p < .001$; see Fig. 2A, left panel), and pleasantness (baseline: positive: $M = 5.55$, $SD = 2.18$, neutral: $M = 4.91$, $SD = 2.48$; post-MIP: positive: $M = 7.11$, $SD = 2.03$, neutral: $M = 4.41$, $SD = 2.07$; $F(1,38) = 16.63$, $p < .001$), but not for sadness (baseline: $M = 1.03$, $SD = 1.83$, post-MIP: $M = 0.80$, $SD = 1.35$, $F(1,38) = 0.66$, $p = .42$). The follow-up independent T-tests showed a significant difference between the positive and the neutral mood group for both feelings of happiness ($t(38) = 4.15$, $p < .001$) and pleasantness ($t(38) = 4.16$, $p < .001$) for the post-MIP measures. Importantly, at baseline, VAS scores for happiness ($t(38) = 1.07$, $p = .29$) nor pleasantness ($t(38) = 0.87$, $p = .39$) differed between groups.

Likewise, for Experiment 2, we found a significant interaction effect between Time and Mood for feelings of happiness (baseline: positive: $M = 4.34$, $SD = 2.67$, neutral: $M = 4.83$, $SD = 2.53$; post-MIP: positive: $M = 6.17$, $SD = 2.22$, neutral: $M = 4.65$, $SD = 2.86$, $F(1,38) = 19.01$, $p < .001$; see Fig. 2B, left panel) and a marginally significant interaction effect for feelings of pleasantness (baseline: positive: $M = 5.14$, $SD = 2.36$, neutral: $M = 4.94$, $SD = 2.24$; post-MIP: positive: $M = 6.14$, $SD = 2.32$, neutral: $M = 4.58$, $SD = 2.58$, $F(1,38) = 4.02$, $p = .052$) while the interaction was not significant for the sadness scores (baseline: $M = 1.15$, $SD = 1.67$; post-MIP: $M = .82$, $SD = 1.10$, $F(1,38) = 1.47$, $p = .23$). Independent T-tests showed, as expected, no difference for reported

happiness ($t(38) = 0.60, p = .56$) and pleasantness ($t(38) = 0.28, p = .78$) between mood groups at baseline. Post-MIP mood measurements showed marginally significant differences between the positive and neutral mood group for post-MIP feelings of happiness ($t(38) = 1.87, p = .069$) and pleasantness ($t(38) = 2.01, p = .052$). These results showed a selective increase in positive affect after the MIP in the positive, but not the neutral mood group.

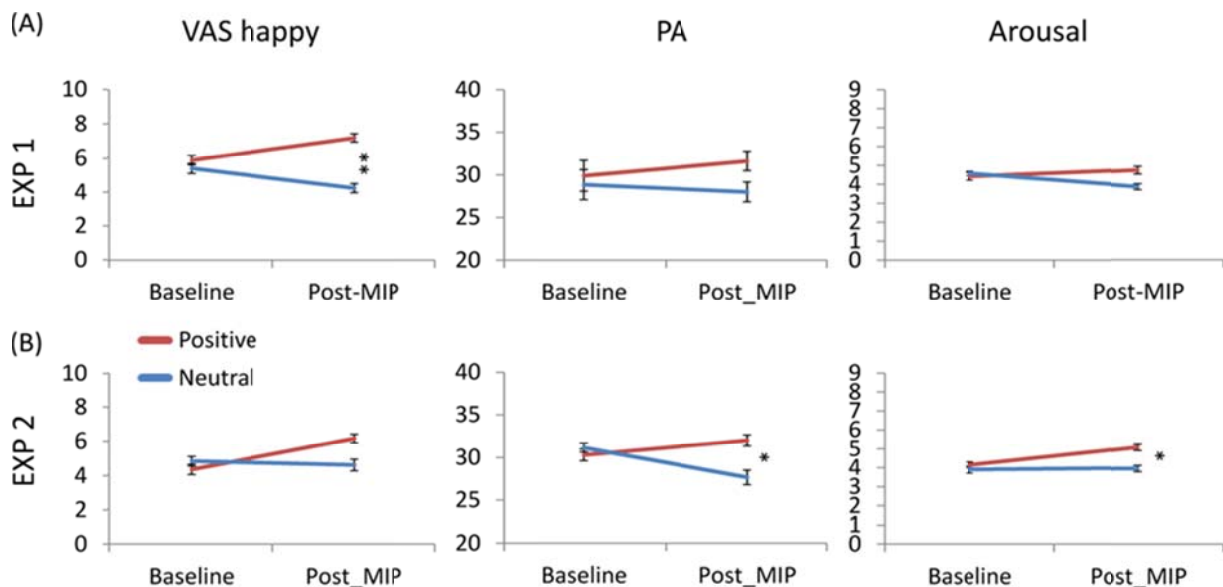


Figure 2. Results for the subjective reports, separately for A) Experiment 1 and B) Experiment 2. Results (means) are shown for the VAS happiness, the Positive Affect scale of the PANAS and the SAM for Arousal. The error bar represents one standard error of the mean.

The ANOVA on the PANAS scores in Experiment 1 showed no significant interaction effect between Time and Mood for the PA scales (baseline: $M = 29.38, SD = 7.93$; post-MIP: $M = 30.68, SD = 6.37, F(1,38) = 1.04, p = .31$; see Fig. 2A, middle panel), nor for the NA scales (baseline: $M = 13.85, SD = 5.13$; post-MIP: $M = 12.33, SD = 3.37, F(1,38) = 1.77, p = .19$).

In Experiment 2, the ANOVA carried out on the PANAS scores showed a significant interaction between Time and Mood effect for the PA scales (baseline: positive: $M = 30.30, SD = 6.14$, neutral: $M = 31.15, SD = 4.57$; post-MIP: positive: $M = 32.00, SD = 5.84$, neutral: $M = 27.65, SD = 7.61, F(1,38) = 19.09, p < .001$). As shown in Fig. 2B (middle panel), this interaction was mostly driven by a decrease in positive affect in the neutral mood group, as opposed to a genuine increase in positive affect in the

positive mood group. A marginally significant interaction effect was found for the NA scales (baseline: positive: $M = 14.15$, $SD = 3.75$, neutral: $M = 12.40$, $SD = 3.07$; post-MIP: positive: $M = 13.25$, $SD = 3.45$, neutral: $M = 12.93$, $SD = 4.65$, $F(1,38) = 3.79$, $p = .059$). Visual inspection indicated this trend was mainly driven by a lower level of NA in the neutral compared to the positive mood group. An independent T-test performed on the PA scores showed no significant difference between the positive and neutral mood group at baseline ($t(38) = 0.50$, $p = .62$), while groups differed significantly from each other in the post-MIP measure of the PA ($t(38) = 2.03$, $p = .05$).

The ANOVA performed on the Arousal scores for Experiment 1 showed a significant interaction effect between Time and Mood (baseline: positive: $M = 4.50$, $SD = 1.76$, neutral: $M = 4.58$, $SD = 1.02$; post-MIP: positive: $M = 4.78$, $SD = 1.82$, neutral: $M = 3.89$, $SD = 1.41$, $F(1,35) = 5.33$, $p = .027$; see Fig. 2A, right panel). However, an independent samples T-test on the Arousal scores showed no significant difference between the positive and neutral mood group after the MIP, $t(38) = 1.65$, $p = .11$, nor at baseline, $t(38) = 0.17$, $p = .86$.

In Experiment 2, similar results were obtained for arousal, as shown by a significant interaction effect (baseline: positive: $M = 4.15$, $SD = 1.39$, neutral: $M = 3.90$, $SD = 1.65$; post-MIP: positive: $M = 5.10$, $SD = 1.50$, neutral: $M = 3.86$, $SD = 1.43$, $F(1,38) = 9.43$, $p = .004$; see Fig. 2B, right panel). Independent T-tests showed a significant group difference after MIP ($t(30) = 2.68$, $p = .01$), but not at baseline ($t(38) = 0.52$, $p = .61$).

Altogether, the subjective reports of these two experiments converge and suggest a significant and selective increase in positive affect (and arousal) after the MIP in the positive mood group, whereas participants in the neutral mood group reported a stable mood throughout the experiment (with a slight decrease in positive affect after the MIP in this control group).

AUT (Experiment 2)

No significant differences between mood groups were found in fluency ($M = 25.70$, $SD = 8.58$; $t(38) = 0.11$, $p = .91$), originality ($M = 11.70$, $SD = 7.63$; $t(38) = 0.08$, $p = .94$) or flexibility ($M = 10.44$, $SD = 2.42$; $t(38) = 0.03$, $p = .97$; see Fig. 3A). We performed power analyses for the different outcome variables of the AUT, based on the mean and the between-groups comparison effect size observed in the present study (fluency, $d =$

0.03; originality, $d = 0.03$; flexibility, $d = 0.01$). These analyses showed that over 10,000 participants ought to be included in each group in order to obtain a significant group difference with the recommended power .80 (Cohen, 1988) for these variables. We also evaluated this based on the meta-analysis assessing positive mood effects on measures of creativity of Baas, De Dreu en Nijstad (2008), showing that the average power for such effects was low (with $r = .15$, transformed to $d = .30$; see Ellis, 2009). This second calculation showed that we would have to test 176 participants per group in order to find significant effects. Hence, although the sample size was modest in Experiment 2, the effect size for a modulation of creativity by positive mood appears to be very small in general.

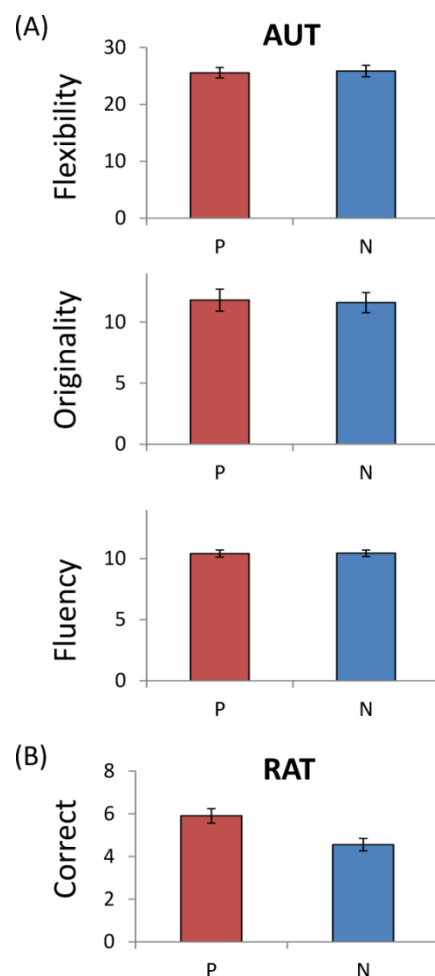


Figure 3. Results (means) for A) the AUT (fluency, originality and flexibility) and B) the RAT. 'P' stands for positive and 'N' for neutral mood group. The error bar represents one standard error the mean.

RAT (Experiment 2)

Similarly, the number of correct responses obtained with the RAT did not differ between mood groups ($t(38) = 1.51, p = .14$), although participants in the positive mood group generated numerically more correct responses than in the neutral mood group (positive: $M = 5.90, SD = 3.02$; neutral: $M = 4.55, SD = 2.63$; see Fig. 3B). Based on these results, we performed a power analysis and found that 71 participants should be tested per group, with a power set to 0.80 (see Cohen, 1988) and a medium effect size ($d = 0.48$) in order to obtain a significant mood effect.

A mixed ANOVA with Mood and Difficulty showed a significant main effect of difficulty ($F(2,76) = 16.70, p < .001$), but no interaction effect with mood ($F(2,76) = 0.57, p = .57$). The main effect of mood failed to reach significance ($F(1,38) = 3.08, p = .10$). Numerically, participants in the positive mood group generated more correct responses than in the neutral mood group, for each of the three difficulty levels (easy: positive: $M = 2.55, SD = 1.39$, neutral: $M = 1.80, SD = 1.51$; medium: positive: $M = 2.30, SD = 1.42$, neutral: $M = 1.75, SD = 1.21$; difficult: positive: $M = 1.05, SD = 1.32$, neutral: $M = 0.80, SD = 0.83$).

Questionnaires

No significant group differences were found in the scores on the trait-related questionnaires in either experiment (all $p > .19$), except for the subscale BAS Fun Seeking in Experiment 2, for which we found that the positive mood group ($M = 5.75, SD = 1.21$) scored lower compared to the neutral mood group ($M = 6.55, SD = 1.19$). These results suggest that the two groups were comparable along these personality characteristics.

A non-parametric analysis performed on the content of the memories used by the participants during the MIP (Experiment 2) showed that participants in the positive mood group reported more memories reflecting happiness ($p < .001$), pride ($p < .001$), joy ($p = .002$) and euphoria ($p = .001$) compared to the neutral mood group, while memories containing serenity were more often used in the neutral mood group ($p = .006$). All other positive emotion contents were only occasionally reported, equally so in both groups (all $ps > .28$).

Psychophysiological results

ZM and CS (Experiment 1). The independent t-test carried out on the mean ZM activity did not show a significant group difference (positive: $M = 2.03 \mu\text{V}$, $SD = 1.15$; neutral: $M = 2.49 \mu\text{V}$, $SD = 2.67$, $t(38) = 0.71$, $p = .48$). Likewise, we did not find a significant group difference for the mean CS activity (positive: $M = 2.42 \mu\text{V}$, $SD = 1.37$; neutral: $M = 3.22 \mu\text{V}$, $SD = 2.09$, $t(38) = 1.42$, $p = .16$), although a numerical decrease in CS activity in the positive compared to the neutral mood group was observed, in line with the assumption of a deactivation of the ‘frowning’ muscle during the encounter of positive mood or affect (Larsen et al., 2003).

Eye blinks (Experiment 2). The Time x Mood ANOVA showed a significant main effect of Time (baseline: $M = 81,33$, $SD = 44,18$; post-MIP: $M = 167,14$, $SD = 68,17$, $F(1,34) = 65.51$, $p < .001$). However, this effect did not interact with mood ($F(1,34) = 0.05$, $p = .94$), nor was the main effect of Mood significant ($F(1,34) = 0.52$, $p = .47$).

DISCUSSION

The goal of this study was twofold. First, we sought to assess whether our elected MIP was efficient to induce and maintain positive affect in a group of participants, when compared to another group of participants receiving a control MIP with neutral content. Changes in mood levels were characterized by means of subjective reports (VASs and questionnaires) and concurrent electrophysiological measurements (either facial EMG or blink rate). Second, we wanted to assess to what extent creative thinking could be influenced by positive mood, when breaking down this construct into divergent vs. convergent thinking. While the induction of positive mood clearly led to a marked increase in positive affect at the subjective level, no similar effects were found for the concurrent psychophysiological measures. Likewise, we did not find evidence for a systematic influence of positive mood on creative thinking, when operationalized as either divergent or convergent thinking. These results are discussed in that order here below.

MIP influences subjective reports but not psychophysiological measures

For the two experiments alike, manipulation checks confirmed that the MIP was effective in enhancing the experience of positive affect, in the positive mood group selectively. The impact of the MIP on the current mood state was most reliably captured by the VASs, showing a clear increase in levels of experienced positive affect in the positive but not the neutral mood group. Moreover, the VAS for feelings of sadness did not change in either group when comparing pre -to post-MIP measurements, indicating that our MIP specifically targeted positive affect. The scores on the positive affect scale of the PANAS also showed a difference between mood groups after the MIP, but only in Experiment 2. This effect seemed to be mainly driven by a decrease in positive affect in the neutral mood group, suggesting that positive mood helped to counteract a natural decline in positive affect over time due to fatigue or other uncontrolled factors. These results confirm that the PANAS may be less sensitive than VASs to capture subtle changes in the mood state of the participants (see Rossi & Pourtois, 2011). Presumably, the change in mood has to be (perceived as) quite substantial before the participant may decide to move up or down a category with the PANAS, while even subtle changes in mood might prompt participants to alter their position on a continuous VAS, especially when using a repeated-measures experimental design. Moreover, the VASs used here, with broad anchor terms, encompassed a wide range of positive affective states, regardless of their origin and nature, while the PANAS mainly focuses on enthusiasm, alertness and other positive emotions high in activation (Crawford & Henry, 2004; Russell & Carroll, 1999; Watson et al., 1988; Watson, Wiese, Vaidya, & Tellegen, 1999). Finally, we also found that subjective reports of arousal were influenced by the MIP, showing either a pre-post MIP decrease in the neutral mood group (Experiment 1) or a pre-post increase in the positive mood group (Experiment 2). These results suggest that our MIP targeting primarily a change in valence (i.e., positive affect) was nonetheless not neutral regarding arousal. This outcome is potentially important in the light of evidence showing that a moderate increase in arousal may enhance cognitive flexibility (De Dreu et al., 2008), and when combined with positive mood it can even boost creative thinking (Baas et al., 2008). However, as outlined in the next section, we did not find evidence for a change in creative thinking after the induction of positive affect with our MIP.

Unlike the subjective reports, our psychophysiological measures (ZM and CS in Experiment 1; blink rate in Experiment 2) failed to reveal a differential effect of positive compared to neutral mood. An important difference between our and previous studies is that we recorded either facial EMG (Experiment 1) or blink rate (Experiment 2) during task performance after the MIP, relative to a baseline measurement. By contrast, earlier studies assessing effects of positive stimuli or affect used passive viewing conditions (see Achaibou et al., 2008; Chermahini & Hommel, 2010; Larsen et al., 2003). However, in this study, we were interested in assessing whether positive mood might remain present during and transfer to a fully orthogonal task following the MIP, as revealed using independent psychophysiological measurements, thereby providing a more objective correlate of positive affect, besides subjective reports that are by definition likely less reliable (e.g., influenced by factors such as social desirability). Presumably, the task itself might have obscured any difference related to positive mood at the psychophysiological level, given that the putative influence of the task on psychophysiological measures is probably larger than the weak influence resulting from the (positive) mood per se. Additionally, the experimental setup with no baseline measure at rest is suboptimal given that it does not allow for comparison of EMG activity within each group, before and after the MIP. Accordingly, it remains to be established whether our MIP might lead to changes in facial EMG (ZM or CS activity) and blink rate when no specific task demands are required.

Creative thinking under positive mood: no straightforward facilitatory effect

Results of Experiment 2 did not confirm a modulatory effect of positive mood on creative thinking. Importantly, neither divergent (AUT), nor convergent thinking (RAT) was influenced by this variable. In the AUT, fluency, flexibility nor originality differed between the two mood groups. Similarly, the number of correct responses on the RAT was not different between groups, although difficulty clearly influenced task performance on this specific creative thinking test in the expected direction. While we obtained higher scores for the AUT for flexibility (Chermahini & Hommel, 2012a) as well as for fluency and originality (Colzato, Ozturk, & Hommel, 2012) compared with other studies using this test in a Dutch speaking population, the scores for the RAT were either higher (Chermahini et al., 2012; Chermahini & Hommel, 2012a), comparable

(Rowe et al., 2007) or lower (Colzato et al., 2012) relative to other studies finding effects of manipulations of the internal state of the participants. Hence, our null findings cannot be explained by a floor effect or an insufficient number of correct responses. While the modest sample size might explain these null findings, an auxiliary power analysis showed that even with several thousands of participants only a modest effect would have been found on the AUT. Importantly, these null findings could not be imputed to an inefficient induction of positive mood with our MIP, as contradicted by the results obtained for the self-reports. Hence, we found a clear dissociation between a successful induction of positive mood on the one hand, and a lack of transfer to creative thinking on the other.

Although speculative, we believe that several variables might have contributed to these null findings for creative thinking, both at the methodological and theoretical levels (see Hennessey & Amabile, 2010). First of all, the change in mood induced by our positive MIP, mainly reflecting positive emotions like happiness and joy, appears to be qualitatively different from positive affect used in earlier studies, reporting either a cost or a gain of positive mood on creative thinking and other higher-order cognitive functions. In these earlier studies, MIPs were primarily based on reward processing (e.g., candy, gifts or funny video's; Isen & Daubman, 1984; Isen et al., 1987; Isen et al., 1991; Van Steenbergen, Band, & Hommel, 2009) or the use of biologically relevant and approach-related (motivational) stimuli, such as food (Gable & Harmon-Jones, 2008, 2010). These approaches reliably differ from our MIP evoking a mild positive mood that did not imply any direct reward or change in motivation. The induction of positive mood in our study was not relevant in terms of task performance or other goals, and characterized by a low intensity in approach motivation. Presumably, our MIP could trigger a rather general and mild change in positive mood, similar to naturally occurring episodes characterized by positive mood in daily life situations that do not have necessarily an obvious, direct source or cause (cf. reward or motivation). Unlike reward, this subtle change in the current affective state of the participant may not be sufficient or optimal to reliably influence prefrontal-based cognition, such as creative thinking (see Byron & Khazanchi, 2012).

Second, it may be that the two tasks used in this study were actually not suited to investigate mood-dependent changes of complex cognitive functions, such as

divergent or convergent thinking. Presumably, many intermediate or latent mental processes take place between the presentation of the words on the screen and the generation of a solution by the participant, such as working memory, sustained attention and cognitive effort and cognitive flexibility (see Baas et al., 2011; De Dreu et al., 2008; Forster & Dannenberg, 2010; Hennessey & Amabile, 2010). It is currently unclear whether positive mood might influence all these steps in a diffuse way, or instead selectively target one of them. Moreover, it is likely that to resolve the task, positive mood might be beneficial for one of these sub-processes, but detrimental for another one, eventually cancelling out any 'raw' and measurable effect of positive mood on creative thinking. In fact, the solutions provided by the participants reflect a combination of all these versatile influences of positive mood on cognition, resulting in an outcome measure that is difficult to interpret or poorly sensitive to subtle changes in positive mood. Moreover, although the AUT and RAT have commonly been used in the literature to measure divergent and convergent thinking respectively, their validity to measure these specific processes can be questioned. In the AUT, participants are instructed to generate 'as many alternate uses as possible', biasing the output towards fluency rather than originality or flexibility. It is possible that instructions emphasizing the importance of producing 'as many *different* alternate uses as possible' might yield other results, perhaps showing a higher sensitivity to mood influences (Davis, 2009). Performance on the RAT on the other hand, is related to performance on certain measures of intelligence (Chermahini et al., 2012), which should by definition be stable and hence not influenced by changes in mood. The choice of the RAT as a measure of convergent thinking is further complicated by its reliance on both divergent and convergent thinking processes and the presumably opposing effects positive mood may have on those two thinking styles.

Finally, so far, no clear consensus regarding the nature of the mood-creativity link has emerged yet in the literature, and existing models do not make clear predictions about their relationship (see Baas et al., 2008; Hennessey & Amabile, 2010). A meta-analysis showed that effect sizes of mood effects on creativity measures are overall small, and the authors stated that 'to make a difference in creative performance, manipulating mood states is not very effective and is unlikely to produce clear and visible changes in creativity' (Baas et al., 2008, p. 797). They further concluded

that the mood-creativity link is probably more complex than only a matter of mood valence. Indeed, at least three additional factors contribute to strengthen this putative relationship: specific task features, mood intensity and attribution of the mood (Davis, 2009). Consistent with the latter factor, previous research showed that reward only affects creative output when it is directly linked to aspects of the task performance (Byron & Khazanchi, 2012), and it is thus plausible that the induction of mood orthogonally to the task obstructs a transfer to creative thinking. Hence, future research is needed to refine or break down the critical cognitive processes involved in creative thinking (Hennessey & Amabile, 2010), in such a way to enable researchers to make better predictions regarding the nature and extent of changes in creative thinking induced by positive mood.

Although the dominant broaden-and-build theory of positive affect bolsters the assumption that positive mood increases creative capacity through its hypothesized broadening effects on attention (Fredrickson, 2001, 2004), here we did not find evidence for this conjecture, despite the fact that our MIP was efficient in inducing positive mood. Importantly, we showed that it was the case both for divergent and convergent thinking, suggesting that putative effects of positive mood on creative thinking are probably more complex than initially thought (see Isen, 2000). Possibly, positive mood might modulate specific components of creative thinking, such as associative thinking. However, the AUT and RAT appear suboptimal to capture such effects, presumably because they each encompass a myriad of cognitive processes, influenced by positive mood in different ways and to different extents. Breaking down creative thinking into a set of fundamental cognitive processes might be valuable to better understand at which level (positive) mood might influence it.

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Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex : evidence from ERPs¹

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ABSTRACT

Recent evidence suggests that not only stimulus-specific attributes or top-down expectations can modulate attention selection processes, but also the actual mood state of the participant. In this study, we tested the prediction that the induction of positive mood can dynamically influence attention allocation and in turn modulate early stimulus sensory processing in primary visual cortex (V1). High-density visual event related potentials (ERPs) were recorded while participants performed a demanding task at fixation and were presented with peripheral irrelevant visual textures, whose position was systematically varied in the upper visual field (close, middle or far relative to fixation). Either a neutral or a positive mood was reliably induced and maintained throughout the experimental session. ERP results showed that the earliest retinotopic component following stimulus onset (C1) strongly varied in topography as a function of the position of the peripheral distractor, in agreement with a near-far spatial gradient. However, this effect was altered for participants in a positive, relative to neutral mood. On the contrary, positive mood did not modulate attention allocation for the central (task-relevant) stimuli, as reflected by the P300 component. We ran a control behavioral experiment confirming that positive mood impaired attention allocation to the peripheral distractors, selectively. These results suggest a mood-dependent tuning of position specific encoding in V1 rapidly following stimulus onset. We discuss these new results against the dominant broaden-and-build theory.

¹ Vanlessen, N., Rossi, V., De Raedt, R., & Pourtois, G. (2013). Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex: evidence from ERPs. *Cogn Affect Behav Neurosci*, 13(1), 60-79. doi: 10.3758/s13415-012-0130-x

INTRODUCTION

Sensory stimulus processing is not only determined by bottom-up physical characteristics, but also by top-down cognitive or affective processes. In this framework, mood has been shown to shape the way incoming information is attended and eventually processed (Gray, 2001, 2004). According to Fredrickson's influential broaden-and-build theory, negative and positive emotions have opposing but complementary functions (Fredrickson & Levenson, 1998): while negative emotions can narrow the thought-action repertoires of an individual, positive affect can substantially broaden thinking styles and these thought-action repertoires. Positive affective states elicit a broadening of the scope of attention (Derryberry & Tucker, 1994), eventually enabling an open (Estrada, Isen, & Young, 1997), creative (Isen, Daubman, & Nowicki, 1987), integrative (Isen, Rosenzweig, & Young, 1991) and flexible (Isen & Daubman, 1984) way of thinking. In a similar vein, cognitive control abilities, and more specifically conflict adaptation, are reduced following the transient induction of positive mood (Van Steenbergen, Band, & Hommel, 2009, 2010).

Interestingly, recent findings suggest that a weakening of inhibitory control processes provides a plausible mechanism to account for a broadening of attention after the induction of positive emotion (Rowe, Hirsh, & Anderson, 2007; Wang et al., 2011). In this framework, loosening up inhibitory processes would result in a broader information processing style, and hence a less narrowed attention focus. As a result, individuals in a happy mood would become more receptive to irrelevant information, allowing distracting stimuli to interfere more strongly with goal-relevant stimuli (Dreisbach & Goschke, 2004). Thus, positive emotion would primarily reduce inhibitory control mechanisms (i.e., decrease attention selectivity), eventually leading to a less selective mode of stimulus processing, consistent with the predictions of the broaden-and-build theory. While this mechanism could, on the one hand, explain an enhanced distractibility under positive mood, it might, on the other hand, also enable people to think in a more creative and flexible way, because they could learn more efficiently from incidental opportunities (Biss & Hasher, 2011; Biss, Hasher, & Thomas, 2010). Whereas many studies have already focused on these gains and drawbacks in higher level cognition and reasoning under positive mood (Ashby, Isen, & Turken, 1999; Biss & Hasher, 2011; Biss et al., 2010; Fredrickson, 2001; Fredrickson & Levenson, 1998; Isen,

2000), the actual *modus operandi* of positive emotion on attention still remains largely underspecified. More specifically, an unanswered question is how positive emotion may dynamically shape and transform attention control mechanisms, such that a broader attentional scope can eventually bias early sensory stimulus processing, leading to the enhancement of both creativity and distractibility. A decreased attention control in this condition might underlie these behavioral phenomena.

Attention control usually refers to different brain mechanisms enabling a fast and efficient selection of relevant information in the environment (Desimone & Duncan, 1995; Posner, Snyder, & Davidson, 1980). Not only perceptual salience, novelty or unexpectedness determine the ease of attention selection (bottom-up factors; see Egeth & Yantis, 1997; Wolfe & Horowitz, 2004), but prior knowledge, expectations as well as mood reliably influence early sensory stimulus processing (top-down factors; see Corbetta & Shulman, 2002). Thus, both top-down and bottom-up attention processes exert control over sensory stimulus processing in such a way to gate the flow of incoming information, and eventually facilitate the selection of relevant stimuli, while filtering irrelevant information from further processing (Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Theeuwes, 2010). Interestingly, it has been suggested that prefrontal cognitive control regions are swiftly recruited in order to downplay the interfering effect potentially created by distractors, and eventually maintain an efficient attention selection process (Lavie, 2005; Lavie, Hirst, de Fockert, & Viding, 2004). However, these attention control systems are dynamic and not immune to changes in affective states (see Desseilles et al., 2009; Gray, 2004; Rossi & Pourtois, 2012; Rowe et al., 2007). Nonetheless, effects of positive emotion on these attention control mechanisms eventually gating early sensory processing as early as in V1 have been much less explored than effects of negative emotion (Stolarova, Keil, & Moratti, 2006; West, Anderson, Ferber, & Pratt, 2011).

Accordingly, the goal of our study was to investigate, using state of the art Event Related Potentials (ERP) methods (Experiment 1) and standard behavioral measures (Experiment 2), possible downside effects of positive mood on early sensory stimulus processing, presumably resulting from a change in top-down attention control mechanisms. Participants performed a demanding task at fixation, while distractors were presented in the upper visual field at an unpredictable time and location relative

to these task relevant stimuli (Schwartz et al., 2005). This set up is suited to explore, using high density EEG measurements, changes in the spatial gradient of visual attention towards the peripheral distractors, while fixation is maintained at a constant location in the center of the screen (Pourtois, Delplanque, Michel, & Vuilleumier, 2008; Rauss, Schwartz, & Pourtois, 2011; Rossi & Pourtois, 2012). Because we used eccentric/peripheral visual stimuli, we could record a reliable C1 ERP component reflecting an early retinotopic encoding of the stimulus in V1, being however sensitive to top-down attention control effects (Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rauss et al., 2011; Rossi & Pourtois, 2012). The C1 usually peaks ~50-100 ms after stimulus onset over central occipito-parietal scalp positions (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Jeffreys & Axford, 1972). In accordance with the cruciform organization of the primary visual cortex and calcarine fissure, the amplitude and polarity of the C1 substantially change as a function of the position of the stimulus in the visual field (Clark, Fan, & Hillyard, 1995).

In Experiment 1, we therefore capitalized on these well-defined electrophysiological properties and investigated whether the C1 component could vary in size and topography not only according to the actual position of the distractor stimulus shown in the upper visual field (i.e. larger negative component for position close to fixation, relative to far), but also with the actual mood of the participant (either happy or neutral). We tested the prediction that the selectivity for early spatial encoding of distractors in V1, at the level of the C1, would decrease after the induction of positive mood. This effect could result from a modulation of top-down attention control mechanisms by positive mood (Rowe et al., 2007), eventually resulting in a decreased position specific selectivity at a more basic perceptual level. More precisely, we surmised that the normal reduction of the C1 with increasing distance of the distractor, relative to fixation, would be less pronounced in participants in a positive mood, relative to a neutral mood, consistent with a broadening of attention.

We also explored possible effects of positive mood on later ERP components in response to the peripheral distractors. Unlike the striate C1, the extrastriate P1, peaking ~100-150 ms post stimulus onset over occipital leads, is mostly sensitive to the content and not to the position of the stimulus within the visual field (Gomez, Clark, Fan, Luck, & Hillyard, 1994; Herrmann & Knight, 2000; Martinez et al., 1999), but can also vary

depending on the affective state of the participant (Moriya & Nittono, 2011). Moreover, the amplitude of the P1 is typically larger for attended, relative to unattended stimuli, consistent with a gain control mechanism of visual attention exerting modulatory effects in the extrastriate visual cortex (Hillyard & Anllo-Vento, 1998; Martinez et al., 1999). Finally, we were also interested in possible effects of mood on the processing of central, task relevant stimuli. The efficiency of central target stimulus processing was mostly assessed by means of the decision-related P300 component, whose amplitude strongly varies with the amount of resources allocated to task demands (Ericsson, Olofsson, Nordin, Rudolfsson, & Sandstrom, 2008; Kok, 2001; Polich, 2007; Polich & Kok, 1995). Moreover, because this component was recently shown to vary with the (negative) affective state of the participant (e.g., Shackman, Maxwell, McMenemy, Greischar, & Davidson, 2011), we tested whether attention allocation towards central (task-relevant) stimuli could also be altered after the induction of positive mood or not.

To corroborate the assumption of a drop in early attention selectivity for the peripheral textures following the induction of positive mood, we ran an additional behavioral experiment. In Experiment 2, participants were asked to explicitly discriminate the content of these peripheral stimuli (in addition to the centrally-presented stimuli at fixation). We reasoned that if the effect of positive mood may correspond to a change in prefrontal attention control mechanisms, and hence early sensory stimulus selectivity, the visual processing of these peripheral stimuli may be impaired, compared to a control condition (i.e. neutral mood).

Previous research has shown that an increased attentional scope is associated with a loss in spatial resolution and processing efficiency, as compared to a detailed processing when the attentional scope is narrowed around a specific portion of the visual field (Carrasco, 2011; Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985; Ivry & Robertson, 1998; Müller, Bartelt, Donner, Villringer, & Brandt, 2003). Thus, if positive mood can broaden the attentional scope, processing over larger portions of the space can cause a drop in spatial resolution, compared to a smaller attentional scope in a neutral mood. Hence, such an impairment in early spatial encoding selectivity would in turn constrain the capacity to perform a visual discrimination of the peripheral stimuli based on the processing of local (geometric) features.

Experiment 2 also enabled us to confirm whether the processing of the centrally presented stimuli would be unchanged in a positive mood, relative to a neutral mood, in line with the results obtained in Experiment 1.

METHODS

Participants

We tested 70 participants who were all right-handed, had normal or corrected-to-normal vision and no history of psychiatric or neurologic disorder according to a self-report questionnaire. All participants were undergraduate psychology students from Ghent University and all gave written informed consent prior to participation. From the thirty-four participants recruited for Experiment 1 (age: $M = 22$; $SD = 2$; 7 males), seventeen were randomly assigned to the positive mood condition and seventeen to the neutral mood condition. One participant in the neutral mood group reported not being able to use imagery, making the implementation of the mood induction procedure (MIP) impossible. Therefore, data for this participant were excluded from further analyses. In Experiment 2, 36 undergraduate students (age: $M = 19$; $SD = 1$; 3 males) were randomly assigned either to the neutral or positive mood condition (18 participants per condition). The data of one participant from the neutral mood group were excluded from further analysis because of excessive slow RTs for the detection of central targets (mean $\pm 2,5$ SDs). Results are reported for the 35 remaining participants. Subjects participated in exchange for course credits (32) or financial compensation (38).

Materials

Mood Induction. We used a between-subjects design to induce either a sustained positive or a neutral/control mood, suited to avoid possible carry-over effects between different mood conditions. Participants were naïve regarding the purpose of the MIP. A cover story was told in order to make participants believe that the experiment concerned the relationship between the processing of visual information and the use of imagination. Mood was induced by means of an imagery procedure where participants were instructed to vividly imagine reliving a happy or neutral autobiographical memory (Holmes, 2006; Holmes, Coughtrey, & Connor, 2008). First, participants were trained in taking a field perspective (i.e. imagining from one's own perspective) during mental

imagery (Holmes, 2006; Holmes et al., 2008). Next, participants were instructed to recall and report an event that happened on a specific day, more than one week ago, which made them feel either very happy (positive mood group) or that did not elicit any specific emotion (neutral mood group) using episodic memory. Participants were then asked to close their eyes and to vividly imagine reliving the recalled experience. Participants were encouraged to use concrete visualizations and to take the requested field perspective while imagining (Watkins & Moberly, 2009; based on Holmes et al., 2008). Participants then imagined the recalled experience for 30 seconds (twice), interrupted by questions about what they could see, hear and feel (based on Watkins & Moberly, 2009). Classical music fragments started to play during the memory recall and continued to play throughout the experiment sessions, such that the music would serve as implicit trigger for the corresponding mood. In Experiment 1, the same (neutral) music samples were played in both mood groups in order to balance possible interference effects created by the music on the recorded EEG signal. However, in order to elicit stronger mood inducing effects and a conditioned context that was better adjusted to the targeted mood, we used ‘happy’ music in the positive mood condition and neutral music in the neutral mood condition in Experiment 2². These music samples were validated in previous research (Bower & Mayer, 1989; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007).

To measure subjective levels of mood, participants were asked to indicate how they felt using the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988) and three 10 centimeters, horizontal Visual Analogue Scales (VAS) for feelings of happiness, pleasantness and sadness. The left anchor of the VAS was labeled ‘Neutral’, while the right one was labeled ‘As happy/pleasant/sad as you can imagine’.

Attention Task. We adapted a standard experimental paradigm (Schwartz et al., 2005; Rauss et al., 2009; Rossi & Pourtois, 2012). The task was programmed using E-Prime, Version 2 (Psychology Software Tools, Inc., 2001). Participants were instructed to

²We performed a control study (n=15) to assess if the music samples alone, without the MIP, could have influenced the behavioral results in Experiment 2. Therefore, participants performed the dual attention task while either positive music fragments (3 blocks) or neutral music fragments (3 other blocks) were played in the background. Subjects were instructed to pay no specific attention to the music. No MIP was administered. The results showed that neutral and positive music samples did not differentially influence accuracy or RTs for the central task, nor for the discrimination of peripheral textures, suggesting that the MIP, and not the use of different music samples alone, modulated attention allocation in the upper visual field (Experiment 2).

carefully attend to a rapid serial visual presentation (RSVP) of short tilted lines (1 cm) at central fixation (Fig. 1). In Experiment 1, participants silently counted the occurrences of deviant lines within each block and reported this value at the end of the block, while in Experiment 2 they were instructed to press a key with their left finger whenever they could detect online the occurrence of a deviant line. Deviant lines were tilted 45° and standard lines 35° counterclockwise from the vertical axis. The ratio standard/target was 4:1, with the number of deviant lines varying between 8 and 12 per block. Because previous studies have confirmed that this task requires central/foveal vision and sustained attention (see Rauss et al., 2009; Rossi & Pourtois, 2012; Schwartz et al., 2005), we used it to ascertain that participants were fixating at the center of the screen where these short lines were presented. Decoupled from this central RSVP, uniform visual textures were shown in the upper visual field at an unpredictable location (i.e. one out of three locations) and time (i.e. variable SOA between central stimulus offset and peripheral texture onset) relative to the central stimuli (Fig. 1A and B). The experiment consisted of a total of 300 central stimuli (i.e., 240 standard and 60 target lines), and 150 peripheral stimuli (i.e., 120 after the presentation of a central standard line and 30 after a central target line). The peripheral stimuli consisted of two arrays of quadrangle elements forming a homogenous visual texture (3° x 34° of visual angle), briefly flashed in the upper visual field at 5.3° (Close), 7.8° (Middle) or 10.3° (Far) from central fixation (see Fig. 1A). Two different types of quadrangle elements (0,5 cm wide x 0,4 cm high or 0,6 cm wide x 0,3 cm high, see Fig. 1C) were used, with 25 presentations of each type at each location.

These peripheral textures were task-irrelevant (i.e., distractors) in Experiment 1, as opposed to Experiment 2 where participants were invited to discriminate the actual content of visual textures (either type 1 or 2, based on the actual quadrangle elements; i.e., dual task setting). In the latter experiment, a fixation cross was presented again at the offset of the visual texture and remained on the screen until participants pressed one out of two keys using their right hand (stimulus-response mapping was alternated across participants). A reminder of the stimulus-response mapping was shown at the beginning of each block. Stimuli were grey and presented against a uniform black background. Participants were seated at 57 cm in front of a 19" CRT screen, with their head movements restrained by a chinrest.

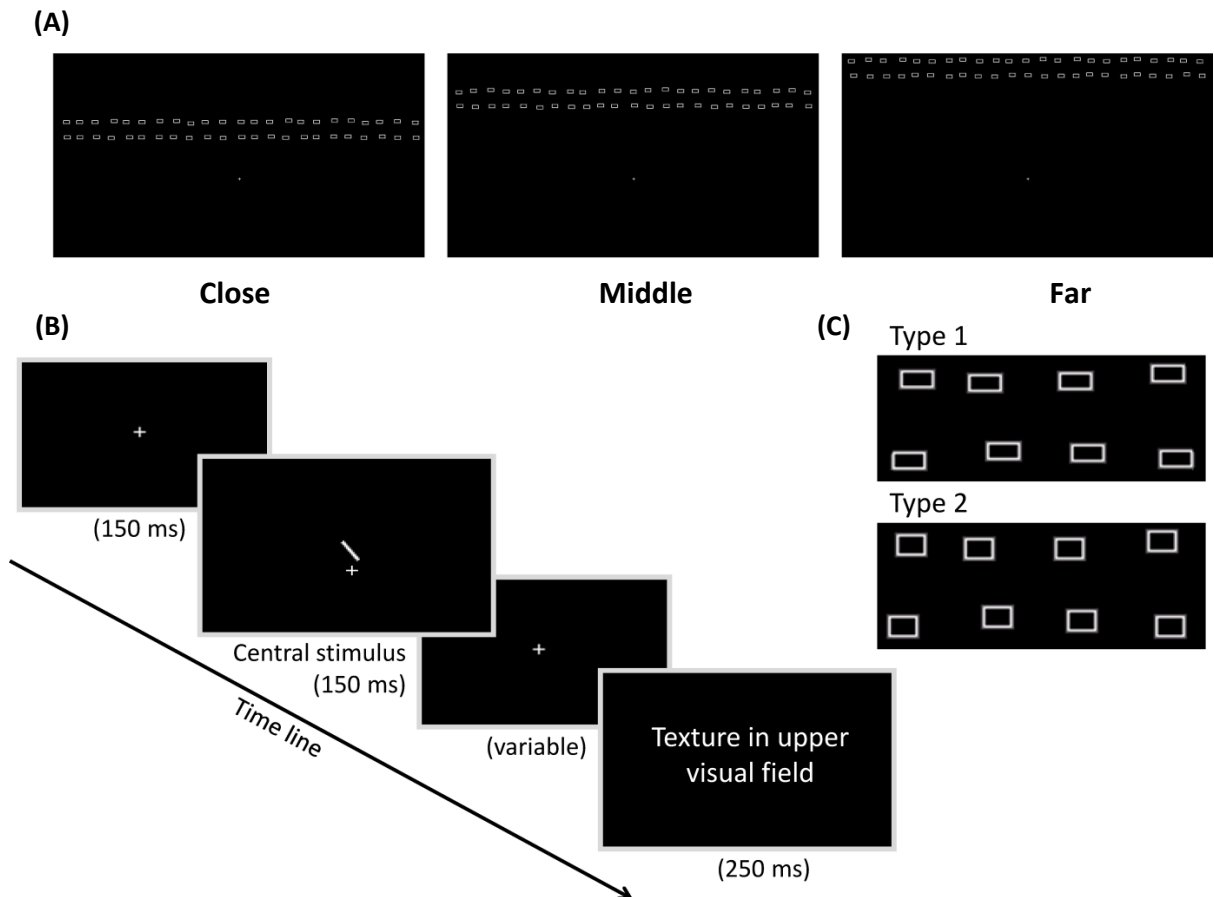


Figure 1. Task. (A) Visual textures were briefly presented in random order at one out of three possible locations in the upper visual field: close to fixation, at middle distance or far from fixation. These textures had to be ignored during the EEG experiment, but were task-relevant in the behavioral experiment. In this case, participants were asked to judge whether the elements forming each texture were either quadratic or rectangles, while keeping fixation in the center of the screen. (B) The main task at fixation (shared across the two experiments) consisted of an oddball line orientation task. Participants were asked to detect covertly (EEG experiment) or overtly (behavioral experiment) deviant line orientations embedded in a RSVP at fixation. Standard lines were tilted 35° counterclockwise, while deviant lines were tilted 45° in the same direction. The ratio between standard and target orientations was 4:1. The fixation cross after the line stimulus was shown for 250-500 ms in the EEG experiment and for 500-750 ms in the behavioral experiment. In half of the trials (random order), a visual texture was briefly presented (250 ms) at one out of three positions in the upper visual field, at a variable time following the presentation of the central line. In the other half, no texture was presented. Hence, the appearance and actual location of the visual textures were unpredictable, and their presentations never overlapped with the centrally presented lines appearing on the screen roughly every 775 ms in the EEG experiment, and every 1025 ms in the behavioral experiment. (C) Half of the peripheral textures were made up by one type of quadrangle elements (0,5 cm wide x 0,4 cm high), whereas the other half had slightly different quadrangle elements (0,6 cm wide x 0,3 cm high), with an equal number of presentations of each type for each of the three locations.

Localizer. In order to identify the C1 and obtain independent evidence that the earliest visual ERP component recorded during the main attention task for the peripheral textures genuinely corresponded to a retinotopic C1, we administered to participants of Experiment 1 two extra blocks of peripheral textures only, under passive viewing conditions at the end of the experimental session (see Rossi & Pourtois, 2012). In these blocks, no RSVP was imposed at fixation. In each block, 120 stimuli were presented in random order, with an even number of presentations at six possible locations (upper or lower visual field: close, middle, or far from fixation). The localizer blocks were administered at the end of the experiment in order to avoid unwanted priming effects, since they remained fully task-irrelevant in Experiment 1, in agreement with previous research (e.g. Rossi & Pourtois, 2012). Moreover, residual effects of (positive) mood were expected to be minimal during these final blocks, because no repetition of the MIP took place prior to them.

Procedure

In Experiment 1, participants were first prepared for EEG recording. Participants completed a practice session containing two blocks of 20 trials (in total, 32 standard lines, 8 target lines), which were repeated until 80% of the (deviant) central lines were reported correctly. Next, positive or neutral mood was induced by means of the MIP, which was shortly (5 min) repeated at the end of Block 3 in order to maintain the targeted mood throughout the experimental session. Participants completed six different blocks of 50 trials each of the attention task. Each trial started with the presentation of a fixation cross (250 ms), followed by a central line (150 ms) at the same location (see Fig. 1B) and again a fixation cross, displayed for the duration of the SOA (average duration in Experiment 1: 375 ms, randomly varying between 250 and 500 ms; in Experiment 2: 625 ms, randomly varying between 500 and 750 ms). After the SOA, in half of the trials a visual texture was flashed for 250 ms at one of three possible locations in the upper visual field; in the other half of the trials, only the fixation cross remained on screen for the same interval. Trials were presented in a semi-random order. The first three stimuli in a block never contained a target line, nor a peripheral distractor. Instructions emphasized the highest accuracy possible for the task at fixation (Experiments 1-2), as well as both accuracy and speed for the two-alternative forced

choice task performed with the peripheral textures (Experiment 2). In addition, instructions given to participants of Experiment 2 clearly emphasized the importance of a high accuracy for the primary task at fixation and the need to maintain attention focused at this central location throughout the whole experiment. VASs and PANAS were administered at the beginning of the experiment (baseline measure), after each MIP, and at the end of the experiment in order to observe possible changes in mood before, during and after the MIP.

Once the experimental session was completed, participants filled out four trait-related/personality questionnaires: the Beck Depression Inventory (BDI; Beck, Steer, Ball, & Ranieri, 1996), the Spielberger State-Trait Inventory – trait version (STAI-T; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983), the BIS/BAS scales (Carver & White, 1994) and the Spontaneous Use of Imagery Scale (Reisberg, Pearson, & Kosslyn, 2003).

To sum up, in both Experiment 1 and 2, participants performed a main oddball detection task at fixation, whereas peripheral textures were briefly flashed during the ISI in the upper visual field at an unpredictable time and location. However, in Experiment 2, these peripheral textures were task-relevant and they required an overt visual discrimination, while in Experiment 1 (EEG) they remained task-irrelevant. Additional methodological differences between the two experiments concerned (i) the music played in the background during the experiment (i.e. same neutral samples for both groups in Experiment 1 vs. neutral or positive samples in Experiment 2), and (ii) specific task demands for the central stimuli (i.e. in Experiment 1, the deviant lines had to be detected and counted silently by the participants before reporting this number at the end of each block, whereas in Experiment 2, participants had to make online a specific key press whenever detecting them).

Analyses of behavioral data

Changes in mood were verified by comparing post to pre-MIP subjective measures of affect. We first computed post-MIP average scores for each VAS and the PANAS administered after the two MIPs and at the end of the experiment. Next, we performed a 2 (Time: baseline vs. post-MIP) x 2 (Mood: neutral vs. positive) mixed ANOVA on the VASs and the PANAS scores, followed by independent T-tests (planned comparisons).

For the four trait-related questionnaires, mean scores were calculated and compared between groups in order to check for possible uncontrolled personality differences between groups.

In Experiment 1, accuracy for the oddball task at fixation was computed for each participant separately by subtracting the reported number from the actual number of deviant lines and the sum of these deviations was computed for the six blocks. Next, these numbers were compared between groups using an independent Student T-test. In Experiment 2, accuracy and reaction times (RTs) for the central task were compared between groups using independent t-tests. Performance for the peripheral textures (accuracy and RTs) was analyzed using mixed ANOVAs, with the within-subject factor Position (close, middle or far) and the between-subject factor Mood (positive vs. neutral). Trials with errors on the central task, as well as RTs exceeding $\pm 2,5$ SDs above or below the individual mean RT on both central and peripheral tasks were excluded from further analysis. The exclusion rate did not differ between the two mood groups (positive: $M = 9.57\%$, $SD = 3.70$; neutral: $M = 7.94\%$, $SD = 3.48$), $t(33) = 1.34$, $p = 0.19$). Statistical analyses were run on 91.22% of the total data.

Greenhouse-Geisser correction was applied when assumptions of sphericity were violated. In these cases, we reported corrected p-values and uncorrected degrees of freedom.

EEG data acquisition and reduction

EEG data were recorded from 128 electrodes placed according to the extended 10-20 EEG system using an elastic cap (Biosemi Active Two System). Vertical and horizontal eye movements were recorded by means of additional bipolar electrodes placed respectively above and below the left eye, and on the outer canthi of both eyes. EEG signals were referenced online to the CMS-DRL ground and continuously sampled at 512 Hz.

EEG signals were referenced offline to the linked mastoids, using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany). Band-pass filters between 0.016 and 70Hz and a notch-filter (50Hz) were used. The filtered data were then segmented into stimulus-locked epochs using a segmentation window of 100 ms pre- and 800 ms post-stimulus onset. Eye-blink artifacts were automatically corrected by

means of the standard procedure put forward by Gratton and colleagues (Gratton, Coles, & Donchin, 1983), and individual epochs were baseline corrected using the entire pre-stimulus interval. Epochs of the EEG containing residual artifacts exceeding $\pm 75\mu\text{V}$ were semi-automatically rejected. Noisy electrodes were interpolated using a spherical splines procedure. Individual averages were computed, separately for each condition. Finally, a 30Hz low-pass filter was applied before the calculation of grand average waveforms.

To characterize and analyze ERPs to the peripheral distractors, we performed a detailed ERP topographic mapping analysis. The added value and underlying principles of this data-driven analysis have been described extensively elsewhere (Michel, Seeck, & Landis, 1999; Murray, Brunet, & Michel, 2008; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Pourtois, De Pretto, Hauert, & Vuilleumier, 2006; Pourtois et al., 2008; Pourtois, Thut, de Peralta, Michel, & Vuilleumier, 2005). Since the C1 is primarily a location-sensitive early visual ERP, the exact same stimulus elicits a different topography and strength of the C1 electric field depending on its actual position in the peripheral visual field (Clark et al., 1995). Accordingly, we used a standard ERP topographic mapping analysis able to capture these changes in the expression of the electric field (i.e. topography) of the C1 as a function of stimulus position. Using a K-means spatial cluster analysis, we first identified in the grand average data the dominant scalp topographies corresponding to the C1 (95-115ms post-stimulus onset) and P1 (165-185ms post-stimulus onset) components generated in response to the peripheral distractors, as well as P300 (400-600 ms post-stimulus onset) in response to the centrally-presented line stimuli. The following standard parameters were used: average reference; number of random trials: 100; smoothing strength (Besag factor) of 10; smoothing half window size of 3; merging of clusters correlating above 0.92; rejection of segments less or equal to 3 time-frames; no sequentializing. These topographic maps were determined objectively using both cross validation (Pascual-Marqui, Michel, & Lehmann, 1995) and Krzanowski-Lai criteria (Pascual-Marqui et al., 1995; Tibshirani, Walther, & Hastie, 2001). Following standard practice, these dominant scalp topographies were then fitted back to the ERPs of each individual participant using spatial fitting procedures to quantitatively determine their representation across subjects and conditions. The Global Explained Variance (GEV, or goodness of fit) was

then used as main dependent variable in standard parametric statistical analyses of variance (ANOVAs) to verify, on the one hand whether mood and position reliably influenced the C1 and/or P1 in response to the peripheral textures, and on the other hand, if mood and stimulus type (standard or target) modulated the P300 in response to task-relevant stimuli.

RESULTS

Experiment 1

Changes in mood: manipulation check

The 2 (Time) x 2 (Mood) mixed ANOVA on the VAS scores showed a significant interaction effect between Time and Mood for feelings of happiness (baseline: positive: $M = 4.48$, $SD = 2.83$, neutral: $M = 4.80$, $SD = 2.92$; post-MIP: positive: $M = 7.57$, $SD = 1.16$, neutral: $M = 4.32$, $SD = 3.00$, $F(1,31) = 23.83$, $p < .001$), and pleasantness (baseline: positive: $M = 4.89$, $SD = 2.72$, neutral: $M = 4.30$, $SD = 3.13$; post-MIP: positive: $M = 7.57$, $SD = 1.12$, neutral: $M = 4.66$, $SD = 3.00$, $F(1,31) = 10.21$, $p = .003$). Next, we compared VAS scores between the positive and the neutral mood group at baseline vs. post-MIP, separately. Independent T-tests showed, as expected, no difference for reported happiness ($t(31) = 0.32$, $p = .75$), nor pleasantness ($t(31) = 0.43$, $p = .56$) between mood groups at baseline. However, post-MIP mood measurements showed a significant difference between the positive and the neutral mood group for feelings of happiness ($t(31) = 4.14$, $p < .001$), and pleasantness ($t(31) = 3.78$, $p = .001$; see Fig. 2. The 2 (Time) x 2 (Mood) mixed ANOVA for the sadness VAS did not show a significant interaction effect (baseline: positive: $M = 0.73$, $SD = 0.97$, neutral: $M = 0.44$, $SD = 0.54$; post-MIP: positive: $M = 0.51$, $SD = 0.73$, neutral: $M = 0.34$, $SD = 0.40$, $F(1,31) = 0.44$, $p = .51$). These results confirmed a significant and selective increase in positive affect after MIP in the positive mood group, but no such change in the neutral mood group.

The 2 (Time) x 2 (Mood) mixed ANOVA on the PANAS scores showed a significant interaction effect between Time and Mood group for the PA scales (baseline: positive: $M = 32.65$, $SD = 5.53$, neutral: $M = 32.88$, $SD = 5.26$; post-MIP: positive: $M = 34.96$, $SD = 4.63$, neutral: $M = 30.54$, $SD = 7.28$, $F(1,31) = 8.69$, $p = .006$), but not for the NA scales (baseline: $M = 23.56$, $SD = 5.81$; post-MIP: $M = 10.89$, $SD = 1.86$, $F(1,31) = 1.24$, $p = .27$). An independent T-test (PA scales) showed a significant difference

between positive and neutral mood group post-MIP, $t(31) = 2.09$, $p = .04$. At baseline, this difference was not significant ($t(31) = 0.54$, $p = .90$).

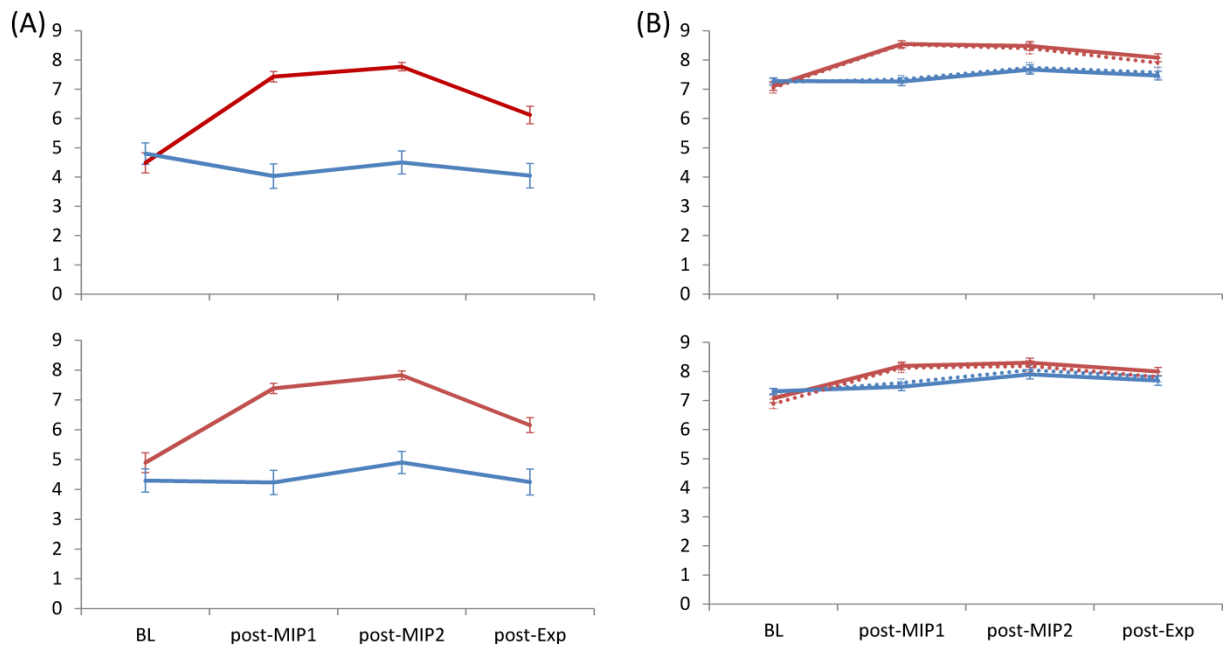


Figure 2. Evolution of levels of positive mood across the four (consecutive) measurement points, separately for the positive mood group (red line) and the neutral mood group (blue line). Mean scores (with 1 S.E.M as error bar) for the happy VAS (upper panel) and pleasant VAS (lower panel) are presented for (A) Experiment 1 and (B) Experiment 2. For Experiment 2, results are shown for all 35 participants (continuous line) vs. 28 participants (14 per group) showing clear effects of mood depending on the MIP (dotted line; see footnote 2 on p. 22).

Behavioral results.

On average, participants in both mood groups had low error rates (sum of absolute deviations in positive group: $M = 4.29$, $SD = 2.78$; neutral group: $M = 4.88$, $SD = 5.60$). There was no significant group difference in accuracy ($t(31) = 0.38$, $p = .71$; see Fig. 3B), suggesting that behavioral performance for the central task was high and balanced between the two mood groups.

ERP results.

P300. The topographical mapping analysis identified three main clusters/topographies during the P300 time interval following the onset of the central tilted lines. We compared the mean GEV values obtained for these three dominant maps using a mixed ANOVA with Stimulus type (standard vs. target) and Map configurations ($n=3$) as within

subjects factors, and Mood (positive vs. neutral) as a between subjects factor. The results showed a significant effect of Stimulus type ($F(1,31) = 4.385, p < .05$), and a significant interaction effect between Stimulus type and Map configuration ($F(2,62) = 15.180, p < .001$) showing that the configuration of the P300 substantially changed depending on the stimulus type (see Fig. 4), in line with previous research (Kim, Kim, Yoon, & Jung, 2008; Kok, 2001; McCarthy & Donchin, 1981; Sawaki & Katayama, 2007). Importantly, no significant main effect of Mood was found ($F(1,31) = 0.016, p = .90$), nor a significant interaction effect between Mood and Map configuration ($F(2,62) = 0.035, p = .96$), indicating that participants in both groups processed standard vs. target central stimuli differentially.

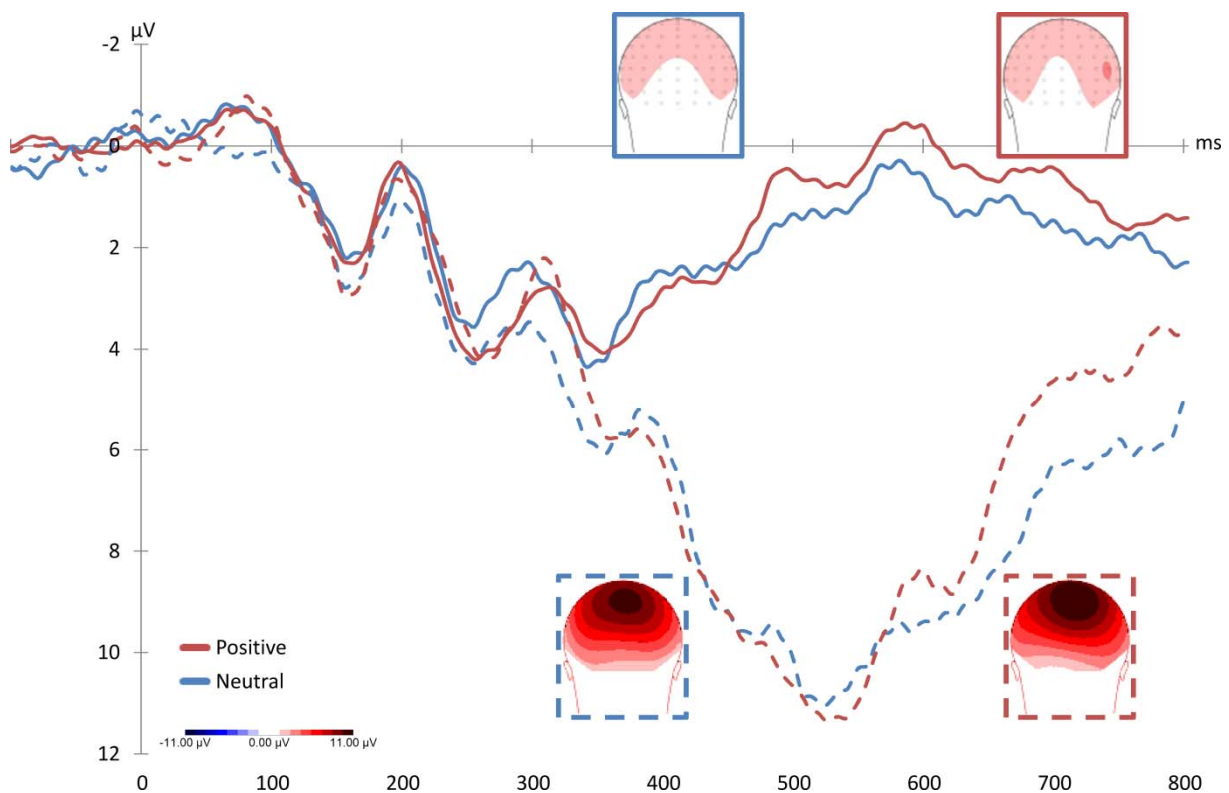


Figure 4. Grand average ERPs to standard (solid) vs. target (dashed lines) central stimuli at a representative midline electrode (POz). A clear P300 was present for target line orientations (dashed line) in the neutral (blue) and positive (red) mood group, whereas this decision-related component was strongly attenuated for standard line orientations (solid line). This conspicuous P300 effect reflecting attention allocation to the target stimuli was similar for the neutral and positive mood groups (see text for numerical values). Topographical voltage maps (back view) for the P300 component (computed during the 400-600 ms post-stimulus onset) are shown for the 2 conditions and 2 groups, separately.

C1. Two main topographies were found during the C1 time window (95-115 ms; see Fig. 5A) following the onset of the peripheral textures. A mixed ANOVA with Map configurations ($n = 2$) and Position (close, middle or far) as within subjects factors, and Mood (positive vs. neutral) as between subject factor was performed on the GEV values extracted for these two C1 topographies. The results showed a significant main effect of Position ($F(2,62) = 7.737, p = .001$), and a significant interaction effect between Position and Mood ($F(2,62) = 8.035, p = .001$). Whereas the former effect confirmed that the topography of the C1 component reliably changed depending on the position of the stimulus in the upper visual field, the latter interaction effect suggested that the induced positive mood influenced this position-specific encoding of the distractor (as reflected by the C1 topography).

Planned comparisons revealed a significant drop of the GEV of the dominant C1 map (i.e. being maximum for the position close relative to fixation) as a function of Position in the neutral mood group (Close vs. Middle, $t(15) = 2.71, p = .02$; Close vs. Far, $t(15) = 2.50, p = .03$), consistent with a non-linear spatial gradient effect. However, this effect was not observed for the C1 of participants in the positive mood group (Close vs. Middle, $t(16) = 0.39, p = .70$; Close vs. Far, $t(16) = 1.20, p = .25$; see Fig. 5B and C). In this group, the explained variance of the dominant C1 topography was not significantly different across the three spatial positions, suggesting a broadening of attention. Together, these results suggest a link between changes in positive mood and position-dependent early brain responses in V1 to these (unattended) textures shown in the upper visual field.

Three dominant maps were found during the C1 time window (95-115ms) for the ERP data recorded during the localizer (upper visual field, see Fig. 6), whereas two dominant C1 maps were found for the C1 recorded during the main task. Presumably, this discrepancy may tentatively be explained by the different task demands (and stimulus parameters for the central stimuli) between these two sessions. Because peripheral textures used in the localizer and in the main task were identical but embedded in different experimental contexts, it is likely that the topographical segmentation data analysis identified slight differences in the actual expression of the C1 map across these two sessions.

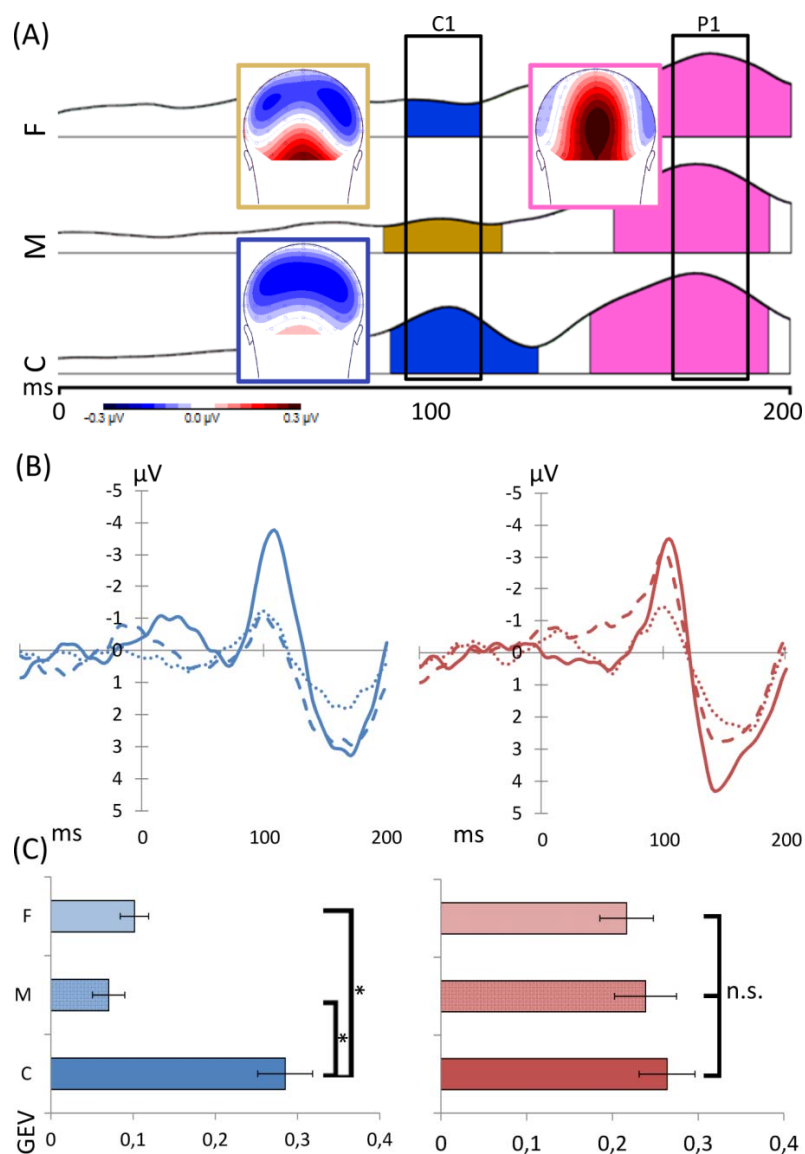


Figure 5. (A) **Results of the topographical ERP mapping analysis.** This analysis identified a main cluster (88-127 ms post-stimulus onset for position close) corresponding to the C1 component, followed by another one corresponding to the P1 component (141-186 ms post-stimulus onset for position close). The corresponding voltage maps (back view) are shown. Following standard practice, amplitude differences were normalized (i.e. the amplitude value at each electrode was divided by the global field power - GFP). (B) Grand average ERPs at electrode POz to visual textures, separately for each group (positive/red or neutral/blue mood) and each position (close/solid line; middle/dashed line; far/dotted line) in the upper visual field. The amplitude of the C1 substantially varied as a function of the position of the textures in the upper visual field, but this effect was stronger for participants in a neutral mood (left panel), compared to a positive mood (right panel). (C) Results (* $p < 0.05$; black bars represent standard errors of the means) of the back-fitting (see methods) of the dominant C1 topography [see blue frame in (A)]. Whereas the GEV of the dominant C1 topography sharply decreased for the middle or far relative to the close position in the neutral mood group (left panel), suggesting a normal spatial gradient effect, this effect was not seen in the positive mood group (right panel) where C1 activity for the far (or middle) position was not significantly lower than for the close position.

A mixed ANOVA with Map configurations ($n=3$) and Position (close, middle or far) as within subjects factors and the between subjects factor Mood (positive vs. neutral) was performed on the GEV values extracted for these maps (localizer). The ANOVA showed a significant interaction effect between Position and Map ($F(2, 62) = 7.71, p < .001$), while the Mood and Map ($F(2,62) = 0.758, p = .47$) as well as Mood and Position ($F(2,62) = 1.53, p = .22$) interactions were non-significant, suggesting a similar early retinotopic encoding of the peripheral textures in both groups. These results suggest that, unlike the C1 recorded during the main attention task, the C1 elicited by the same peripheral distractors during the localizer run (passive viewing) was not reliably influenced by mood. Importantly, a systematic comparison of topographies and waveforms for the C1 deflection recorded during the localizer vs. main attention task to the same peripheral textures confirmed that this early negative component unambiguously corresponded to a genuine C1 deflection, showing the expected polarity reversal as a function of the lower vs. upper visual presentation (see Fig. 6).

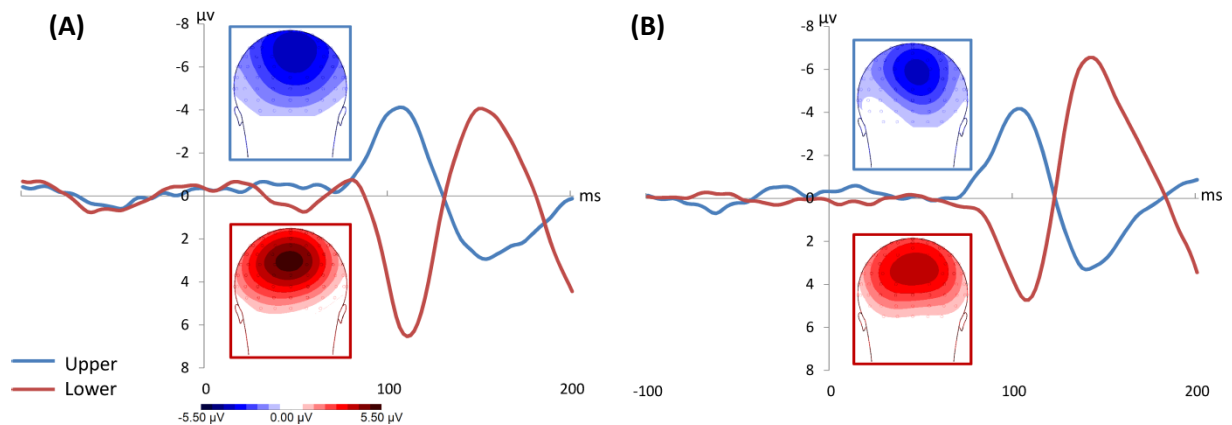


Figure 6. Results of the localizer. Grand average ERPs at electrode POz to peripheral visual textures presented close to fixation, separately for the upper (blue line) and lower visual field (red line) (a) for the neutral mood group and (b) for the positive mood group. These ERPs confirm that in both groups a diagnostic C1 polarity reversal was equally present, early on following stimulus onset over occipito-parietal electrodes along the midline, for visual stimulations in the upper vs. lower visual field, consistent with the electrophysiological signature of this early retinotopic visual component (Rauss, et al., 2009). The corresponding voltage maps (back view) are shown. Maps show normalized amplitude differences (i.e. the amplitude value at each electrode was divided by the GFP).

P1. During the time interval of the P1 (165-185ms) following the onset of the peripheral textures (main task), a single dominant topographical component was found to account

for the ERP signal across the three positions (close, middle or far; see Fig. 5A). A mixed ANOVA with Position (close, middle, far) as within subjects factor and Mood (positive, neutral) as between subject factor on the GEV values extracted for this dominant P1 topography did not show any systematic variation with the position of peripheral textures ($F(2,62) = 2.06, p = .14$), confirming that this extrastriate component was most likely responding to the content, rather than the position of these stimuli. Moreover, this analysis showed that there was no significant main effect of Mood ($F(1,31) = 1.11, p = .30$), nor a significant interaction effect between Mood and Position ($F(2,62) = 0.85, p = .43$).

Questionnaires

T-tests performed on the questionnaire data failed to reveal any significant group difference (BDI: $t(31) = 0.29, p = .78$; STAI-T: $t(31) = 0.30, p = .77$; SUIIS: $t(31) = 0.08, p = .23$, BIS/BAS, BIS: $t(31) = 0.53, p = .60$, BAS Drive $t(31) = 0.61, p = .55$, BAS Fun: $t(31) = 0.12, p = .91$, BAS Reward: $t(31) = 0.09, p = .93$), suggesting that the observed ERP differences for the processing of the peripheral textures between the two groups could not be explained by uncontrolled group differences along these specific personality traits.

Experiment 2

Changes in mood: manipulation check

The 2 (Time) x 2 (Mood) mixed ANOVA on the VAS scores showed a significant interaction effect between these two factors for feelings of happiness (baseline: positive: $M = 7.11, SD = 1.29$, neutral: $M = 7.28, SD = 0.87$; post-MIP: positive: $M = 8.37, SD = 1.04$, neutral: $M = 7.46, SD = 1.12, F(1,33) = 15.07, p < .001$) and pleasantness (baseline: positive: $M = 7.08, SD = 1.25$, neutral: $M = 7.32, SD = 0.83$; post-MIP: positive: $M = 8.16, SD = 1.06$, neutral: $M = 7.69, SD = 1.10, F(1,33) = 4.51, p = .04$; see Fig. 2), but not for feelings of sadness (baseline: positive: $M = 1.33, SD = 1.56$, neutral: $M = 0.75, SD = 0.66$; post-MIP: positive: $M = 0.61, SD = 0.55$, neutral: $M = 0.58, SD = 0.41, F(1,33) = 2.41, p = .13$). Planned comparisons confirmed that there was no significant group difference at baseline in reported feelings of happiness ($t(33) = 0.450, p = .51$), pleasantness ($t(33) = 0.665, p = .656$), nor sadness ($t(33) = 1.409, p = .17$). Post-MIP VAS

scores differed significantly between positive and neutral mood group for feelings of happiness ($t(33)= 2.481, p = .018$), but did not reach significance for pleasantness ($t(33)= 1.306, p = .20$) or sadness ($t(33)= 0.215, p = .83$). Altogether, these results confirmed an increase in happiness after the MIP in the positive mood group, but no change in the neutral mood group.

By contrast, the 2 (Time) x 2 (Mood) mixed ANOVA on the PANAS scores showed no significant interaction effect for the PA scales (baseline: $M = 32.40, SD = 5.41$; post-MIP: $M = 32.19, SD = 5.44, F(1,33) = 1.97, p = .17$), nor for the NA scales (baseline: $M = 12.34, SD = 2.33$; post-MIP: $M = 11.26, SD = 1.56, F(1,33)= 0.28, p = .60$).

Attention task

Central stimuli. Participants' accuracy was high in both groups (positive: 88.65%, $SD = 6.66$; neutral: 91.84%, $SD = 6.05$). There was no significant difference between the two groups in accuracy ($t(33)= 1.49, p = .15$; see Fig. 3B). Neither the amount of false alarms, (positive: $M = 4.89, SD = 9.06$; neutral: $M = 2.41, SD = 3.62, t(33)= 1.05, p = .30$), nor omissions (positive: $M = 22.17, SD = 10.83$, neutral: $M = 17.71, SD = 10.39, t(33)= 1.24, p = .22$), differed significantly between the two groups. Likewise, RTs for correct detections were balanced between groups (positive: $M = 499.70, SD = 97.68$; neutral: $M = 456.22, SD = 61.66, t(33)= 1.56, p = .13$).

These results confirmed that participants correctly attended and maintained fixation to the central RSVP, and that positive mood induction did not simply affect the processing of these centrally-presented lines, relative to neutral mood.

Peripheral stimuli. The 2(Mood: neutral vs. positive) x 3(Position: close, middle, or far) mixed ANOVA performed on the mean accuracy scores revealed a significant main effect of Position ($F(2,66) = 16.10, p < .001$), showing, as expected, a monotonic decrease of performance as a function of Position relative to fixation (Fig. 3A): position close, $M = 80.14, SD = 15.62$; position middle, $M = 78.03, SD = 15.14$; position far, $M = 69.96, SD = 14.33$. Accuracy differed significantly between positions far and middle ($t(33)= 4.13, p < .001$), as well as between far and close ($t(33)= 4.83, p < .001$). However, mean accuracy did not differ significantly between close and middle ($t(33)= 1.41, p = .17$). Importantly, this analysis also revealed a significant main effect of mood, indicated

by an overall lower accuracy in the positive mood group ($M = 71.22$, $SD = 12.57$) when compared to the neutral mood group ($M = 80.15$, $SD = 13.11$, $F(1,33) = 2.23$, $p = .03$; see Fig. 3A). The interaction effect between Mood and Position was not significant ($F(2,66) = 0.36$, $p = .70$), indicating that the effect of mood did not differ across the three positions. Planned comparisons showed a significant difference between positive and neutral mood group for position far ($t(33) = 2.43$, $p = .02$) and for position close ($t(33) = 2.13$, $p = .04$), but no such difference between positive and neutral mood group for position middle ($t(33) = 1.61$, $p = .12$). Hence, accuracy for the peripheral textures was overall lower for participants in a positive mood, relative to a neutral mood. This result may be interpreted as a general drop in attention selectivity for the textures shown in the upper visual field for participants with a positive mood³. Analysis of RTs for correct responses confirmed that Position reliably influenced the speed in a predictive way ($F(2,66) = 13.49$, $p < .001$), with faster decisions for peripheral textures shown close to fixation ($M = 517.73$, $SD = 136.01$), relative to the middle position ($M = 564.06$, $SD = 155.62$, $t(34) = 3.72$, $p < .001$), or far position ($M = 582.87$, $SD = 151.21$, $t(34) = 4.49$, $p < .001$). The RT difference between middle and far was not significant ($t(33) = 1.44$, $p = .16$). There was a significant interaction effect between Mood and Position ($F(2,66) = 3.13$, $p = .05$), showing a monotonic increase of RT with increasing distance from fixation in the neutral mood group, but not for the positive mood group. No main effect of Mood was found ($F(1,36) = 1.04$, $p = .32$).

Questionnaires

Comparisons performed on the personality questionnaire data failed to reveal any significant difference between the two mood groups (BDI: $t(33) = 0.25$, $p = .80$; STAI-T: $t(33) = 0.39$, $p = .70$; SUIIS: $t(33) = 0.25$, $p = .80$; BIS/BAS: BIS: $t(33) = 0.26$, $p = .80$, BAS Drive: $t(33) = 0.31$, $p = .76$, BAS Reward Responsiveness: $t(33) = 0.82$, $p = .42$ scales), except for the BAS Fun Seeking scale, with a (marginally) significantly higher score in the

³When we analyzed the changes in levels of positive mood following the MIP (taking into account VAS and PANAS scores concurrently), we found that 7 out of 35 participants showed an unusual pattern. Three participants assigned to the neutral mood group showed an increase in positive mood while four participants assigned to the positive mood group showed a weak or no increase in positive mood following the MIP. We performed additional refined statistical analyses excluding the data of these 7 subjects but we did not observe any change in the performance for the central task (effect of group was still non-significant; $t(26) = 1.18$, $p = .25$), nor for the visual discrimination of the peripheral textures (effect of group was still significant; $F(1,26) = 4.50$, $p < .05$).

neutral ($M = 6.59$, $SD = 1.12$) compared to the positive ($M = 5.44$, $SD = 2.09$) mood group ($t(33) = 2.00$, $p = .054$).

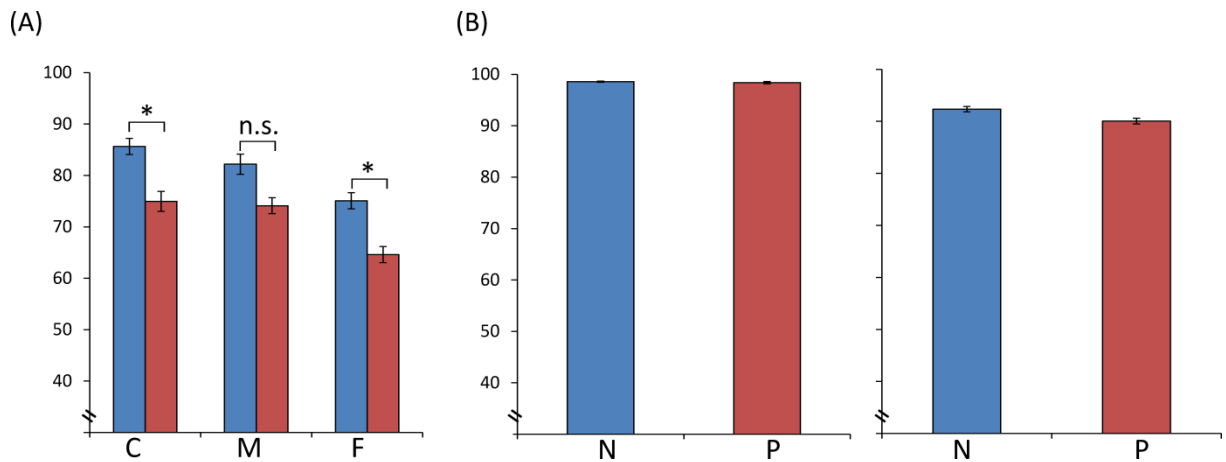


Figure 3. (A) Accuracy rates for the identification of peripheral textures (Experiment 2) show a decrease in accuracy with increasing Position from fixation (C/close to fixation; M/middle position; F/far from fixation). However, an overall lower accuracy in the positive mood group (red) relative to the neutral mood group (blue) was found ($* p < .05$; black bars represent standard errors of the means). (B) Accuracy rates for the oddball line orientation task at fixation for the EEG experiment (left panel). Trials for which participants correctly detected a target (or correctly rejected a non-target) were counted and these numbers were then converted to percentages (bearing in mind that in total 300 trials were presented). Results for the behavioral experiment (right panel). In each experiment, no accuracy difference was found between the positive (P) and neutral (N) mood group.

DISCUSSION

The results of our study show that positive mood can alter the earliest cortical stage of stimulus processing, presumably taking place in V1 (i.e. C1 component; Rauss et al., 2011). More specifically, our ERP findings show that the expression (topography) of the C1 to unattended peripheral distractors shown in the upper visual field strongly varies according to the position (close, middle or far) of these textures relative to central fixation. However, this early spatial gradient effect is clearly altered during positive, relative to neutral, mood. In line with a broadening of spatial attention with positive emotion, the dominant topography of the C1 was equally strong regardless of the position of the texture in the upper visual field for participants experiencing positive affect, whereas the C1 of participants in the neutral mood condition showed a clear and sharp topographical change according to the same manipulation (see Fig. 5B and C). Importantly, these results were obtained even though mood did not influence

performance and decision-related ERP responses (i.e., P300) to the centrally presented visual stimuli, suggesting that an enhanced level of positive affect had primarily an influence on covert attention allocation towards peripheral (unattended), as opposed to central (attended) stimuli. We discuss the implications of these new findings below.

Positive emotion broadens attention

In order to assess the influence of positive mood on attentional processes, participants were randomly assigned to either a positive or neutral MIP. Given that this MIP consists of self-relevant imagery and music, the observed changes in positive affect may be attributed to the modulation of higher-level cognitive or affective processes, as opposed to mere phasic reward (Hickey, Chelazzi, & Theeuwes, 2010; Kringelbach & Rolls, 2004; Pessoa & Engelmann, 2010; Rolls, 2000; Van Steenbergen et al., 2009) or the selective induction of approach-motivated affect (Gable & Harmon-Jones, 2008, 2010). In contrast, the novel MIP we used rather elicited a positive mood characterized by low intensity in approach motivation, since the emotions evoked were not relevant in terms of any specific (task) goal⁴. The results of the manipulation check showed that the MIP was successful in increasing subjective feelings of positive mood, selectively in the positive mood group. However, manipulation check did not include complementary measures of arousal. Hence, it is possible that not only positive valence, but also arousal accounted for changes in attention control processes following the induction of positive mood in our study. Consistent with previous research (Ashby et al., 1999), we surmise that this change in positive mood following the MIP may be associated with a sustained increase in dopaminergic levels in specific cortical and subcortical structures, related to executive functions. Nonetheless, it remains unclear at this stage whether the elected

⁴Our results suggest that non-verbal VASs may be more sensitive than the PANAS to capture subtle changes in positive mood (Rossi & Pourtois, 2011), given that in Experiment 2, pre-post change in mood was only found with the VASs. As the change in affective state after our MIP is mild, such a change might be better captured by an instrument that can pick up small variations along a continuous scale (cf. VAS), as opposed to a limited number of discrete categories (cf. PANAS). Moreover, the presence of verbal labels for the PANAS may prevent participants from deviating substantially in their estimations in a repeated measures design. Moreover, the positive affect scale of the PANAS is principally measuring ‘positively valenced affects’ (Watson, Wiese, Vaidya, & Tellegen, 1999), high in activation (Russell & Carroll, 1999) and how much the participant enjoys engaging with his/her environment (Crawford & Henry, 2004). By contrast, the VASs we used in this study assess current positive feelings regardless of their origin/nature and independently from the level of activation they may elicit. Given the individualization of our MIP, the general scope of the VASs might be better suited than the PANAS in order to capture subtle changes in mood.

positive MIP actually yielded either phasic or tonic changes of dopamine levels in targeted prefrontal regions.

Previous studies already showed that changes in positive mood are related to changes in cognitive functions, including the use of a more open (Estrada et al., 1997), creative (Isen et al., 1987), integrative (Isen et al., 1991) or flexible (Isen & Daubman, 1984) thinking style. Taken together, these results point to a role of positive affective states as being able to trigger a broadening of the attentional scope (Derryberry & Tucker, 1994). Based on this evidence, Fredrickson and colleagues (Fredrickson, 2001; Fredrickson & Levenson, 1998) advocated in the broaden-and-build theory that negative mood would prompt a narrowing of thought-action tendencies and attentional focus, while positive mood would on the contrary broaden people's thought-action repertoires and attentional scope. This way, mood provides human organisms with an adaptive and flexible mechanism enabling to efficiently cope with changing environmental demands, by dynamically modulating the way incoming information is processed and eventually stored in memory systems (Gray, 2004).

However, the evidence showing that positive affect can trigger a genuine broadening of the visual attentional scope and induce a more global information processing style is scarce. Previous studies used mainly cognitive control or interference tasks, such as the flanker task (Rowe et al., 2007). Rowe and colleagues (2007) found that in positive mood, flankers had a greater interference effect on central task-relevant stimuli relative to neutral and sad mood, even when the spacing between target and flankers was increased. This broadening effect seems to be related to changes in the extrastriate visual cortex, at the level of the P1 (Moriya & Nittono, 2011). These results show an increased proneness to distraction and are consistent with a broadened attention in positive mood (Fredrickson, 2001; Fredrickson & Levenson, 1998), even though a direct link between positive mood and changes in attention control mechanisms remains difficult to establish, based on these studies. Because these interference tasks primarily rely on several cognitive processes beyond attention (e.g. executive functions and cognitive control, see Botvinick, Braver, Barch, Carter, & Cohen, 2001), it is unclear whether positive mood can causally lead to a change in the attention focus and in turn gate early sensory stimulus processing. Therefore, the main goal of our study was to address this question using a standard visuo-spatial task (Rauss et al.,

2009; Rauss et al., 2011; Rossi & Pourtois, 2012; Schwartz et al., 2005), capitalizing on the high temporal resolution provided by ERPs to track attention-dependent changes in early sensory processing triggered by the earlier induction of a positive mood.

Neurophysiological mechanism underlying broadening of attention

Participants were asked to perform a demanding oddball detection task at fixation, ensuring that voluntary attention was properly locked to this position in the visual field, but leaving enough attentional resources available for the covert processing of visual distractors (EEG experiment) or overt processing of exogenous task-relevant visual textures (behavioral experiment). These uniform visual textures were briefly flashed in the upper visual field at an unpredictable time and variable location. Using ERP measurements, we could thus track electrical brain activity unambiguously elicited either by the central or peripheral stimuli, and assess at which stage their respective sensory processing was modulated by the induction of positive mood. We reasoned that if positive mood truly broadens attention scope, then the sensory processing of the unattended peripheral distractors should be altered, especially for the unattended stimuli shown at the most extreme spatial location relative to fixation.

Our new ERP results confirm this conjecture and show that the earliest stage of stimulus processing in V1, as indexed by the C1, is influenced by the location of the distractor in the upper visual field, as well as by mood. The amplitude and polarity of the C1 systematically varies with the position of the stimulus in the visual field, reflecting an early retinotopic encoding effect (Clark et al., 1995). Using a standard ERP topographic mapping analysis (Pourtois et al., 2008), we found that in a neutral mood, participants showed a non-linear reduction of the topographical C1 component with increasing distance between the distractor and fixation, reflecting the spatial sensitivity of the C1 (Clark et al., 1995). However, participants in the positive mood group did not show such a spatial gradient effect. Hence, the spatial gradient of the C1 found in the neutral mood group was blurred after the induction of positive mood, showing a drop in selectivity for the early spatial encoding of distractors in V1. These findings show an interaction effect between bottom-up sensory processing, guided by low level stimulus information (Egeth & Yantis, 1997; Wolfe & Horowitz, 2004), in this case the spatial location of the distractor stimulus shown in the upper visual field (Rauss et al., 2011)

and top-down factors (Buschman & Miller, 2007; Corbetta & Shulman, 2002; Marois & Ivanoff, 2005; Theeuwes, 2010) such as the current mood state of the participant (Gray, 2004; Rossi & Pourtois, 2012).

Of note, we found that this effect of mood on early sensory processing of the distractors was task-specific, mood dependent and selective for the C1 component. During the localizer, we found that the C1 component to these same peripheral distractors was not influenced anymore by mood, although the electrophysiological properties of the C1 were very similar in the main attention task and localizer (see Fig. 6). This might be explained by mood effects fading out during the recording of the localizer blocks and/or the task differences between the localizer (i.e. passive viewing conditions) and the main task blocks. In this sense, the absence of mood effects on the localizer blocks might indicate a specific effect of positive mood on active filtering of irrelevant information, instead of an aspecific influence of this factor on the mere early bottom up processing of visual stimuli in V1. However, future studies are needed to assess and better characterize (short scale) time-dependent fluctuations of effects of (positive) mood, and how they may influence early visual and attention brain processes (including the C1 component). More specifically, whether positive mood alters spatial properties selectively or feature-based components of (selective) attention (or both) requires additional empirical validation. Likewise, given the existing evidence showing opposite effects of positive vs. negative mood on the global vs. local information processing style (Gable & Harmon-Jones, 2008, 2010; Gasper & Clore, 2002; Rowe et al., 2007), additional work is needed as well in order to assess whether positive mood primarily influences the information processing style overall, or instead, is best characterized by process-specific changes concerning attention control mechanisms.

Unlike the C1 component, analyses of the extrastriate P1 component (Hillyard & Anllo-Vento, 1998; Martinez et al., 1999) failed to reveal any change as a function of stimulus position in the upper visual field, consistent with previous ERP findings (Clark et al., 1995). Likewise, mood had no effect on the topographical properties of the P1 component. However, given the strong anatomical connections between the prefrontal cortex and the parietal and occipital cortices, a modulatory effect of positive mood remotely influencing not only early visual areas (including V1), but also the extrastriate visual cortex (and hence the P1 component) appears more likely. Moreover, our

observation of a C1-selective effect of the positive mood could also be explained by the specific task demands and stimulus parameters used in our study. The elected experimental paradigm likely promoted attention competition/selection primarily in the spatial domain (see also Rossi & Pourtois, 2012). We surmise that a modulation of the P1 component by (positive) mood could also be found if different task demands and stimulus characteristics would be used, for example dot probe or cueing tasks (see Pourtois, Grandjean, Sander, & Vuilleumier, 2004).

Another important finding of our study was to show that mood did not change the processing of the centrally presented/task-relevant stimuli, in both experiments. As expected, the amplitude of the P300 component was strongly influenced by task demands (Kim et al., 2008; Kok, 2001; McCarthy & Donchin, 1981; Sawaki & Katayama, 2007), being larger for perceived (deviant) targets than for standards. However, this effect was not different between the two mood groups, in agreement with earlier ERP studies (Moriya & Nittono, 2011; Rossi & Pourtois, 2012). Moriya and Nittono (2011) used a flanker task, but they did not report any reliable effect of either positive or negative mood on the amplitude of the P300 component. They concluded that attention might only be influenced by mood at early stages of stimulus processing, as opposed to response selection and decision processes. Rossi and Pourtois (2012) also confirmed that neither positive nor negative mood influenced the amplitude of the target-related P300 component (as well as accuracy at the behavioral level), using an adapted version of the experimental paradigm used in this study. In their ERP study, participants were instructed to attend to a RSVP at fixation, consisting of the same line segments as in the current study. In some trials, a deviant line orientation was presented and these deviant lines had to be detected by participants (ratio standard-target line orientations was 4:1). Perceptual load for these central stimuli was manipulated in this study, such that the detection task could be easy, intermediate or difficult. Participants performed this task under either a positive or a negative affective state (within-subject design). Results showed that the target-related P300 component, as well as accuracy at the behavioral level, varied strongly and in a predictive direction depending on task difficulty. However and importantly, mood did not interact with these effects, including for the easiest and most difficult level of task difficulty. By contrast (and similarly to the present study), in this earlier study mood altered the early

visual processing of (unattended) peripheral distractors, suggesting that (state-dependent) affect mainly influenced peripheral (and unattended stimuli) as opposed to central vision (and the processing of attended stimuli). The new ERP results presented in this study (see Experiment 1) are compatible with this interpretation and they confirmed an asymmetry between central/attended and peripheral/unattended locations for effects of mood or affect on (early) visual perception. In contrast, another study did find a modulation of the P300 component by negative affective state (threat of shock, Shackman et al., 2011). Hence, it remains unclear if the decision-related P300 component can be modulated by affective state. More generally, our results suggest that positive mood may lead to qualitatively different effects during sensory processing and decision making processes for task-relevant stimuli, relative to negative emotions. Future ERP studies comparing more directly effects of positive vs. negative mood are needed in order to assess whether not only early sensory processing stages (e.g. C1 component), but also later decision-related processes are equally influenced by these opposite affective states or not. Likewise, it appears necessary to explore further the likely dependency of some of these ERP components to specific neurotransmitter systems. In particular, given that positive mood is thought to be mediated by specific dopaminergic systems (Ashby et al., 1999), some of the present ERP effects could tentatively be related to changes in these dopaminergic systems. In this regard, studies linking the P300 component either to dopaminergic (see Pogarell et al., 2011) or adrenergic inputs (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich, 2007) provide important hints on the actual organization of the underlying brain architecture and neural systems mediating effects of (positive) mood on attention.

More generally, our findings suggest that effects of positive mood were specific to the processing of the peripheral, task-irrelevant stimuli and they did not influence task-relevant, central stimuli. This result allows us to rule out the possibility that changes in early sensory processing at the level of the C1 for the peripheral visual textures were explained by systematic behavioral performance imbalances between mood groups for the task at fixation. The behavioral data collected during the EEG experiment and the additional behavioral experiment, showing no difference in accuracy nor in RTs between mood groups for the task at fixation, further support this conclusion.

Additional information regarding the nature and extent of the selective change produced by positive mood was provided by the additional behavioral experiment. We reasoned that if the effect of positive mood may correspond to a drop in early spatial encoding selectivity, as our new ERP results for the C1 suggest, the capacity to discriminate subtle geometric differences between different peripheral stimuli may be impaired in positive mood, compared to neutral mood, given the intrinsic attention competition exerted by the three non-overlapping spatial positions in the upper visual field. This new result is compatible with earlier findings in the literature, showing that a larger attentional scope may lead to an associated loss in processing efficiency and spatial resolution (as compared to a smaller scope; Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985) and that this is reflected in a decreased neural signal change in the corresponding retinotopic area (Müller et al., 2003). These results provide support for the assumption of a trade-off effect between the size of the attentional focus and the efficiency/resolution of visual (spatial) processing (Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985; Ivry & Robertson, 1998; Müller et al., 2003). In line with this reasoning, when peripheral textures became task-relevant and had to be discriminated (Experiment 2), accuracy dropped as a function of the distance of the textures relative to fixation. Similarly to these previous findings showing a drop in efficiency of stimulus processing when the attentional scope was broadened, we found that participants in the positive mood group committed on average substantially more discrimination errors than participants in the neutral mood group across the three positions. Combined together with our new C1 results showing an altered sensitivity between the three positions in the upper visual field in positive relative to neutral mood (Experiment 1), this decrease in accuracy in the positive mood group might suggest a drop in attention selectivity across these three positions in the upper visual field (Experiment 2). However, some caution is needed when comparing directly the results of both experiments, given that they differ along several dimensions. While working memory is presumably taxed similarly in both experiments by the central RSVP, in Experiment 2 peripheral textures were also task-relevant and required an explicit visual discrimination, possibly triggering a more open attention focus compared to the task-irrelevant distractors in Experiment 1. Moreover, if we assume a general limited resources account for attention capacities (see Marois & Ivanoff, 2005), then increasing

task demands may block or dampen effects of (positive) mood on early visual perception. Nonetheless, in Experiment 1, we found clear evidence for an effect of position of textures in the upper peripheral visual field at the level of the C1, indicative of a change in the distribution of spatial attention in this portion of the visual field, as well as a significant modulation of this effect by the positive mood. Future studies are needed to assess whether task-relevance of peripheral textures reliably influences the size and extent of positive mood effects (on early visual perception). The results of this study (Experiment 2) show that despite a dual task setting and a (high) working memory load, positive mood could still exert a modulatory effect on the ability to discriminate peripheral textures shown in the upper visual field, an effect which presumably arises early following stimulus onset in the primary visual cortex when the location of these textures were precisely/retinotopically encoded (see results of Experiment 1).

Presumably, if positive emotion broadens attention, the distractor or location specificity may be impaired because attention is by definition operating over a potentially more expanded region. Changes in dopaminergic-dependent prefrontal attention control mechanisms under positive mood could underlie these early visual perception effects (Ashby et al., 1999). However, the actual mechanism linking positive mood, dopamine, and cognitive processes is not yet fully understood, partly due to the existence of several dopamine receptor types and different dopaminergic-dependent neuromodulation pathways, connecting to different (sub)cortical brain regions. It is likely that the influence of sustained positive mood (as achieved in this study) on specific cognitive processes, such as attention, actually concerns tonic changes in dopamine levels, as opposed to mere phasic fluctuations. Alternatively, it has been suggested that phasic dopamine increases in prefrontal cortex, elicited by stimuli that are rewarding or reward-predicting, serve as a pervasive gating signal. Accordingly, we surmise that the positive MIP, instructing participants to focus on a personal experience of positive mood, served as a reward cue for the participants, hence likely influencing the phasic dopamine release in this region, even though future studies are needed to corroborate this conclusion.

Broadening through decreased inhibition?

The alteration in early sensory processing of the distractors under positive mood (and its behavioral effect) might be explained by a change in higher-level attention control mechanisms (Corbetta & Shulman, 2002; Lavie, 2005). It is possible that resources left over and not consumed by the main oddball task at fixation may be used to process covertly these peripheral stimuli (Lavie, 1995, 2005; Lavie et al., 2004; Lavie & Tsal, 1994), and this effect could be exacerbated under positive mood. Hence, positive mood may not influence sensory processing in V1 directly, but rather (tonically) loosen the normal top-down control exerted by prefrontal attention control regions onto V1 (see also Rossi & Pourtois, 2012). Therefore, the effect of positive mood in our study might very well operate at this level and interfere with the normal recruitment of prefrontal cognitive control regions aimed at downplaying the distraction effect induced by these peripheral visual textures. These prefrontal regions primarily include the dorsolateral prefrontal cortex (Miller & Cohen, 2001; Posner & Presti, 1987), as well as the anterior cingulate cortex (Posner & Petersen, 1990; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Interestingly, because both regions are receiving strong dopaminergic inputs from the midbrain and basal ganglia, and because positive mood may be associated with a tonic change in these dopaminergic brain systems (Ashby et al., 1999), the observed changes in V1 after the induction of positive mood in our study may tentatively be linked to these distant prefrontal effects, or alternatively to a more global change in the fronto-parietal network supporting the endogenous control of attention (Corbetta & Shulman, 2002). In other words, positive mood might affect these prefrontal inhibitory systems (Wang et al., 2011), eventually leading to a change in early sensory processing in V1, given the strong anatomical projections from these prefrontal areas to early sensory cortices, including V1 (Van Essen, Anderson, & Felleman, 1992). Hence, because of this decreased prefrontal control or inhibitory mechanism, positive emotion alters the early sensory processing in V1, and hence the attention selectivity, revealing in turn a downside of positive emotion on early visual cognition (see also the results of the behavioral experiment corroborating this conclusion). One may assume that a similar release in prefrontal inhibitory control may explain a variety of effects observed under positive mood, including a more global (as opposed to local) processing style (Gable & Harmon-Jones, 2010), a higher susceptibility to distraction during

interference tasks (Rowe et al., 2007), a lower adaptation following conflict detection (Van Steenbergen et al., 2010), as well as eventually an enhanced creative style (Isen, 2000; Isen & Daubman, 1984; Isen et al., 1987; Isen et al., 1991). However, it should be mentioned that the focus of our study was on how ‘low-level’ attentional and visual processes could be modulated by (transient and short-lived) changes in levels of positive mood, as opposed to alterations of high-level cognitive functions, such as creativity, reasoning, problem solving or language. Interestingly, it is plausible to assume that a common ‘basic’ process might underlie changes seen in a broad range of cognitive functions after the induction of positive emotion. More specifically, a substantial decrease in frontal inhibitory processes following the induction of positive mood, such as postulated in earlier research or models (Rowe et al., 2007, Biss & Hasher, 2011; Biss et al., 2010), might possibly explain, although indirectly, the present ERP results, as well as a wide range of behavioral phenomena previously reported in the literature, including the adoption of a more creative and flexible information processing style. Additional brain-imaging studies are needed, however, to link more directly changes in such prefrontal inhibitory control mechanisms with the induction of positive mood, and finally try to causally relate these putative changes in higher prefrontal brain regions with specific alterations during early sensory processing or attention control, as revealed in our study.

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Feeling happy enhances early spatial encoding of peripheral information automatically: electrophysiological time-course and neural sources¹

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ABSTRACT

Previous research showed that positive mood may broaden attention, although it remains unclear whether this effect has a perceptual or post-perceptual locus. In this study, we addressed this question using high density event-related potentials (ERP) methods. We randomly assigned participants to a positive or neutral mood condition. Then, they performed a demanding oddball task at fixation (primary task ensuring fixation) and a localization task of peripheral stimuli shown at three positions in the upper visual field (secondary task) concurrently. While positive mood did not influence behavioral performance for the primary task, it did facilitate stimulus localization on the secondary task. At the electrophysiological level, we found that the amplitude of the C1 component (reflecting an early retinotopic encoding of the stimulus in V1) was enhanced in the positive compared to the neutral mood group. Importantly, this effect appeared to be largely automatic, because it occurred regardless of the task relevance of the peripheral stimulus, and prior to top-down gain control effects seen at the level of the subsequent P1 component. This early effect was also observed irrespective of a change of the target-related P300 component (primary task) by positive mood. These results suggest that positive mood can automatically boost the spatial encoding of peripheral stimuli early on following stimulus onset. This effect can eventually underlie the broadening of spatial attention which has been associated with this specific mood state.

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INTRODUCTION

The broaden and build effects of positive emotions

The importance of positive emotions in psychological wellbeing has increasingly gained researchers' interest since Fredrickson published her influential broaden-and-build theory (Fredrickson, 2001, 2004). At the heart of this theory lies the idea that positive and negative emotions exert opposite influences on cognitive functions: whereas negative mood would trigger a narrowing of the attentional scope and behavioral repertoire, positive mood on the other hand would fuel broader thought-action tendencies and expand the attentional focus (Fredrickson & Branigan, 2005). Evidence supporting this theory comes from Derryberry and Tucker (1994), who found an association between positive mood and a larger attentional scope, and from Isen and her colleagues, who showed that positive affect enables a flexible (Isen & Daubman, 1984), creative (Isen, Daubman, & Nowicki, 1987), integrative (Isen, Rosenzweig, & Young, 1991) and open (Estrada, Isen, & Young, 1997) way of processing information and seeking solutions (see Isen, 2000 for a review).

An expansion of the attentional focus might be crucial to the benefits of positive mood for higher order cognitive functioning, and different paradigms have been set up to reveal such an effect, including flanker and other interference tasks. While some studies found evidence for a broadening effect of positive mood (Moriya & Nittono, 2011; Rowe, Hirsh, & Anderson, 2007), others failed to replicate this effect (Bruyneel et al., 2013; Finucane, Whiteman, & Power, 2010; Huntsinger, Clore, & Bar-Anan, 2010; Martin & Kerns, 2011). These discrepant results might stem from the fact that these earlier studies primarily used interference tasks, which are not pure measures of spatial attention, but instead rely more heavily on executive functions and cognitive control (Botvinick, Braver, Barch, Carter, & Cohen, 2001). Because conflict and competition among multiple responses are induced by these interference tasks, it is likely that the effects reported in some of these earlier studies concern post-perceptual stages of processing rather than a genuine broadening of the attentional focus early on following stimulus onset. Hence, using these tasks, it remains unclear whether positive mood influences early or late stages of information processing during attention selection.

Costs and benefits of a broadening of attention under positive mood

To overcome these limitations, we previously validated a task enabling us to titrate effects of positive mood on early stages of visual processing and attention selection, both at the EEG and behavioral levels (Vanlessen, Rossi, De Raedt, & Pourtois, 2013). In this earlier study, participants were randomly assigned to either a neutral or a positive mood induction condition that consisted of a standard guided imagery procedure (Holmes, 2006; Holmes, Coughtrey, & Connor, 2008). Next, they performed a demanding oddball detection task in the center of the screen, used to ensure fixation throughout the experimental session. Orthogonally, distractors (i.e., unattended textures) were briefly flashed at different eccentricities in the upper visual field at an unpredictable time and location relative to these central stimuli. These task parameters were therefore suited to study two major components of attention control concurrently: top-down attention selection (indexed by the processing of the central stimuli) and bottom-up attention capture (indexed by the covert or implicit processing of the peripheral distractors; Corbetta & Shulman, 2002; Schwartz et al., 2005).

At the EEG level, these two processes were formally operationalized by amplitude changes at the level of the P300 and C1 components, respectively. Oddball targets elicited a conspicuous P300 component relative to standards, in line with previous results (Rossi & Pourtois, 2012). However, this effect was not influenced by positive mood. The C1 elicited by the peripheral distractors varied in amplitude with their actual spatial position, being larger for textures shown close to fixation compared to further away in the upper visual field (Clark, Fan, & Hillyard, 1995). Remarkably, this near-far gradient effect was influenced by positive mood, indicated by a less sharp decrease of the C1 amplitude with increasing eccentricity for participants in the positive compared to the neutral mood group. Given that the C1 corresponds to the earliest sweep of activation in the primary visual cortex following stimulus onset (Jeffreys & Axford, 1972; Rauss, Schwartz, & Pourtois, 2011), we interpreted these results as reflecting an early influence of positive mood on the processing of peripheral distractors (bottom-up component of attention). Moreover, the direction of this ERP effect was compatible with a broadening of attention under positive mood, as if in this specific mood state attention was readily allocated to peripheral distractors falling far away relative to fixation.

At the behavioral level, we reasoned that this neurophysiological effect would not necessarily translate as a measurable advantage in the processing of the content of these stimuli as a function of positive mood. Earlier studies investigating the effects of a broadened attentional scope showed a trade-off between the size of the attentional focus and the spatial resolution within that focus (Castiello & Umiltà, 1990; Eriksen & Yeh, 1985; Ivry & Robertson, 1998), with corresponding effects at the neural level (Müller, Bartelt, Donner, Villringer, & Brandt, 2003). Thus, when attentional resources are spread over a larger portion of the visual field, this gain in spatial attention is somehow counteracted by a loss regarding the processing of the details and local information. In line with this prediction, we found in our previous study (Vanlessen, et al., 2013) that participants in the positive mood group showed a drop in accuracy for processing the content (i.e., local elements) of these textures shown in the upper visual field, compared to the participants in the neutral mood group. However, this behavioral effect was evidenced only in a control experiment where no EEG was recorded concurrently (Vanlessen, et al., 2013). Hence, we could link these behavioral effects with the changes observed at the level of the C1 only indirectly. Moreover, the question remains whether positive mood could be associated with a gain (as opposed to a cost) regarding the processing of these peripheral stimuli at the behavioral level, when task instructions emphasize the processing of global elements or coarse information, rather than local discrimination. Presumably, if positive mood automatically broadens attention to these peripheral stimuli, then the processing of a more global property, such as location (as opposed to their local content) might be facilitated, compared to a neutral mood condition.

Rationale of the present study

To address these questions, we adapted in this study our previous paradigm (Vanlessen, et al., 2013) and we instructed participants to attend to the location of peripheral stimuli shown in the upper visual field (secondary task), besides monitoring a stream of rapidly presented stimuli in the center of the screen (primary task, RSVP identical to our previous study). Importantly, high density (i.e., 128 channels) EEG was continuously recorded enabling us to concurrently characterize changes in top-down attention control (P300 component) and early sensory processing (C1 amplitude) induced by

positive mood. While central fixation was ensured by means of the primary task², participants were asked to pay attention (peripheral vision) to the location of the peripheral stimuli shown at an unpredictable time and location relative to the central RSVP. More specifically, we asked them to detect overtly (by means of a specific button press) the appearance of textures shown randomly at a predefined target position (in the middle of the upper visual field), while ignoring the two other competing locations (either above or below the target position). This way, we could obtain a behavioral estimate of participants' ability to localize stimuli shown in the upper visual field. Given the size and shape of the peripheral textures used in our study (see Methods), this task required to process global spatial information, as opposed to their local elements, as in our previous study (Vanlessen, et al., 2013).

Following the C1, we also assessed whether the extrastriate P1 component to the peripheral stimuli might be influenced by 'targetness' and positive mood. Previous studies already reported that this component, peaking around 100-150 ms after stimulus onset, was sensitive to manipulations of selective attention, being larger for attended compared to unattended stimuli (Anllo-Vento, Luck, & Hillyard, 1998; Martínez et al., 1999). Accordingly, we could assess whether peripheral stimuli shown at the attended location in the upper visual field (i.e., the middle position) would elicit a larger P1 than those shown at the unattended locations (i.e., either below or above the middle position). We could also test whether positive mood could influence this gain control mechanism.

Moreover, for each of the three locations in the upper visual field, we also used two different texture elements to assess whether positive mood could blur the spatial resolution in the upper visual field (see Vanlessen, et al., 2013) and hence lead to a drop in their discrimination, as indexed by the N1 component (Vogel & Luck, 2000). Although participants were not instructed to pay attention to the content of the textures (they were instructed to localize them), we reasoned that the N1 component would give us an indirect correlate of their covert discrimination in the extrastriate visual cortex. An extensive pilot testing was carried out to select two textures that were able to elicit a

² The terms 'primary' and 'secondary' do not obey to a hierarchy among these two tasks, but these adjectives are used throughout the manuscript to make a clear distinction between the task at fixation ('primary') and the concurrent spatial localization task in the upper visual field ('secondary').

similar C1 component but a different N1 component (see Methods). If positive mood broadens attention to these peripheral stimuli while at the same time it decreases their spatial resolution, we surmised that the amplitude of the N1 component would be significantly less influenced by the texture content in the positive, relative to the neutral mood group.

This revised paradigm allowed us to extend our previous ERP findings (Vanlessen et al., 2013) in several ways. First, we could assess whether the early broadening of attention seen previously at the level of the C1 could be deemed ‘automatic’ (i.e., occurring regardless of the fact that the peripheral stimuli were task-relevant or not). Possibly, making the peripheral stimuli task-relevant could impede an early modulation of the C1 by positive mood, because additional processes were required to treat them explicitly. Second, we could test whether the putative broadening of attention after the induction of positive mood would be accompanied by a behavioral facilitation for the processing of the spatial location of these peripheral stimuli, compared to a neutral mood condition. Third, we could explore whether stages of sensory processing subsequent to the C1 might also be influenced by positive mood. More specifically, we could evaluate whether selective attention to these peripheral stimuli (P1 component) and their subsequent implicit discrimination (N1 component) could also be modulated by positive mood, besides the C1. Finally, we could examine whether, with this dual task setting, positive mood might potentially alter the processing of the central stimuli shown during the RSVP (both at the behavioral and ERP levels).

Using this paradigm, we formulated the following predictions. (i) We hypothesized that, at the behavioral level, participants in the positive mood group would better discriminate the location of the peripheral stimuli, compared to participants in the neutral mood group. This prediction was formulated based on earlier studies linking positive affect with a preference for global information processing (Basso, Schefft, Ris, & Dember, 1996; Gasper & Clore, 2002; Srinivasan & Hanif, 2010) and a broader focus of attention (Fredrickson, 2001; Moriya & Nittono, 2011; Rowe, et al., 2007). Unlike previous studies using primarily conflict or interference tasks (Moriya & Nittono, 2011; Rowe, et al., 2007), a strength of this paradigm was the possibility to relate positive mood to a genuine benefit in the spatial localization of peripheral stimuli, consistent with a broadening of attention. (ii) Critically, we predicted that the

C1 elicited by the peripheral stimuli would be larger in magnitude in the positive relative to the neutral mood group, indicating an early gating of attention towards these peripheral stimuli in the primary visual cortex that may underlie a broadening of attention in this specific mood state (Fredrickson, 2001; Vanlessen, et al., 2013). (iii) Besides the C1, we also explored whether positive mood could influence selective attention to these peripheral stimuli (P1 component), as well as their implicit discrimination (N1 component). Given that the extrastriate visual P1 component varies in amplitude with selective attention (Heinze et al., 1994; Mangun, Buonocore, Girelli, & Jha, 1998; Pourtois, Grandjean, Sander, & Vuilleumier, 2004), we reckoned that this component would be larger for target textures (i.e., middle position in the upper visual field) compared to textures serving as distractors (above and below this specific location). For the subsequent N1 component, we predicted that its amplitude would vary depending on the texture content. Because we already found a drop in spatial resolution for these peripheral textures in our previous study (see Vanlessen, et al., 2013), we surmised that positive mood could blur this N1 effect. (iv) Finally, regarding the primary task, we predicted that the (oddball) target stimuli embedded in the RSVP would elicit a larger P300 compared to the standard stimuli (see Moriya & Nittono, 2011; Rossi & Pourtois, 2012; Vanlessen, et al., 2013 for similar findings), indicating a clear detection of these target stimuli. We also expected participants to detect most of them (see also Rossi & Pourtois, 2012; Vanlessen, et al., 2013). Given that several previous ERP studies consistently found this P300 effect regardless of changes in the affective state of the participant, we had no reason to expect positive mood to alter this pattern for the P300 component (Rossi & Pourtois, 2012; Vanlessen, et al., 2013). Accordingly, we did not expect changes for the primary task (both at the behavioral and ERP levels) depending on the (positive) mood.

MATERIALS AND METHODS

Participants

Forty-two undergraduate students from Ghent University participated in this study (age: $M = 22$; $SD = 2$; 6 male participants per group). According to a self-report questionnaire, all participants had normal or corrected-to-normal vision and no history

of psychiatric or neurological disorders. All participants gave written informed consent prior to participation. Participants were randomly assigned to either a positive or a neutral mood condition. The data of two participants from the positive mood group were excluded from further analysis: one participant suffered from repeated migraine attacks during the experiment; another one showed excessive low accuracy for the secondary task (accuracy of 1.41% for target detection). Hence, twenty participants per mood group were included in the final sample. The study protocol was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee.

Materials

Mood Induction. Participants received either a positive or a neutral/control mood induction in a between-subjects design. The MIP used in our previous study (Vanlessen, et al., 2013) was found to be successful in eliciting the desired (positive or neutral) mood state in participants and was therefore used again in the current study. The MIP consisted of an imagery procedure in which participants were instructed to vividly imagine to re-experience an autobiographical memory (Holmes, 2006; Holmes, et al., 2008). The MIP was preceded by imagery exercises (i.e. holding and manipulating a lemon) in order to train participants to imagine from their own perspective (Holmes, 2006; Holmes, et al., 2008). During the MIP, participants were asked to recall and report a specific situation they experienced at least one week before the experiment, that made them feel either very happy (positive mood condition) or neutral (neutral mood). Next, participants closed their eyes and tried to vividly imagine reliving the reported experience for 30 seconds. Then, the experimenter asked the participants questions about the sensations they could experience during imagination, in order to encourage concrete imaginations from the requested perspective (Watkins & Moberly, 2009; based on Holmes et al., 2008). Next, participants imagined the recalled experience for another 30 seconds. During both the memory recall and the experimental task, experimentally validated classical music fragments were playing in the background in order to implicitly trigger the associated mood (Bower & Mayer, 1989; Mitterschiffthaler, Fu, Dalton, Andrew, & Williams, 2007). Participants were instructed to pay no attention to the music. We ensured participants remained naïve regarding the

purpose of the MIP using a cover story making them believe that the experiment concerned the relationship between the processing of visual information and the ability to use imagination.

Changes in subjective levels of mood following the MIP were measured by means of three questionnaires: the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988), the Self-Assessment Manikin for Arousal (SAM; Bradley & Lang, 1994) and three 10 centimeters, horizontal Visual Analogue Scales (VAS) for the feelings happiness, pleasantness and sadness. The left anchor of the VAS was labeled 'Neutral', while the right one was labeled 'As happy/pleasant/sad as you can imagine'.

Main Task. Participants performed a dual task deriving from an experimental paradigm validated previously (Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rossi & Pourtois, 2012, 2013; Schwartz, et al., 2005). The primary task was used to ensure sustained central/foveal vision throughout the experimental session and measure top-down attention control mechanisms. It consisted of a RSVP of short lines (1 cm) at central fixation, that could be either standard lines (tilted 35° counterclockwise from the vertical axis) or target lines (tilted 45°), with a 4:1 standard/target ratio (see Fig. 1A).

Participants made a key press on a response box upon target detection (using a pre-defined key). The secondary task was decoupled from this foveal RSVP and entailed the localization of visual textures shown in the upper visual field. These stimuli were presented at an unpredictable location and time (i.e. variable SOA between central stimulus and peripheral texture) relative to the central stimuli. Central and peripheral stimuli never overlapped in space nor time.

The peripheral stimuli consisted of visual textures ($3^{\circ} \times 34^{\circ}$ of visual angle) organized in two horizontal lines that were constituted of either crosses (0.8 x 0.9 cm) or snowflake-like elements (0.9 x 1 cm, see Fig. 1C), with an equal number of presentations of each type at each location (at 5.3°, Close; 7.8°, Middle; or 10.3°, Far from central fixation). Based on a pilot EEG study, we selected these two textures because they elicited a reliable amplitude difference at the level of the N1, indexing a rapid discrimination of the content between these two textures (i.e., the snowflake-like texture elicited a larger N1 amplitude than the crosses), while they both elicited a clear

and similar C1, our main ERP component of interest. However, this variation along the texture content was task-irrelevant (and unknown to the participants), whereas the actual spatial location of the peripheral stimulus was the task-relevant stimulus dimension (secondary task). Participants were instructed to detect overtly any peripheral texture stimulus appearing in the middle position in the upper visual field (using another pre-defined key). Thus, participants responded with one of two predefined keys of the response box for the central targets and with the other one for peripheral targets; this stimulus-response mapping was counterbalanced across participants. In addition, participants were instructed to withhold responding for textures appearing randomly at one of the two other competing positions. Thus, the non-target peripheral stimuli (i.e., textures shown either below or above this middle location, resulting in distractors appearing close to fixation or far from it; see Fig. 1B) did not require any manual response.

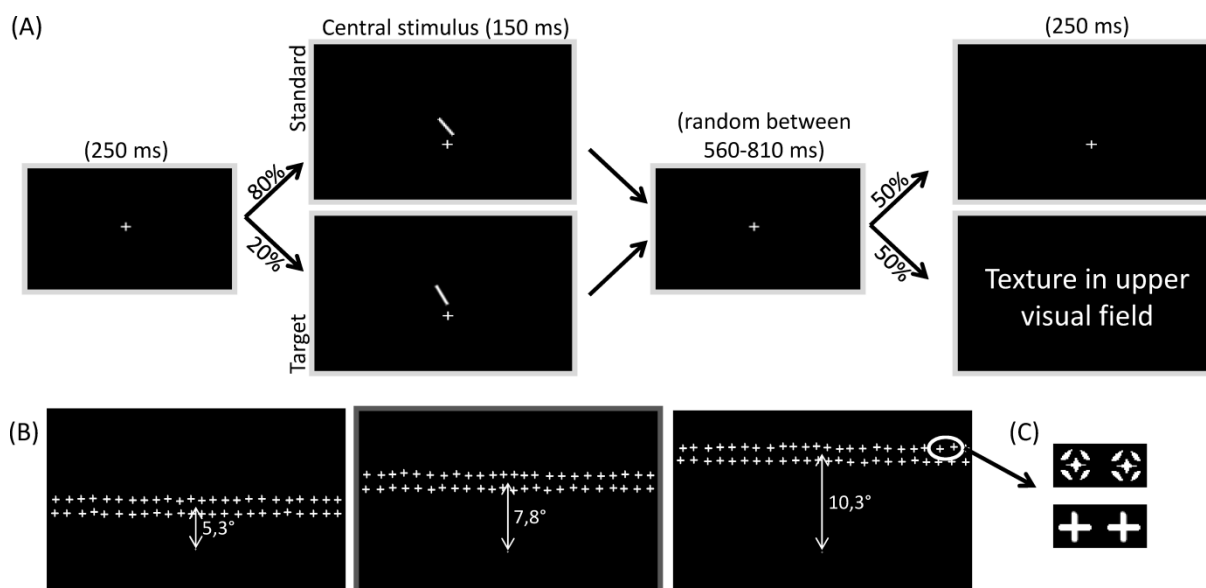


Figure 1. Stimuli and task. A) Participants performed a dual task consisting of a demanding oddball task at fixation and a localization task (with peripheral vision) of textures shown at three concurrent spatial positions in the upper visual field. Stimuli at fixation and peripheral textures never overlapped in space nor time. B) Visual textures at the three possible positions in the upper visual field: close, middle or far relative to fixation. Only the middle position was task-relevant and required an overt response. C) Half of the peripheral textures were made up by snowflake-like elements, while the other half consisted of ‘crosses’, with an equal number of presentations of each type at each of the three locations. Texture content was task-irrelevant.

Localizer. When the main task was completed, participants received two additional blocks containing peripheral stimuli only under passive viewing conditions (no RSVP at fixation; mere fixation required). These peripheral stimuli were shown at six non-overlapping positions, i.e., the same three positions relative to fixation as in the main task (close, middle and far in the upper visual field), as well as the three symmetric positions in the lower visual field. A total of 480 stimuli (240 per block) were presented in random order and were equally divided over the six possible locations and with an equal number of each texture subtype at each position. Due to a technical problem, the data of one participant in the positive mood group could not be saved properly.

These two additional blocks were employed to confirm that the first Visual Evoked Potential (VEP) elicited by the peripheral textures during the main task corresponded to a reliable retinotopic C1 component (see Rossi & Pourtois, 2012; Vanlessen, et al., 2013). Hence, we used these ERP data as an independent localizer for the C1 component. Following standard practice, this was achieved by contrasting upper vs. lower visual field stimulations and showing the expected polarity reversal for this early striate component (manifested by a negative C1 amplitude for stimuli shown in the upper visual field, but a positive C1 amplitude at the same early latency following stimulus onset for the same stimuli shown in the lower visual field; see Clark, et al., 1995; Jeffreys & Axford, 1972; Rauss, et al., 2011). These properties (latency, amplitude, polarity and topography) allowed us to confirm that the earliest component generated during the main task (peripheral stimuli) corresponded to a C1 component likely generated in the fundus of the calcarine fissure. A primary source of the C1 in V1 was further confirmed by source localization methods (see here below).

Given that the MIP was not repeated prior to these two blocks, we surmised that residual effects of positive mood ought to be minimal (see Table 1 for direct confirmation), and thus would no longer exert an influence on the C1 amplitudes (as confirmed by our ERP results, see here below). We could also have administered these localizer blocks prior to the first MIP in order to avoid any possible carryover effect of the mood. However, we did not opt for this possibility for methodological reasons, because we did not want to draw the attention of the participants to these peripheral stimuli before the start of the experimental session. We wanted to avoid a ‘priming’ effect that might have contaminated the C1 recorded for the same peripheral stimuli

during the main task or altered the efficiency of the cover story told to the participants during the first MIP.

Questionnaires. Participants completed three trait-related questionnaires: the Beck Depression Inventory (BDI; Beck, Steer, Ball, & Ranieri, 1996), the BIS/BAS scales (Carver & White, 1994) and the Dutch Resilience scale (Rs; Portzky, Wagnild, De Bacquer, & Audenaert, 2010). These questionnaires were used to confirm balanced (low) depression level, activation/inhibition and resilience between the two groups.

Procedure

Participants were first prepared for EEG recording and then completed two practice blocks (in total containing 45 trials, of which 8 central target lines), which were repeated until 80% accuracy for central target detection was reached. Next, the positive or neutral MIP was administered, after the field perspective training phase (duration: about 20-25 minutes). The MIP was shortly repeated (for five minutes) after blocks 3 and 6, in order to maintain the targeted mood until the end of the task. At the beginning of each trial, a fixation cross was presented (250 ms), followed by a central stimulus (150 ms), which could be a standard stimulus (in 80 percent of the trials) or a target stimulus (20 percent of the trials) requiring an overt response. The central stimulus was followed by another fixation cross (displayed during the SOA with an average duration of 685 ms, randomly varying between 560 to 810 ms). In half of the trials, the fixation cross stayed on the screen for another 250 ms; in the other half, a peripheral texture was briefly presented for the same period (250 ms) at one out of the three possible locations in the upper visual field (see Fig. 1A). Next, a fixation cross was presented for 1500 ms before the next trial started. Although the textures could be presented at three possible locations above fixation, participants only had to respond to textures shown in the middle position (i.e. 7.8° from fixation). The task consisted of a total of 450 central stimuli (i.e., 360 standard and 90 target lines), of which 225 were followed by a peripheral stimulus (i.e., 180 after the presentation of a central standard line and 45 after a central target line). Trials were presented in a semi-random order: the first three stimuli in a block never contained a central target line, nor a peripheral texture. Instructions emphasized accuracy and speed for both the primary and

secondary tasks and a reminder of the stimulus-response mapping for both the central and the peripheral stimuli was shown at the beginning of each block. Instructions also stressed central fixation to carry out the primary task, while the secondary task had to be made using peripheral vision (in the upper visual field). At the end of the main task, participants received two blocks of 240 trials of peripheral textures under passive viewing conditions ('localizer'). All stimuli were grey and presented against a uniform black background. Each participant completed 9 blocks containing 50 trials each, seated at 57 cm from a 19" CRT screen, with their head movements restrained by a chinrest. The task was programmed using the E-Prime Version 2 software (Psychology Software Tools, Inc., 2001).

VASs, PANAS and SAM for Arousal were administered at the beginning of the experiment (baseline measure), after each MIP and at the end of the experiment, in order to assess directional changes in positive mood after the MIP, compared to baseline. After completion of the experimental tasks, participants received questions about the stimulus content of the textures presented in the upper visual field: they were asked to rate how many different texture types they think were presented in the upper visual field during the main task, how certain they were about their response and to what extent they had paid attention to the texture content. Next, participants completed the three trait-related questionnaires.

Analyses of behavioral data

To verify if mood scores changed post- compared to pre-MIP, we first calculated the average values for each VAS, PANAS and SAM administered after each MIP. Next, we compared the post-MIP scores with the baseline measure for these scales by performing separate 2 (Time: baseline vs. post-MIP) x 2 (Mood: neutral vs. positive) mixed ANOVAs on the VASs, PANAS and SAM scores as well as independent samples T-tests to further establish the specificity of the mood change in the positive mood group. Mean scores for the trait-related questionnaires were compared between mood groups using independent sample T-tests.

For the oddball task at fixation (primary task), accuracy was calculated taking into account all types of errors (i.e., false alarms to standard stimuli and missed target stimuli). We used independent samples T-tests to assess differences in accuracy and

mean reaction times (RTs) for correct responses between mood groups. The accuracy for the secondary task was analyzed by means of mixed ANOVAs with Position (close, middle or far) as within-subjects and Mood (positive vs. neutral) as between-subjects factor. Mean RTs for the detection of target textures (Middle position in the upper visual field) were analyzed using an independent samples T-test with Mood as between-subjects factor. All T-tests were two-tailed.

Trials with errors for the primary task and/or RTs exceeding $\pm 2,5$ SDs above or below the individual mean RT for the primary or secondary task were excluded from further analysis. The number of removed trials was balanced between the two mood groups (positive: $M = 3.61\%$, $SD = 3.08$; neutral: $M = 4.84\%$, $SD = 4.97$, $t(38) = 0.94$, $p = .35$). Statistical analyses were run on 95.77% of the total data. Effect sizes were reported for all analyses. More specifically, we reported partial eta squared for the ANOVAs and Cohens' d (based on the observed means and standard deviations; see Lakens, 2013) both for the independent and paired T-tests.

EEG data acquisition and reduction

EEG was continuously recorded from a Biosemi Active Two System, using 128 AgAgCl electrodes. EEG signals were referenced online to the CMS-DRL electrodes and sampled at 512 Hz. Vertical oculograms were recorded through additional bipolar electrodes placed respectively above and below the left eye. The data reduction method using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany) was identical for the main task and the localizer blocks.

EEG signals were referenced offline to the linked mastoids and band-pass filters between 0.016 and 70Hz, and a notch-filter (50Hz) were applied. Next, the EEG data were segmented relative to the onset of either central or peripheral stimuli (stimulus-locked epochs; segmentation window of 160 ms pre- and 740 ms post-stimulus onset). In order to avoid contamination by the processing of and response to the target stimuli at fixation, individual ERPs for the peripheral textures were only included in the averages when they followed a central standard stimulus that did not require any response (and did not elicit a P300).

Artifacts due to eye blinks were automatically corrected by means of the standard Gratton et al. algorithm (Gratton, Coles, & Donchin, 1983). A spherical splines

procedure was used for interpolating noisy channels. The epochs were baseline-corrected using the entire 160 ms pre-stimulus interval. Epochs containing residual artifacts were semi-automatically rejected using an absolute voltage criterion of $\pm 75 \mu\text{V}$ exceeding baseline. Using this procedure, 79% of the epochs were found to be artifact-free. For the main task, averages were calculated separately per participant for target and standard stimuli (primary task), and for peripheral stimuli at each position (Close, Middle or Far). For the localizer blocks, individual averages were calculated for the three positions above vs. below fixation.

Given its typical centro-parieto-occipital scalp distribution, the P300 component was identified at electrode positions A19, A20 and A21 (midline; with A19 corresponding to electrode Pz in the International 10–20 System and A21 to POz); A5, A18 and A17 (left hemisphere); and A32, A31 and A30 (right hemisphere). We calculated the mean amplitude of the P300 per electrode during the time window spanning from 490 to 690 ms post-stimulus onset for the target and standard stimuli separately (primary task). We used this specific time window because it best encompassed the P300 component for all participants over posterior parietal electrodes. For the peripheral stimuli (secondary task), a semi-automatic peak detection was applied on the individual averages in order to score the latency and amplitude of the C1 and P1 in both the main task and the localizer blocks, as well as the N1 in the main task (Picton et al., 2000). Then, for each of these deflections separately, we computed the mean amplitude around the peak using a 20 ms interval (10 ms before and 10 ms after the peak). The C1 was defined as a negative ongoing peak with the greatest amplitude between 25 and 85 ms post-stimulus onset over occipito-parietal electrode positions A19/Pz, A20 and A21/ POz (midline); A5, A17 and A18 (left hemisphere); and A32, A31 and A30 (right hemisphere). The P1 component was defined as the first positive deflection following the C1, peaking between 75 and 150 ms post-stimulus onset. The P1 was measured at slightly more occipital (lower) electrode positions compared to the C1: A21/ POz, A22 and A23/Oz (midline); A15/O1, A16, A17 and (left hemisphere); and A28/O2, A29, A30 (right hemisphere). Finally, the N1 component was identified as the first negative wave following the P1, reaching its highest amplitude between 155 and 215 ms post-stimulus onset at electrode positions A8, A9, A10/PO7; B11/P8, B12 and B13 on the left hemisphere; and B5, B6, B7/PO8,

D29, D30 and D31/P7 on the right hemisphere. These electrode positions were selected based on the topographical properties of the current data set. Statistical analyses were performed on the amplitude values pooled across the selected electrodes.

Separate mixed ANOVAs were used for the analysis of the mean amplitudes of the P300, C1, P1 and N1 components. For the P300, we used a mixed ANOVA with Stimulus (standard vs. target) as within-subjects factor, and Mood (positive vs. neutral) as between-subjects factor. The C1 (main task and localizer) and P1 data were submitted to mixed ANOVAs with Position (close, middle or far) as within-subjects factor, and Mood (positive vs. neutral) as between-subjects factor. For the analysis of the N1, we applied a mixed ANOVA with Position (close, middle or far) and Texture (crosses vs. snowflakes) as within-subjects factors, and Mood (positive vs. neutral) as between-subjects factor. Two-tailed paired or independent samples T-tests were used to perform post-hoc comparisons. We also performed ANOVAs on the peak latencies of these ERP components. However, these analyses did not show significant effects of mood on their latencies (all $p > .18$ for main or interaction effects involving mood as a factor). Therefore, we report the results obtained for the mean amplitudes of these components only. Whenever normality assumptions were violated, corrected p-values were used. As was the case for the analyses of the behavioral data, partial eta squared and Cohens' d were reported.

Finally, to corroborate the assumption of generators located primarily in the striate visual cortex for the C1 component, we used standardized low-resolution brain electromagnetic tomography (sLORETA, Pascual-Marqui, 2002). sLORETA solutions are computed within a three-shell spherical head model co-registered to the MNI152 template (Mazziotta et al., 2001). sLORETA estimates the 3-dimensional intracerebral current density distribution in 6239 voxels (5 mm resolution), each voxel containing an equivalent current dipole. This 3-dimensional solution space in which the inverse problem is solved is restricted to the cortical gray matter. The head model for the inverse solution uses the electric potential lead field computed with a boundary element method applied to the MNI152 template (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002). Scalp electrode coordinates on the MNI brain are derived from the international 5% system (Jurcak, Tsuzuki, & Dan, 2007). A direct statistical comparison

between the two groups for the C1 component was carried out using a stringent non-parametric randomization test (relying on 5000 iterations).

RESULTS

Changes in mood: manipulation check

The 2 (Time) x 2 (Mood) ANOVA on the VAS scores showed a significant interaction effect between Time and Mood for feelings of happiness (baseline: positive: $M = 5.42$, $SD = 2.72$, neutral: $M = 4.51$, $SD = 2.84$; post-MIP: positive: $M = 7.87$, $SD = 1.71$, neutral: $M = 4.17$, $SD = 2.74$; $F(1,38) = 58.83$, $p < .001$, $\eta p^2 = 0.61$), and pleasantness (baseline: positive: $M = 5.76$, $SD = 2.60$, neutral: $M = 4.76$, $SD = 2.76$; post-MIP: positive: $M = 7.62$, $SD = 1.76$, neutral: $M = 4.41$, $SD = 2.50$; $F(1,38) = 17.84$, $p < .001$, $\eta p^2 = 0.32$), but not for sadness (baseline: $M = 0.50$, $SD = 0.80$, post-MIP: $M = 0.77$, $SD = 0.91$, $F(1,38) = 1.48$, $p = .23$, $\eta p^2 = 0.04$; see Table 1 for a break-down of the happiness vs. sadness mean values obtained for the different measurement moments and groups, separately). Next, we compared VAS scores between the positive and the neutral mood groups at baseline vs. post-MIP, using independent T-tests. As expected, post-MIP mood measurements showed a significant difference between the positive and the neutral mood group for both feelings of happiness ($t(38) = 5.13$, $p < .001$, $d = 1.62$; see Fig. 2A) and pleasantness ($t(38) = 4.69$, $p < .001$, $d = 1.48$; see Fig. 2B). Importantly, at baseline, groups did not differ for reported happiness ($t(38) = 1.04$, $p = .25$, $d = 0.33$) nor pleasantness ($t(38) = 1.17$, $p = .95$, $d = 0.37$). These results show a selective increase in positive affect after MIP in the positive, but not in the neutral, mood group (see also Table 1).

The 2 (Time) x 2 (Mood) ANOVA on the PANAS scores showed a significant interaction effect between Time and Mood for the PA scales (baseline: positive: $M = 31.60$, $SD = 5.58$, neutral: $M = 30.95$, $SD = 6.72$; post-MIP: positive: $M = 32.95$, $SD = 6.02$, neutral: $M = 28.77$, $SD = 6.98$, $F(1,38) = 7.00$, $p = .012$, $\eta p^2 = 0.16$), but not for the NA scales (baseline: $M = 12.25$, $SD = 2.33$; post-MIP: $M = 11.43$, $SD = 1.89$, $F(1,38) = 2.56$, $p = .118$, $\eta p^2 = 0.06$). An independent samples T-test showed a significant difference between the positive and neutral mood group on the post-MIP PA scores, $t(38) = 2.03$, $p = .05$, $d = 0.64$ (see Fig. 2C). At baseline, this difference was not significant ($t(38) = 0.33$, $p = .65$, $d = 0.11$). These results show that while positive affect in the neutral mood

group substantially decreased from baseline to post-MIP, no similar blunting of positive affect was seen in the positive mood group.

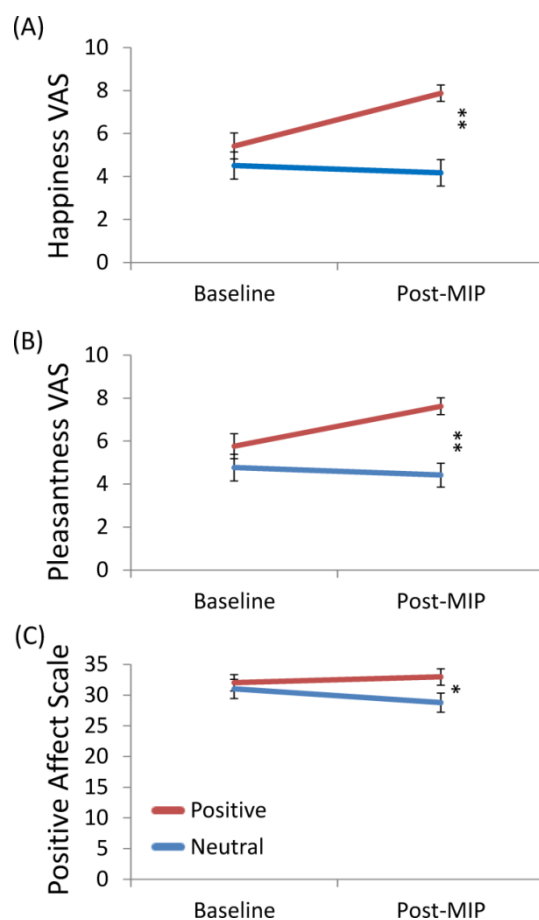


Figure 2. Mood scores at baseline and after the MIP (average of the different measurements following the first MIP) of A) the VAS for feelings of happiness and B) feelings of pleasantness, and C) the positive affect scale of the PANAS. VAS scores for happiness and pleasantness increased after the MIP in the positive mood group, while they remained unchanged after the MIP (relative to the baseline) in the neutral mood group. The positive affect measured with the PANAS decreased during the experiment in the neutral mood group, but remained stable in the positive mood group. ** indicates a significant effect with $p \leq .001$ and * $p \leq .05$; error bars represent 1 S.E.M.

The 2 (Time) x 2 (Mood) ANOVA on the SAM for Arousal scores showed a significant interaction effect between Time and Mood (baseline: positive: $M = 4.22$, $SD = 1.22$, neutral: $M = 3.63$, $SD = 1.61$; post-MIP: positive: $M = 5.22$, $SD = 1.75$, neutral: $M = 3.21$, $SD = 1.32$, $F(1,35) = 8.52$, $p = .006$, $\eta p^2 = 0.20$). An independent samples T-test on the Arousal scores showed a significant difference between the positive and neutral mood group (with higher subjective levels of arousal in the former compared to the

latter group), $t(35) = 4.20$, $p = .001$, $d = 1.30$ after the MIP, but not at baseline, $t(35) = 1.26$, $p = .22$, $d = 0.41$.

Table 1. Mean VAS scores (1 standard deviation) obtained for the feelings happiness and sadness at the different measurement points during the experiment, separately for the positive and the neutral mood group. These results show a steep increase of happiness following the first MIP in the positive mood group, exclusively. High levels of happiness were also maintained throughout the experiment in this group. By contrast, levels of sadness were low and balanced between the two groups.

VAS	Group	Baseline	MIP1	MIP2	MIP3	After last block
Happiness	Positive	5.42 (2.72)	8.01 (1.77)	7.66 (1.94)	7.95 (1.82)	5.54 (2.69)
	Neutral	4.51 (2.84)	4.23 (2.78)	4.20 (2.79)	4.07 (2.88)	3.87 (2.89)
Sadness	Positive	0.61 (0.73)	0.54 (0.89)	0.42 (0.66)	0.53 (0.95)	0.51 (0.60)
	Neutral	0.60 (0.79)	0.91 (1.32)	0.71 (0.76)	0.70 (0.82)	0.74 (1.45)

Behavioral results.

Primary task

Participants reached high levels of accuracy, equally so in each mood group (positive group: $M = 96.65$, $SD = 2.93$; neutral group: $M = 96.51$, $SD = 3.62$, $t(38) = 0.13$, $p = .90$, $d = 0.04$). Likewise, RTs for correct target detection did not differ significantly between groups, although the RTs in the positive group were numerically shorter (positive group: $M = 482.866$, $SD = 85.39$; neutral group: $M = 524.21$, $SD = 69.27$, $t(38) = 1.68$, $p = .10$, $d = 0.53$). Together, these results show a balanced performance between the two mood groups for the primary task, confirming one of our predictions. Moreover, the high accuracy in each group suggests that participants maintained fixation in the center of the screen throughout the experimental session and processed the textures in the upper visual field with peripheral vision (see also Rossi & Pourtois, 2013).

Secondary task

A mixed ANOVA performed on the mean accuracy scores with Position and Group as factors showed a significant effect of Position (Close: $M = 91.33$, $SD = 8.64$; Middle: $M = 84.16$, $SD = 14.64$, Far: $M = 86.24$, $SD = 13.26$, $F(2,76) = 4.02$, $p = .022$, $\eta^2 = 0.10$). The interaction effect of Position and Group ($F(2,76) = 0.93$, $p = .40$, $\eta^2 = 0.02$), as well as the main effect of Group ($F(1,38) = 0$, $p = .99$, $\eta^2 < .001$), were not significant. A post-hoc independent samples T-test performed on the RTs for target detection showed that participants in the positive mood group ($M = 593.79$, $SD = 108.14$) identified the target textures faster than participants in the neutral mood group ($M = 667.72$, $SD = 82.76$, $t(38) = 2.43$, $p = .020$, $d = 0.77$). These results confirmed our second prediction.

To evaluate the presence of a possible trade-off between the primary and the secondary task, we performed an auxiliary correlation analysis showing however no relation between them regarding accuracy ($r = .082$, $p = .61$). A positive relation was found ($r = .36$, $p = .023$) for the speed with these two tasks, indicating that participants who were faster with the primary task were also faster with the secondary. Hence, these results confirm that high accuracy for the primary task was not compensated by low accuracy for the secondary task or vice versa.

Primary and secondary task combined

We also performed an ANOVA on these RT data with Mood as between-groups factor and Task as within-groups factor. The rationale for this control analysis was to assess whether the substantial RT facilitation ($d = 0.77$) as a function of positive mood observed for the secondary task could be dissociated from the (non-significant) RT facilitation found for the primary task with positive mood. This analysis showed significant main effects of Task ($F(1,38) = 72.04$, $p < .001$, $\eta^2 = 0.66$) and Group ($F(1,38) = 6.31$, $p = .06$, $\eta^2 = 0.14$); however, the interaction effect between the two factors failed to reach significance ($F(1,38) = 1.30$, $p = .26$, $\eta^2 = 0.03$). Moreover, using G*Power, we estimated that we would need to test at least 64 participants per group to achieve a significant group difference for the primary task, with a medium effect size ($d = 0.50$) and a power of 0.80. Accordingly, these results suggest that positive mood likely led to a general RT facilitation (including the primary and secondary tasks), however, we lacked sufficient power to reveal this effect for the primary task.

Questionnaires

No significant group differences were found regarding the trait-related variables, including the BIS/BAS (BIS: $t(38) = 0.36$, $p = .72$, $d = 0.11$, BAS Drive $t(38) = 0.58$, $p = .56$, $d = 0.18$, BAS Fun: $t(38) = 0.10$, $p = .92$, $d = 0.03$, BAS Reward: $t(38) = 0.43$, $p = .67$, $d = 0.14$) and the Dutch Resilience Scale ($t(38) = 0.35$, $p = .73$, $d = 0.11$). These results suggest that group differences found at the behavioral and ERP levels were not confounded by obvious personality differences between the two groups. However, a post-hoc independent samples T-test performed on the BDI scores did show a significant group difference, with a somewhat surprising higher level of (subclinical) depression in the positive mood group ($M = 9.85$, $SD = 8.02$), compared to the neutral mood group ($M = 4.80$, $SD = 4.54$; $t(38) = 2.45$, $p = .019$, $d = 0.77$). However, this unexpected group difference regarding levels of depression did not prevent participants in the positive mood group to increase their positive mood following the MIP, compared to participants assigned to the neutral mood group (see behavioral results here above). Furthermore, these BDI scores did not correlate with behavioral performance (RT and ACC) for the primary or secondary task, nor with the P300 to central targets or C1 to peripheral stimuli (all $p > .24$).

Post-experiment questions related to the texture content showed balanced results between the two groups. In each mood group, eight out of 20 participants correctly estimated the number of different textures ($n = 2$) that appeared in the upper visual field during the main task. The level of confidence in their estimation was also balanced between the two groups ($M = 4.04$, $SD = 2.39$; $t(38) = 1.51$, $p = .14$, $d = 0.48$), as was their subjective rating regarding the extent to which they paid attention to the texture content ($M = 3.08$, $SD = 2.16$; $t(38) = 1.25$, $p = .22$, $d = 0.40$).

ERP results.

Primary task

P300. The mixed ANOVA showed, as expected, a significant main effect of Stimulus type ($F(1,38) = 211.78$, $p < .001$, $\eta p^2 = 0.85$). A post-hoc paired samples T-test showed that the P300 amplitude elicited by target stimuli ($M = 11.45$, $SD = 0.67$) was significantly larger than the P300 to standard stimuli ($M = 3.49$, $SD = 0.28$, $t(38) = 12.83$, $p < .001$, $d =$

2.44, see Fig. 3), indicating that oddball target stimuli were detected and processed differently compared to standards.

Additionally, the ANOVA also showed a significant interaction effect between Stimulus type and Mood ($F(1,38) = 12.19, p = .001, \eta p^2 = 0.24$). This interaction was driven by a larger P300 for the target stimuli in the positive mood group ($M = 13.34, SD = 3.94$) compared to the neutral mood group ($M = 9.55, SD = 3.78, t(38) = 3.11, p = .004, d = 0.98$), while the P300 amplitude to the standard stimuli did not differ between groups ($t(38) = 0.043, p = .97, d = 0.01$, see Fig. 3). This interaction suggests that participants in the positive mood group likely detected targets more easily than the neutral mood group. However, as reported here above, this neurophysiological effect was not accompanied by a change at the behavioral level (balanced accuracy and mean RTs for the primary task between the two groups).

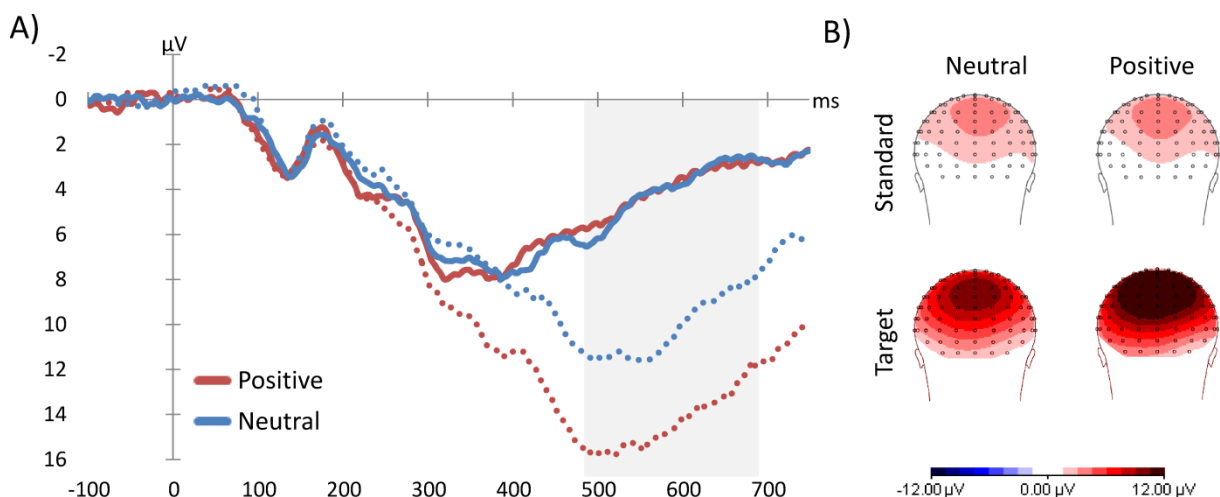


Figure 3. A) *Grand average ERPs to central stimuli (primary task) recorded at a representative posterior parietal midline electrode position (A20). A clear increase of the P300 component was found for oddball target stimuli (dashed line) compared to standard stimuli (solid line). However, the target P300 was larger in the positive (red) compared to the neutral (blue) mood group. No group difference was found for the P300 in response to the standard stimuli. The P300 was scored as the mean ERP activity recorded during a prolonged time interval (spanning from 490 to 690 ms post-stimulus onset; demarked by the grey frame). Note that negative values are plotted upwards.* B) *Corresponding voltage maps (back view) for the P300 component for the standard and target stimuli, separately for the positive and the neutral mood group.*

Secondary task

C1. The mixed ANOVA revealed a significant main effect of Position ($F(2,76) = 16.95, p < .001, \eta p^2 = 0.31$; Fig. 4A and B). Planned comparisons showed a drop in C1 amplitude with increasing eccentricity (see also Vanlessen, et al., 2013). The C1 was larger in magnitude for peripheral stimuli shown at the close position ($M = -4.03, SD = 2.32$) relative to both the middle position ($M = -1.95, SD = 1.91; t(39) = 4.94, p < .001, d = 0.98$), and the far position ($M = -2.12, SD = 1.95; t(39) = 4.74, p < .001, d = 0.89$). The C1 did not differ between the middle and far position ($t(39) = 0.49, p = .63, d = 0.09$). Importantly, this analysis also showed a significant main effect of Mood, showing a greater C1 amplitude to peripheral stimuli (regardless of their position) in the positive ($M = -3.24, SD = 1.46$) compared to the neutral mood group ($M = -2.16, SD = 1.35, F(1,38) = 5.95, p = .019, \eta p^2 = 0.14$; see Fig. 4).

The independent localizer blocks enabled us to ascertain that this early component recorded during the main task was a C1 component. A direct visual comparison between the main task and localizer blocks showed that the C1 had the same morphology and topography in these two sessions. Second, we found a clear-cut polarity reversal for this component depending on which part of the visual field (either upper or lower) was stimulated with these textures (see Fig. 5A and B), confirming that this early component had a striate origin (Kelly, et al., 2013).

The ANOVA performed on the mean C1 amplitudes for the stimuli presented in the upper visual field during the localizer blocks yielded a significant main effect of position ($F(2,74) = 19.94, p < .001, \eta p^2 = 0.35$), suggesting a linear decrease of the C1 amplitude with increasing eccentricity (close vs. middle: $t(38) = 4.61, p < .001, d = 0.85$; close vs. far: $t(38) = 5.58, p < .001, d = 1.23$; middle vs. far: $t(38) = 2.21, p = .03, d = 0.48$). Unlike the main task, no main effect of Mood ($F(2,74) = 0, p = .99, \eta p^2 < 0.001$), nor an interaction effect between Position and Mood ($F(2,74) = 1.59, p = .21, \eta p^2 = 0.04$) was found for the C1 in this analysis (localizer blocks), suggesting that when the MIP was ceased, modulatory effects of positive mood on this early retinotopic component were no longer present.

For the main task, results of the source localization algorithm (sLORETA) confirmed that the larger C1 in the positive compared to the neutral mood group was associated with enhanced activity in the primary visual cortex (see Fig. 4D).

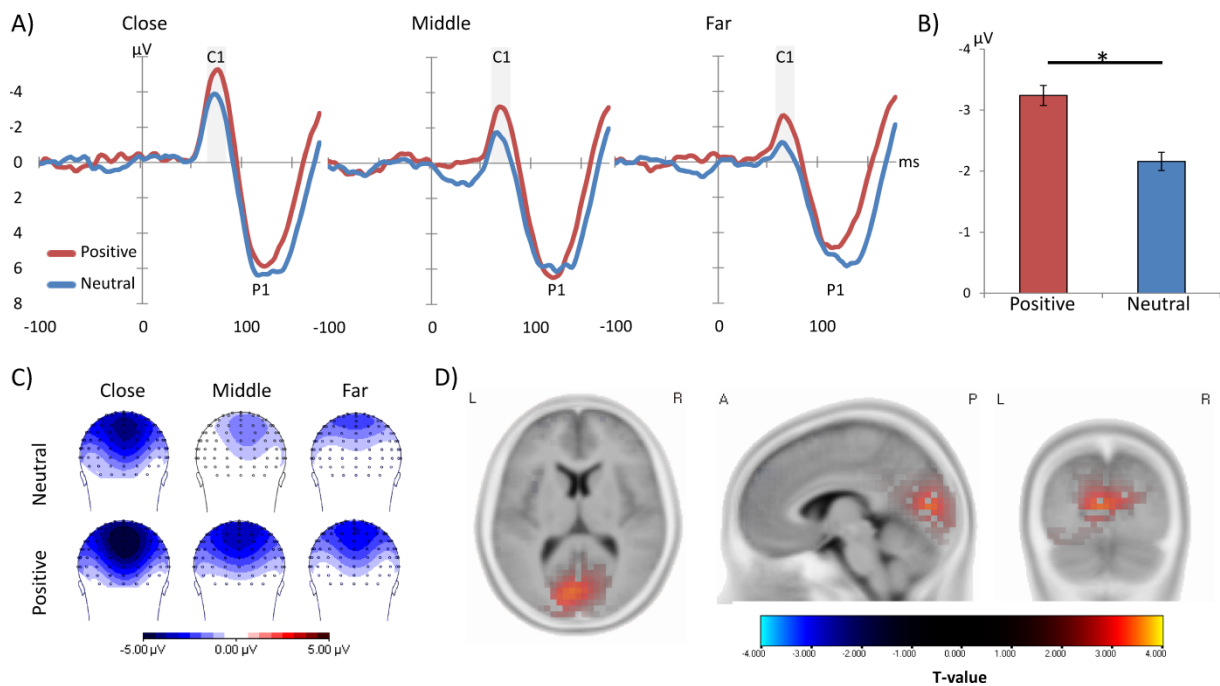


Figure 4. A) *Grand average ERPs to peripheral textures shown in the upper visual field recorded at a representative posterior parietal midline electrode position (A21/POz), separately for the three positions. While the amplitude of the C1 monotonically decreased with increasing eccentricity relative to fixation, it was systematically larger in the positive (red) compared to the neutral (blue) mood group. Note that only the Middle position was task-related. The C1 was scored in individual averages as the mean ERP activity recorded during a 20 ms interval around the peak (demarcated by the grey frame). Negative values are plotted upwards.* B) *Across the three positions, the C1 was larger in the positive (red) compared to the neutral mood group (blue). * indicates a significant effect with $p \leq .05$; error bars represent 1 S.E.M.* C) *Corresponding voltage maps for the C1, separately for each stimulus position and each group.* D) *Direct statistical comparison in the inverse solution space (sLoreta) between the positive mood group ($n = 20$) and the neutral mood group ($n = 20$) for the C1 (peak amplitude) generated in response to the peripheral textures (all three positions aggregated). This analysis revealed a significantly higher activation in the positive compared to the neutral mood group encompassing early visual areas (Brodmann areas 17 and 18). The maximum activation ($t(39) = 3.44, p < .005$) was found in $x = -5, y = -80, z = 10$ (MNI coordinates), corresponding to the vicinity of the calcarine fissure. This statistical analysis is based on a stringent non-parametric randomization test (relying on 5000 iterations), and provides corrected p-values.*

P1. The mixed ANOVA showed a main effect of Position ($F(2,76) = 6.57, p = .002, \eta^2 = 0.15$), in such a way that the close ($M = 6.32, SD = 3.07$) and middle position ($M = 6.08, SD = 3.13$) led to a larger P1 than the far position ($M = 4.91, SD = 2.75; t(39) = 2.98, p = .005, d = 0.48$; and $t(39) = 3.12, p = .003, d = 0.40$ for these two comparisons,

respectively) (see Fig. 5C). The amplitude of the P1 was balanced for the Close and Middle positions ($t(39) = 0.59, p = .56, d = 0.08$).

The observation that the amplitude of the P1 did not decrease monotonically with increasing eccentricity (like the C1 did) is compatible with earlier studies that have reported enhanced P1 effect for attended vs. unattended stimuli (Anllo-Vento, Luck, & Hillyard, 1998; Martínez, et al., 1999). Attended stimuli were textures shown in the middle position of the upper visual field in the present case. For this location, the P1 was reliably larger than for the far position (where no overt discrimination was required). However, the P1 was equally large in size for the middle and close positions. This could be explained by the fact that in our experimental design, attention had to be allocated to two non-overlapping positions concurrently (i.e., the center of the screen and the middle part of the upper visual field). In these conditions, visual stimuli appearing between these two anchors (textures shown at the close position) somehow received priority alike during the competition for attention selection (Castiello & Umiltà, 1992; Heinze, Luck, et al., 1994; Jans, Peters, & De Weerd, 2010). At any rate, the results obtained for the P1 clearly showed that the middle position was prioritized or attended relative to the far position, given the specific task demands (secondary task).

Unlike the C1 component, no significant main effect of Mood was found for the P1 component ($F(1,38) = 0.24, p = .63, \eta p^2 = 0.006$), nor a significant interaction effect between Mood and Position ($F(2,76) = 1.41, p = .25, \eta p^2 = 0.04$; see Fig. 4 and 5C).

N1. The mixed ANOVA yielded a significant main effect of Texture ($F(1,38) = 16.17, p < .001, \eta p^2 = 0.30$) (see Fig. 5D). However, no main effect of Position or Mood, nor interaction effects between these factors reached significance (all $p > .05$; all $\eta p^2 \leq 0.05$). This finding suggests that although the texture content was kept task-irrelevant, the two textures elicited a differential activation (presumably in the extrastriate visual cortex) early on following stimulus onset, at the level of the N1 (Luck, Woodman, & Vogel, 2000; Vogel & Luck, 2000). However, positive mood did not alter this early discrimination process (as we surmised it might have been the case if a broadening of attention under positive mood would also be accompanied by a drop in spatial resolution).

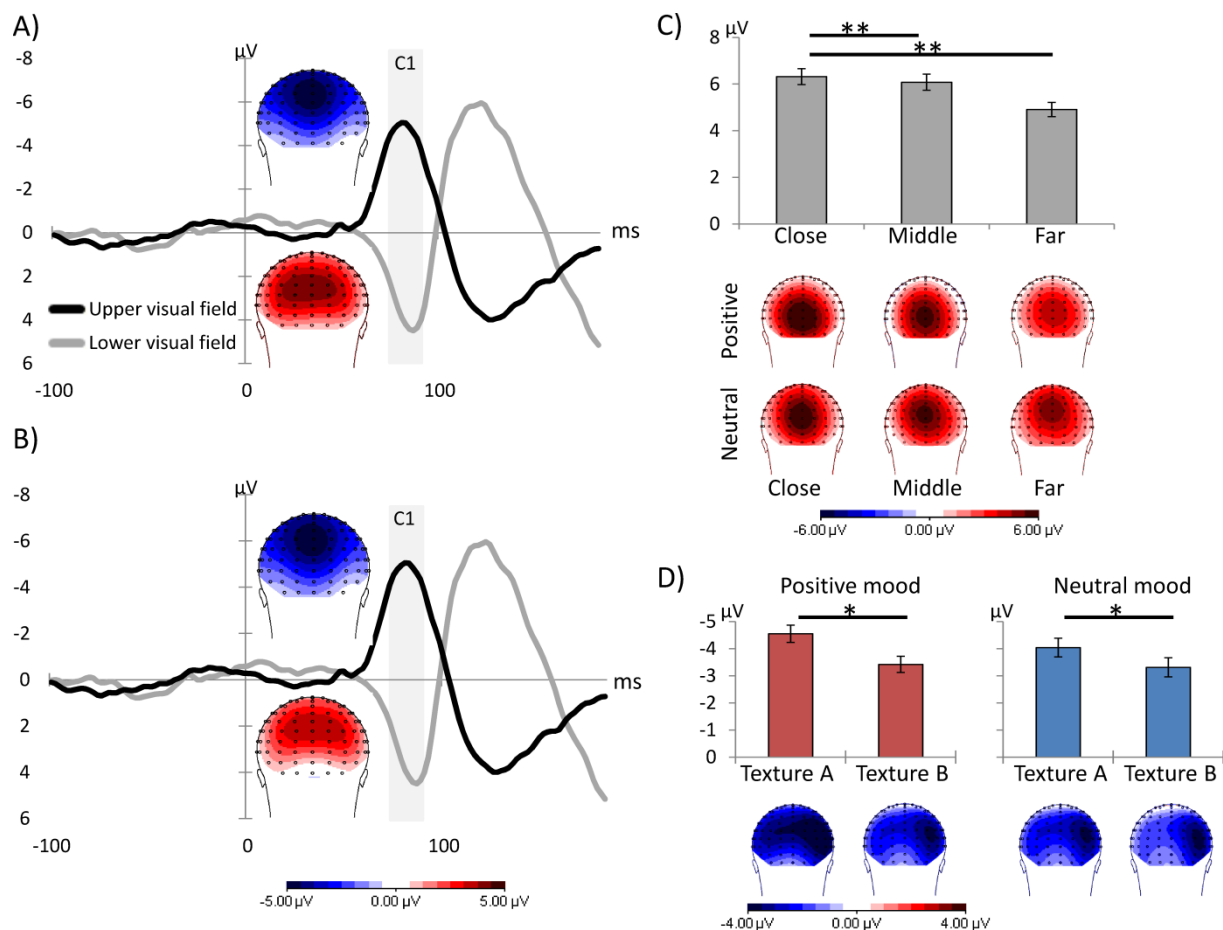


Figure 5. Grand average ERPs to peripheral stimuli (Close position) recorded at a representative posterior parietal midline electrode position (A21/POz), separately for textures shown in the upper (black line) and in the lower visual field (grey line) (localizer blocks); and for A) the positive and B) the neutral mood group (Localizer). In each group, a conspicuous polarity reversal was evidenced for the C1 as a function of the position of the stimulus in the visual field (i.e., upper visual field presentations were associated with a negative deflection while lower visual field presentations were associated with a positive deflection at the same latency). The corresponding voltage maps are shown. C) For the P1 (main experimental session; secondary task), the analysis showed a reduced amplitude for the Far position, relative to the two other positions, without a modulation by (positive) mood. The corresponding voltage maps are shown for a time window of 105-125 ms post-stimulus onset. D) For the N1 (main experimental session; secondary task), the analysis showed that the texture made up of snowflakes (Texture A) elicited a larger N1 (the voltage maps are shown for an interval of 105-125 ms post-stimulus onset), than the texture made up of crosses (Texture B), equally so in each group (positive/red and neutral/blue). ** indicates a significant effect with $p \leq .005$ and * $p \leq .01$; error bars represent 1 S.E.M.

DISCUSSION

In this study, we sought to investigate, using ERP measurements, whether positive mood could influence the early retinotopic processing (indexed by the C1 component; see Rauss, et al., 2011) of attended and task-relevant stimuli shown in the upper visual field at various locations/eccentricities relative to fixation, in agreement with a broadening of spatial attention associated with this specific mood state (Ashby, Isen, & Turken, 1999; Fredrickson, 2001, 2004). To test this prediction, participants were assigned either to a neutral/control or positive mood condition, and they performed a dual task involving an oddball detection at fixation and a localization task in the periphery of the upper visual field, while high-density EEG was recorded concurrently. Results showed that our MIP was efficient and successful to elicit a reliable and sustained change in positive affect (see Table 1). Positive mood influenced target processing at fixation (primary task), indicated by a larger P300 component. Importantly, the C1 component to all peripheral textures (secondary task) was substantially enhanced in the positive compared to the neutral mood group, regardless of whether the textures were targets or not. Moreover, in the positive mood group, participants detected targets faster than in the neutral mood group. No differential effect of positive mood was found for the subsequent P1 or N1 component. However, these two extrastriate components varied in amplitude in a predictive way: while the P1 was enhanced for attended relative to unattended stimuli (Heinze, Mangun, et al., 1994; Hillyard & Anllo-Vento, 1998), the amplitude of the N1 changed depending on the texture content (Vogel & Luck, 2000). These results suggest that positive mood can boost the early spatial encoding of the peripheral stimuli in the primary visual cortex selectively, before top-down attention control mechanisms gate sensory processing in the extrastriate visual cortex. Hereafter, we discuss the implications of these new neurophysiological results.

Early and automatic broadening of attention with positive mood

Our results show that positive mood influenced the earliest cortical stage of stimulus processing in V1, indexed by the C1. As expected, the amplitude of the C1 reliably decreased with increasing eccentricity relative to fixation (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Jeffreys & Axford, 1972; Rauss, et al., 2011). This result

indirectly suggests that foveal vision was used to process the RSVP at fixation (primary task), and that the peripheral stimuli shown in the upper visual field (secondary task) were therefore processed with peripheral vision. Additional source localization analyses confirmed that the C1 component had a striate origin. Strikingly, the C1 was substantially larger in the positive compared to the neutral mood group uniformly across the three positions used in the upper visual field, despite the fact that only one of them (i.e., the Middle one) had actually to be attended. At the behavioral level and consistent with one of our predictions, we found that participants in the positive mood group discriminated the location of these peripheral stimuli faster than in the neutral mood group, although without a gain in accuracy. Accordingly, the putative broadening of attention following the induction of positive mood seems to be associated with a facilitation in processing of the location of peripheral stimuli. However, the fact that this RT facilitation (secondary task) could not be dissociated from a general speeding up during target processing (see behavioral results) suggests that positive mood had probably larger effects than we hypothesized, and also influenced target processing at fixation (primary task).

The new findings obtained for the C1 component suggest in turn an early and automatic boost of the early spatial encoding of these textures in the positive compared to the neutral mood group, which might eventually underlie a broadening of spatial attention in this specific mood state (Fredrickson, 2001, 2004). They also extend our previous results showing that a broadening of spatial attention captured by this early C1 component can also be observed when the peripheral stimuli are directly task-relevant, and not simply used as distractors (Vanlessen, et al., 2013; see also Table 2). Importantly, this early mood-dependent C1 effect was evidenced before top-down attention control mechanisms operating at the level of the P1 and yielding classical gain control effects for attended, relative to unattended stimuli took place (Hillyard & Anllo-Vento, 1998; Martínez, et al., 1999). Unlike the preceding C1, the amplitude of the P1 was not modulated by positive mood, but rather by the targetness of the peripheral stimuli (and hence the amount of selective attention presumably allocated to them). In accordance with our prediction, our results showed that the P1 was enhanced for the middle position, compared to the far position, in line with research showing increased P1 amplitudes for attended compared to unattended stimuli in conditions of sustained

attention (Heinze & Mangun, 1995). Interestingly, unattended stimuli at the close position also elicited an enhanced P1 component. This result can be explained by the fact that peripheral textures shown at this location appeared between the main focus of attention in the center of the screen (primary task) and the secondary focus of attention likely anchored in the middle of the upper visual field (secondary task). Because spatial attention cannot be split into two independent or separate foci simultaneously (Castiello & Umiltà, 1992; Heinze, Luck, et al., 1994; Jans, et al., 2010), these stimuli, like the ones shown at the (attended) middle position, received enhanced processing in the extrastriate visual cortex (P1 effect), compared to the ones shown at the far position.

Altogether, these ERP results suggest a dissociation between an early automatic broadening of attention taking place in the striate cortex (C1) under positive mood, and top-down attention gain control mechanisms operating in the extrastriate visual cortex (P1) at a later latency following stimulus onset and independent of mood. Even though the results obtained for the C1 (and P1 to a lesser degree) suggest that these peripheral stimuli were processed with peripheral vision, we did not monitor however the actual position of the eyes during the experiment, and therefore we cannot formally exclude the possibility of saccadic eye movements towards the upper visual field. To remedy this limitation, future studies should include the online monitoring of the eye position (using eye-tracking methods).

As predicted, the subsequent N1 component was influenced by the type of textures shown in the upper visual field (with two types shown equally often in random order), however, this effect was not influenced by positive mood, as we had predicted. These results suggest that a rapid and implicit discrimination occurred between these two texture types (Vogel & Luck, 2000), equally so in each group. Contrary to one of our predictions, we did not find evidence for a reduced spatial resolution (and hence diminished N1 discrimination process) accompanying the broadening of attention after the induction of positive mood. In our previous study (Vanlessen, et al., 2013), such an effect was found when the content (rather than the position) of the peripheral stimuli became task-relevant. Hence, our results suggest that the likely tradeoff effect between a broadening of attention and a reduced spatial resolution (Castiello & Umiltà, 1990; Eriksen & Yeh, 1985; Ivry & Robertson, 1998) following the induction of positive mood

could entail different processing stages following stimulus onset. Whereas the broadening of attention would mainly involve the early and automatic retinotopic encoding of the stimuli in the striate cortex (C1 component), the concurrent diminished spatial resolution would concern later processing stages indexed by the P1 and N1 components, which are known to be generated after the C1 component in the extrastriate visual cortex (Martínez, et al., 1999).

Table 2. Systematic comparison between the results obtained in our previous ERP study (Vanlessen et al., 2013) and the current results. These symbols (and adjectives) reflect the direction of the effect found when comparing the positive mood group to the neutral mood group. For example, ‘larger’ means that the positive group showed a larger component as compared to the neutral group. Note that this systematic comparison between these two studies is made difficult because of reliable methodological differences between them. In Vanlessen et.al, 2013, no (secondary) task with the peripheral textures was required while EEG was recorded concurrently (Experiment 1). In a control experiment without EEG (Experiment 2), participants were instructed to discriminate the content of these peripheral stimuli, regardless of their location (‘what’ task), besides the primary task. In the current study, participants had to localize these peripheral stimuli, regardless of their content (‘where’ task). Despite these methodological differences across the two studies, we found that the amplitude of the C1 to the peripheral textures was augmented (either in topography in Vanlessen et al., 2013 or amplitude in the present case) in the positive compared to the neutral mood group. N/A: Not Applicable.

		Vanlessen et. al, 2013		Current study
		Exp 1	Exp 2	
EEG measurement		yes	no	yes
Primary task		Detection	Detection	Detection
Behavior	ACC	=	=	=
	RT	N/A	=	Numerically faster
ERP	P300	=	N/A	Larger
Secondary task		N/A	Discrimination	Localization
Behavior	ACC	N/A	Lower	=
	RT	N/A	=	Faster
ERP	C1	Larger (topography)	N/A	Larger (amplitude)
	P1	=	N/A	=
	N1	N/A	N/A	=

The observation of a component specific modulation of early sensory processing by positive mood (here at the level of the C1) might be explained by the use of a simple task (secondary task), mostly tapping into spatial localization abilities in the present case. Because the amplitude of the C1, unlike the subsequent P1 or N1, is primarily sensible to the position of the stimulus in the visual field (as opposed to its content), it is therefore not entirely surprising to find a modulation of this early component, selectively. Should we have used other task demands (focusing for example on the content rather than the position of these peripheral stimuli), maybe the experimental outcome would have been then slightly different, with modulations of the P1 and N1 amplitude by positive mood alike, besides the C1. A modulation of the P1 component following the induction of positive mood was already reported previously (Moriya & Nittono, 2011). On the other hand, given that we already found a similar selective modulation of the C1 component by positive mood when no task was required with these peripheral stimuli (see Vanlessen, et al., 2013; see also Table 2), we are inclined to conclude that these amplitude modulations of early sensory processing in V1 (C1 effect) are deemed ‘automatic’, in the sense of occurring prior to and independently from later attention gain control or task effects (usually occurring at the level of the P1 or N1 in the extrastriate visual cortex). In this framework, positive mood would therefore be associated with a short, ‘phasic’ broadening of spatial attention, the locus of which would be restricted to the first sweep of activation in the primary visual cortex following stimulus onset. Whether or not this early gating effect in V1 by positive mood is compatible with the concurrent modulation of specific long-distance neural pathways (connecting the prefrontal cortex and amygdala to the occipital lobe; see Pourtois, Schettino, & Vuilleumier, 2013) or neurotransmitter systems (e.g., dopaminergic-related; see Ashby, Isen, & Turken, 1999) remains an open question for future research.

More generally, our new results add to the growing literature showing systematic amplitude variation of this early retinoptic component not only as a function of changes in (top-down) attention control mechanisms (Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss, et al., 2009), but also the current mood state of the participant or specific emotional factors (Pourtois, et al., 2004; Rossi & Pourtois, 2012; Stolarova, Keil, & Moratti, 2006; Weymar, Keil, & Hamm, 2013). These amplitude changes during early sensory processing in the primary visual cortex by emotion or mood occurring at the

level of the C1 all share in common the fact that they are fast, usually component specific and orthogonal to more classical effects of load or selective attention (Handy, Soltani, & Mangun, 2001). As such, they could be deemed 'automatic' to some extent (Moors & De Houwer, 2006), and likely occur via dynamic modulations or plasticity in specific neural routes connecting mesio-temporal lobe structures and the ventral prefrontal cortex to the occipital lobe, including the primary visual cortex (Amaral, Behniea, & Kelly, 2003; Gschwind, Pourtois, Schwartz, Van De Ville, & Vuilleumier, 2012; Pourtois, Schettino, & Vuilleumier, 2013; Vuilleumier, 2005).

Positive mood influences top-down attention and early sensory processes independently

Besides the C1 to the peripheral stimuli, we also found that positive mood influenced target processing at fixation (primary task), indicated by a larger P300 for participants in the positive than the neutral mood group. This result was unexpected. Because in each group target stimuli elicited a much larger P300 than standard stimuli (see Fig. 3), this results suggests an enhanced processing of these target stimuli in the positive group (Kim, Kim, Yoon, & Jung, 2008; McCarthy & Donchin, 1981; Sawaki & Katayama, 2007), even though this neurophysiological effect did not translate into a gain in accuracy or RT speed. This finding suggests that positive mood was associated either with an enhanced efficiency or fluency (or less effortful control) during the primary task (see Polich, 2012), or alternatively, that because arousal (besides positive emotion) was also augmented in the positive mood group, the target P300 was in turn increased in amplitude in this group (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich & Kok, 1995). In our study, we did not find, however, a positive relation between changes in subjective levels of arousal following the MIP and the amplitude of the P300 to the target stimuli (primary task). Nonetheless, future studies are needed to assess the specific or respective contribution of arousal vs. positive valence on the observed neurophysiological effects (C1 and P300).

It is important to mention that effects of positive mood on the early sensory processing of the peripheral stimuli (C1 component) cannot be explained by a general modulatory effect of this mood state that would influence the C1 to these peripheral stimuli and the P300 to the central targets equally or uniformly. First, at the behavioral

level, we did not find evidence for a tradeoff between the two tasks. Moreover, we included and analyzed VEPs (C1, P1 and N1) to the peripheral stimuli if and only if they followed (central) standard stimuli (that did not require any response and were associated with a reduced P300 component of similar size in both groups). Accordingly, our results (C1 component) are not confounded by potential lingering ERP activities or carry-over effects from the preceding target-related (central) stimulus (P300 effect). In this context, influences of positive mood on the early sensory processing of the peripheral stimuli (C1 component, corresponding to a broadening of attention) are orthogonal to changes in target processing with this specific mood state (P300 component). To lend further support to this claim, we submitted the amplitude values of the C1 and P300 component to the same ANOVA, including three factors: Task (primary vs. secondary), Condition (non-target vs. target), and Group (positive vs. neutral)³. We reasoned that if the effects of positive mood are dissociable for the central (primary task) and peripheral stimuli (secondary task), then this control analysis should reveal a significant interaction effect between these factors. The results showed a significant three-way interaction ($F(1,38) = 5.75, p = .02, \eta p^2 = 0.13$), confirming that (positive) mood did not boost ERP activity in general, but dissociable effects were evidenced for the primary and secondary task. Whereas positive mood enhanced the C1 component to all peripheral stimuli regardless of their ‘targetness’ (indicated by a significant main effect of Group; see ERP results for the secondary task), it did enhance the P300 for the central stimuli, but only when they were targets (indicated by a significant interaction effect between Group and Condition; see ERP results for the primary task). Combined together, these results suggest that positive mood can probably exert effects on stimulus processing and attention control mechanisms at multiple levels and through specific modulations in distinct neural networks.

Conclusions

Our new ERP results show that positive mood can lead to a boost in early sensory processing in V1 (C1 component) related to the spatial position of task-related

³ We used the amplitude of the P300 for the primary task, whereas the absolute amplitude values of the C1 were used for the secondary task. The non-target condition refers to the standard stimuli in the primary task, and the positions Close and Far in the secondary task.

peripheral stimuli, selectively. A larger C1 component in the positive than neutral mood group is consistent with the broaden-and-build-theory (Fredrickson, 2001, 2004). This gain in spatial perception and in turn broadening of attention following the induction of positive mood can be seen as automatic because it is rapid, not modulated by task demands, and it takes place before top-down attention gain control mechanisms come into play and eventually gate the processing of attended compared to unattended locations or stimuli (P1 effect). Moreover, positive mood was found to influence the processing of central target stimuli (P300), irrespective of these changes in early sensory processing for the peripheral stimuli (C1). Altogether, these findings bolster the assumption that positive mood may broaden spatial attention by means of modulatory effects of sensory processing in V1 rapidly following stimulus onset. Whether these modulatory effects depend on specific neurotransmitter systems (e.g., dopamine; see Ashby, et al., 1999) remains an unanswered question. Moreover, additional imaging studies are needed to better characterize the neural pathways likely involved in these early mood-dependent sensory modulations in the primary visual cortex, given that their sources might very well implicate remote and distant brain regions in the limbic system and prefrontal cortex (Pessoa, 2008; Pourtois, et al., 2013; Vuilleumier, 2005).

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Increased perceptual load undoes the broadening of attention by positive mood:

Time-course and topographic-evoked potential mapping

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ABSTRACT

Independent lines of research showed that perceptual load and positive mood can each influence selective attention and early visual perception in opposite ways (narrowing and broadening, respectively). In this study, we sought to explore whether these two factors might therefore compete with one another, when they are combined together within the same experimental design. Participants were allocated to a positive or a neutral mood condition and then performed a dual task, while high density EEG was recorded. The dual task consisted of an oddball detection task at fixation (being either easy - low load or more difficult - high load), and a spatial localization task of peripheral stimuli shown in the upper visual field (for which task difficulty was kept constant). We explored changes in the amplitude of the C1 component generated in response to these peripheral stimuli depending on load and mood concurrently. ERP results showed a decreased C1 in the high compared to the low load condition, however, without any modulation by positive mood. These new neurophysiological results suggest that narrowing effects created by load can outweigh broadening effects accompanying positive mood, revealing a hierarchical organization in different attention control processes acting on a common perceptual pathway in V1 rapidly following stimulus onset.

INTRODUCTION

Attention selection mechanisms are manifold (Chun, Golomb, & Turk-Browne, 2011; Corbetta & Shulman, 2001; Pourtois, Schettino, & Vuilleumier, 2013). Usually, one makes a distinction between 'structural' factors, such as perceptual load for example, and more subtle factors, such as mood. Cumulating psychophysiological evidence suggests that these two factors can each reliably gate early sensory processing following stimulus onset in the primary visual cortex (V1), as indexed by amplitude-variations of the striate C1 component.

The C1 is the earliest visual evoked potential (VEP), which is generated ~50-80 ms following stimulus onset in V1 (Clark, Fan, & Hillyard, 1995; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Foxe & Simpson, 2002; Jeffreys & Axford, 1972). The C1 has several electrophysiological properties which make it compatible with an early retinotopic encoding of the stimulus in lower tier visual cortex (Kelly, Gomez-Ramirez, & Foxe, 2008). Among them, the C1 shows a reversal in polarity depending on the position of the stimulus in the visual field. The C1 has a negative amplitude for stimuli shown in the upper visual field, whereas it has a positive amplitude for the exact same stimuli shown in the lower visual field. This distinctive feature is compatible with the cruciform organization of the calcarine fissure and in turn with the main generators of this early VEP being located in the striate visual cortex (Rauss, Schwartz, & Pourtois, 2011).

Earlier imaging studies already demonstrated that V1 is not impermeable to changes in top-down attention control arising in the fronto-parietal network (Rees, Frith, & Lavie, 1997; Schwartz et al., 2005; Slotnick, 2003). Increasing perceptual load at fixation led to a smaller BOLD fMRI response in V1 to peripheral distracters, compared to a low load condition, suggesting that the attentional bottleneck was flexible and could operate as early as in V1, in agreement with the tenets of the load theory of selective attention (Lavie, 1995; Lavie & Tsal, 1994). Under high perceptual load, because most of the resources are consumed by the (difficult) task at hand, attention selection operates early following stimulus onset (i.e., the peripheral distractor stimuli are filtered out). On the other hand, under low perceptual load, the resources left over by the (easy) task may spill over to the peripheral (distractor) stimuli, eventually resulting in a larger response to them, compared to the high load condition.

Recently, several psychophysiological studies corroborated this conclusion by showing that the amplitude of the C1 was influenced by top-down attention control mechanisms (Poghosyan & Ioannides, 2008; Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss et al., 2009). For example, Rauss et al. (2009) found that the C1 was smaller in amplitude for peripheral distractors when perceptual load at fixation increased, relative to a low load condition (but see Ding, Martinez, Qu, & Hillyard, 2013 for opposite results). Likewise, Kelly et al. (2008) showed a larger C1 to attended, relative to unattended eccentric stimuli. These results add to the growing literature showing that attention selection processes, likely operating within the frontal and parietal cortex (see Corbetta & Shulman, 2001), can gate early sensory processing taking place in the occipital cortex, including in V1 (Poghosyan & Ioannides, 2008; Slotnick, 2003).

Besides load and structural factors, the mood of the participant per se is able to change attention selection processes. According to the broaden-and-build theory (Fredrickson, 2001, 2004), negative and positive mood influence attention in opposite ways: while a negative affective state triggers a narrowed attentional scope, positive feelings promote a broadening of the attentional focus. Recently, we found evidence for a signature of these opposite attention-related effects in V1, at the level of the C1 component. After the induction of state anxiety and negative affect, we found that the amplitude of the C1 to peripheral distractors was lower, compared to a neutral mood condition (Rossi & Pourtois, 2012). By contrast, after the induction of positive mood, we found that the C1 component was larger for peripheral distractors, compared to a neutral mood condition (Vanlessen et al., 2013). Accordingly, the affective state of the participant can also influence the way incoming sensory information is processed in V1 and in turn attended (see also Supèr, van der Togt, Spekreijse, & Lamme, 2003). Thus, perceptual load and positive affect can each influence early sensory processing in V1, as indexed by amplitude modulations of the C1 to peripheral stimuli, in opposite directions however: while increasing perceptual load leads to a narrowing of the attentional focus (reduced C1; see Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Rossi & Pourtois, 2012), increasing positive mood seems to broaden the attentional focus (increased C1 component; see Vanlessen, Rossi, De Raedt, & Pourtois, 2013, 2014). Interestingly, these two effects appear therefore to exert modulatory influences on a common perceptual pathway in V1. Accordingly, the question arises as to which extent

modulatory effects of positive mood in V1 during early sensory processing (Vanlessen et al., 2013) could overcome the typical narrowing effect created by perceptual load in the same area, at the same early latency following stimulus onset (Rauss et al., 2009), when these two factors are brought about concurrently and thus in direct competition. To date, no study has explored yet synergistic effects of perceptual load and positive mood on attention selection processes, using EEG methods. Because we previously showed that a larger C1 component to peripheral stimuli after the induction of positive (compared to neutral) mood was observed equally when these stimuli were distractors (Vanlessen et al., 2013) or became task-relevant (Vanlessen et al., 2014), we conjectured that positive mood could influence early sensory processing in V1 ‘automatically’ (i.e., regardless of changing task demands). Therefore, here we tested the prediction that positive mood could undo the strong narrowing or filtering effect created by load in V1, as indexed by the C1 component.

To test this hypothesis, we adapted the paradigm previously designed by Vanlessen et al. (2014), in which participants performed a primary task at fixation (corresponding to a ‘low’ load condition and ensuring fixation) while localizing peripheral stimuli shown in the upper visual field at different eccentricities (secondary task). In the current study, we changed perceptual load of the primary task such as to compare a Low Load (LL) condition to a High Load (HL) condition, across different blocks. The secondary task (with constant task difficulty) consisted of the detection of peripheral stimuli presented at one specific (i.e., Middle) position, while ignoring two other competing positions in the upper visual field (i.e., either Close or Far from fixation; see Vanlessen et al., 2014 for a similar procedure). Importantly, participants were first allocated to either a positive or a neutral mood induction procedure (MIP) and then performed the dual task, while high density EEG was recorded. This way, we could compare the C1 component generated in response to the exact same, attended peripheral stimuli across different contexts varying systematically in perceptual load at fixation and mood.

We formulated several predictions. With respect to the secondary task, (i) we expected a decreased C1 to the attended peripheral stimuli in the HL compared to the LL condition, in line with previous ERP studies (Rauss et al., 2009; Rossi & Pourtois, 2012). Moreover, we hypothesized a lower accuracy in the HL compared to the LL

condition (Rossi & Pourtois, 2013). (ii) Crucially, we expected that positive mood would enhance the C1, relative to a neutral mood condition, irrespective of load. As a corollary, we expected a better discrimination of the location of the peripheral stimuli in the positive compared to the neutral mood group. (iii) We also predicted that the subsequent P1 component to the peripheral stimuli would be modulated in amplitude by the two concurrent attention manipulations, equally so in both groups. More specifically, attended peripheral stimuli should elicit a larger P1 compared to unattended stimuli (see Vanlessen et al., 2014). Moreover, the P1 ought to be larger for peripheral stimuli in the LL compared to the HL condition (Handy, Soltani, & Mangun, 2001; Heinze et al., 1994; Mangun, Buonocore, Girelli, & Jha, 1998). Regarding the primary task, (iv) we predicted that targets would elicit a larger P300 compared to standard stimuli, indicating a clear discrimination between the two types of stimuli. Furthermore, we anticipated that this effect would be larger in the LL compared to the HL condition, showing a more effortful oddball detection in the latter compared to the former condition (Kim, Kim, Yoon, & Jung, 2008; Rossi & Pourtois, 2012). Likewise, we expected a larger P300 oddball effect in the positive compared to the neutral mood group, with a possible gain in accuracy, regardless of load (see Vanlessen et al., 2014).

METHODS

Participants

Forty-one undergraduate students from Ghent University participated in this study (age: $M = 22$ years; $SD = 4$; 12 male participants) after giving written informed consent. All participants reported having normal or corrected-to-normal vision and no history of psychiatric or neurologic disorders. We randomly assigned them to a positive or neutral mood condition. One participant from the positive mood group was excluded because she did not complete all test blocks, and two others because of excessive artifacts in the recorded EEG signal. The final sample included 38 participants (i.e., 20 in the neutral mood group and 18 in the positive mood group).

Materials

Mood Induction. We used the same MIP as in our previous ERP studies (Vanlessen et al., 2013, 2014). We told participants that the experiment concerned the relationship

between visual information processing and the ability to use imagination. Four 10 centimeters, horizontal Visual Analogue Scales (VAS) for feelings of happiness, pleasantness, sadness and arousal were used to quantify subjective levels of mood. In the three first VASs, the left anchor of the VASs was labeled 'Neutral', while the right one was labeled 'As happy/pleasant/sad as you can imagine'. The VAS for arousal was labeled with images from the Self-Assessment Manikin of Arousal (SAM; Bradley & Lang, 1994) indicating very low arousal on the right anchor, and very high arousal on the left.

Attention Task. We adapted a standard experimental paradigm (Schwartz et al., 2005; Rauss et al., 2009; Rossi & Pourtois, 2012) to a dual task (see Vanlessen et al., 2014). The primary task consisted of a rapid serial visual presentation (RSVP) of one centimeter tilted lines at fixation and ensured sustained foveal fixation. The task was an oddball detection task containing standard lines not requiring a response, and target lines that had to be detected overtly (by means of manual key presses). Two levels of difficulty were used in the primary task: in LL, the standard lines (tilted 35° counterclockwise from the vertical axis) were easily distinguishable from the targets (tilted 45°; see Vanlessen et al., 2014), while in HL, the targets (tilted 38°) had a smaller angular difference compared to the standard lines, making them harder to tell apart (see Fig. 1A). Note that the frequent standard lines were physically identical across these two load levels. The standard/target ratio was 4:1 in both conditions.

Decoupled from this foveal RSVP, visual textures were presented in the upper visual field, at an unpredictable location (at 5.3°, Close; 7.8°, Middle; or 10.3°, Far from central fixation; see Fig. 1B) and time (i.e. variable SOA between central stimulus offset and peripheral texture onset) relative to the central stimuli. Hence, central and peripheral stimuli never overlapped in space nor time. The peripheral stimuli consisted of visual textures (3° x 34° of visual angle) organized in two horizontal lines that were constituted of short horizontal lines (0.1 x 0.9 cm), with an equal number of presentations at each location. Participants were instructed to detect peripheral stimuli appearing at the middle position in the upper visual field by making a key press, while ignoring the same stimuli presented either close or far from fixation (see Vanlessen et al., 2014).

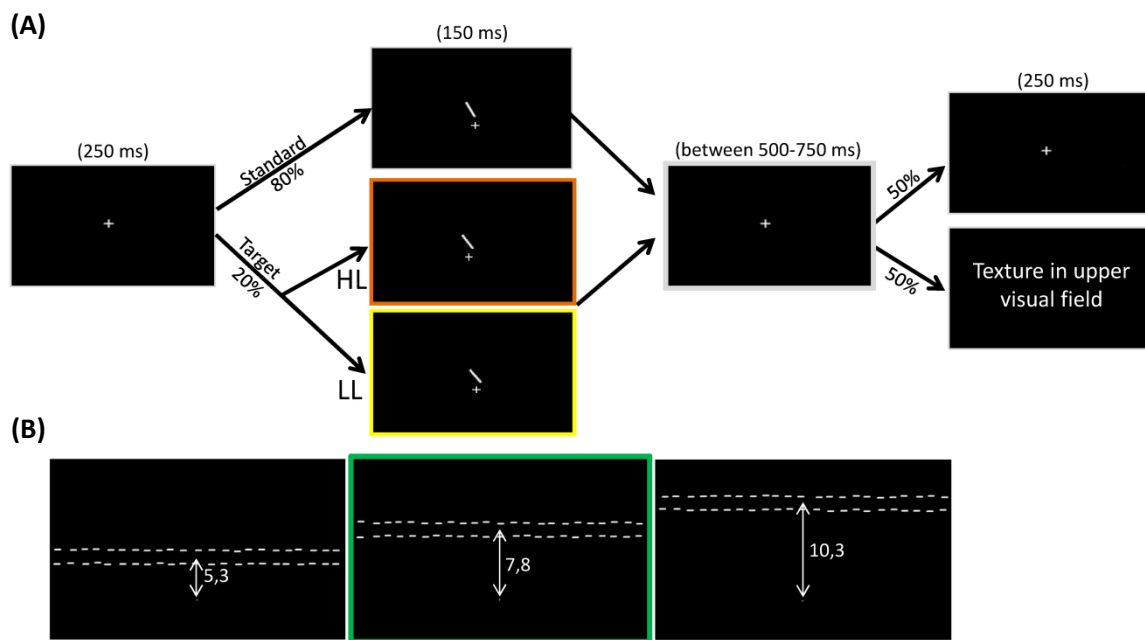


Figure 1. Stimuli and task. A) Participants performed a dual task consisting of an oddball task at fixation that imposed either a LL (yellow frame) or a HL (orange frame); and a localization task of textures shown randomly at three positions in the upper visual field. Stimuli at fixation and peripheral distractors never overlapped in space nor time. B) Visual textures at the three possible positions in the upper visual field: Close, Middle or Far relative to fixation. Only the middle position was task-relevant and required an overt response (green frame).

The stimulus-response mapping for the primary and secondary tasks was counterbalanced across participants and a reminder was shown at the beginning of each block. Participants were seated at 57 cm in front of a 19" CRT screen, with their head movements restrained by a chinrest. The task was programmed using the E-Prime Version 2 software (Psychology Software Tools, Inc., 2001). All stimuli were grey and presented against a uniform black background.

Localizer. At the end of the main session, participants completed two extra blocks of peripheral stimuli without the (foveal) RSVP under passive viewing conditions, to confirm that the first VEP elicited by the peripheral textures during the main attention task genuinely corresponded to a retinotopic C1 (see Rossi & Pourtois, 2012; Vanlessen et al., 2013, 2014). The stimuli were identical to the ones used in the main task, presented at the positions Close, Middle and Far relative to fixation, randomly above and below fixation.

Questionnaires. Participants filled out the Beck Depression Inventory (BDI; Beck, Steer, Ball, & Ranieri, 1996).

Procedure

Participants were first prepared for EEG recording and then completed at least four practice blocks (two for the LL and two for the HL). The blocks were repeated until 80% of the central targets were detected correctly. Next, the MIP was administered and shortly repeated after blocks 3, 6 and 9, in order to keep the neutral or positive mood present during the entire duration of the task (see Fig. 2). Each trial consisted of a fixation cross (250 ms), followed by a central stimulus (150 ms) and again a fixation cross (displayed during the SOA with an average duration of 625 ms, randomly varying between 500 to 750 ms). The fixation cross remained displayed during this interval in half of the trials. In the other trials, a peripheral texture was briefly presented (250 ms) at the Close, Middle or Far position in the upper visual field (see Fig. 1A). Trials were presented in a semi-random order: the first three trials in a block never contained a central target nor a peripheral texture. Instructions emphasized accuracy and speed for both the primary and secondary tasks. The task consisted of 600 central stimuli (i.e., 300 in the LL and 300 in the HL condition), of which half was followed by a peripheral stimulus (i.e., 240 after the presentation of a central standard and 60 after a central target stimulus in each load condition). All participants completed six LL and six HL blocks, containing 50 trials each. The order of LL and HL blocks was counterbalanced across participants. At the end of the main task, participants received two additional blocks (localizer) of 240 trials of peripheral textures (i.e., 6 positions x 40 repetitions per position), followed by the Beck Depression Inventory (BDI; Beck et al., 1996).

The four VASs were administered at the beginning of the experiment, after each MIP, and at the end after the last block of the main attention task (before the localizer).

Analyses of behavioral data

We performed two separate ANOVAs on the VAS scores. First, we calculated the average values for the different VASs after the four MIPs. Next, we performed 2(Time: baseline vs. post-MIP) x 2(Mood: neutral vs. positive) mixed ANOVAs for each VAS to

assess changes in mood after the MIP compared to baseline. Second, we performed 2(Load: LL vs. HL) x 2(Group: positive vs. neutral) mixed ANOVAs on the average VAS scores collected after blocks of LL (see Fig. 2, yellow arrows) and blocks of HL (orange arrows). Mean scores for the BDI were compared between mood groups using independent sample T-tests.

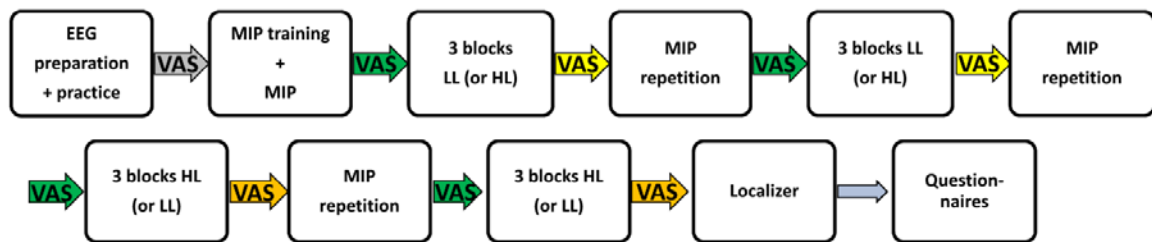


Figure 2. Procedure. VAS were administered at baseline (grey arrow), after all MIPs (green arrow), after LL blocks (yellow arrow) and after HL blocks (orange arrow). The order of LL and HL blocks was counterbalanced across participants.

Mixed ANOVAs with the within-subjects factor Load (low vs. high) and between-subjects factor Mood (positive vs. neutral) were used to analyze accuracy and reaction times (RTs) for the central oddball task, and RTs for the correct detection of targets in the secondary task separately. The accuracy for the secondary task was analyzed by means of a mixed ANOVA with Load (low vs. high) and Position (close, middle or far) as within-subjects factors and Mood (positive vs. neutral) as between-subject factor. All significant effects were followed-up by T-tests. All T-tests were two-tailed.

Trials with RTs exceeding $\pm 2,5$ SDs above or below the individual mean RT on either task were excluded from further analysis. An equal proportion of trials was excluded based on this criterion in both mood groups (positive: $M = 1.43\%$, $SD = 0.43$; neutral: $M = 1.45\%$, $SD = 0.44$; $t(36) = 0.24$, $p = .81$). In addition, trials with errors on the primary task were also excluded from further analysis (positive: $M = 7.08\%$, $SD = 3.21$; neutral: $M = 10.69\%$, $SD = 5.99$, $t(36) = 2.28$, $p = .03$). This difference was due to different accuracy scores between the two mood groups in the HL condition (see behavioral results section). Statistical analyses were run on 91.02 % of the total data.

EEG data acquisition and reduction

The EEG data recording and reduction were identical to (Vanlessen et al., 2014). Using this procedure, we kept 74.23% of the epochs. For the primary task, averages were calculated per participant for standard and target stimuli separately, and for peripheral stimuli at each position apart (close, middle and far position); all separately for LL and HL. For the localizer blocks, individual averages were calculated separately for the three positions above vs. below fixation.

The P300 component (primary task) was identified on electrode positions A19, A20 and A21 (midline), A5, A18 and A17 (left hemisphere) and A32, A31 and A30 (right hemisphere), given its typical centro-parietal-occipital scalp distribution. The mean amplitude during the time window spanning from 493 to 693 ms post-stimulus onset was computed per electrode, for the central target and standard stimuli and for each load condition separately.

By means of a semi-automatic peak detection, we identified the C1 (secondary task) on the individual averages in both the main task and the localizer blocks, as well as the P1 in the main task (Picton et al., 2000). The C1 was defined as the largest negative peak between 25 and 100 ms post-stimulus onset on occipital electrode positions A19, A20 and A21 (midline), A5, A18 and A17 (left hemisphere) and A32, A31 and A30 (right hemisphere). The P1 was measured at slightly more occipital electrode positions compared to the C1: A21, A22 and A23 (midline), A17, A16 and A15 (left hemisphere) and A30, A29 and A28 (right hemisphere) and was defined as the first positive deflection following the C1, peaking between 75 and 200 ms post-stimulus onset. These electrode positions were selected based on the conspicuous topographical properties of these two early visual components. Only the C1 to peripheral stimuli following a standard central stimulus (and hence not contaminated by a preceding target processing and motor response) was included in the analysis (see also Vanlessen et al., 2014 for a similar procedure). The mean amplitude was computed during a time window of 20 ms around the detected peak for the C1 or P1, separately for each electrode position and condition. Statistical analyses were performed on the average values of the selected electrodes.

Separate mixed ANOVAs were used for the analysis of the mean amplitudes of the P300, C1 and P1 components. For the P300, we used a mixed ANOVA with Stimulus

(standard vs. target) and Load (low vs. high) as within-subjects factors, and Mood (positive vs. neutral) as between-subjects factor. The C1 and P1 data were submitted to mixed ANOVAs with Position (close, middle or far) and Load (low vs. high) as within-subjects factors, and Mood (positive vs. neutral) as between-subjects factor. The C1 data of the localizer blocks were submitted to an ANOVA with Position (close, middle or far, for the upper visual field only) as within-subjects factor. Post-hoc comparisons were performed using two-tailed T-tests. When normality assumptions were violated, corrected p-values were reported.

In addition, we performed a detailed topographic mapping analysis of the C1 and the P1 component generated in response to the peripheral distractors (see Michel, Seeck, & Landis, 1999; Murray, Brunet, & Michel, 2008; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Pourtois, De Pretto, Hauert, & Vuilleumier, 2006; Pourtois, Thut, de Peralta, Michel, & Vuilleumier, 2005). We used a standard K-means clustering technique to identify the dominant scalp topographies in the grand averages data, corresponding to the C1 (60-86 ms post-stimulus onset) and the P1 (117-156 ms post-stimulus onset) at each position separately, using the following parameters: average reference; number of random trials: 100; smoothing strength (Besag factor) of 10; smoothing half window size of 3; merging of clusters correlating above 0.92; rejection of segments less or equal to 5 time-frames; no sequentializing. Both cross validation (Pascual-Marqui, Michel, & Lehmann, 1995) and Krzanowski-Lai criteria (Pascual-Marqui et al., 1995; Tibshirani, Walther, & Hastie, 2001) were used to objectively determine the number of dominant topographical maps. Next, these dominant topographies were fitted back to the individual ERP data of each participant using spatial fitting procedures enabling to quantify their expression across subjects and conditions. We extracted the Global Field Power (GFP), reflecting the strength of the electric field (either for the C1 or P1) at this specific latency (either 60-86 ms or 117-156 ms post-stimulus onset) (see Lehmann & Skrandies, 1980; Murray et al., 2008). For each component separately, these GFP values were eventually submitted to a mixed-model ANOVA with the within-subjects factors Position and Load, and the between-subjects factor Mood.

RESULTS

Changes in mood: manipulation check

The ANOVA comparing the VAS scores at baseline with the scores obtained after the MIP indicated a significant interaction between Time and Mood for both feelings of happiness ($F(1,36) = 11.74, p = .002$) and pleasantness ($F(1,36) = 5.96, p = .02$).

Importantly, post-MIP scores showed significant group differences for feelings of happiness (Positive: $M = 625.56, SD = 175.14$; Neutral: $M = 403.29, SD = 201.25$; $t(36) = 3.61, p = .001$; see Fig. 3A) and pleasantness (Positive: $M = 609.71, SD = 172.49$; Neutral: $M = 437.88, SD = 187.98$; $t(36) = 2.93, p = .006$), while groups did not differ at baseline for reported happiness ($t(36) = 0.67, p = .51$), nor pleasantness ($t(36) = 0.82, p = .42$).

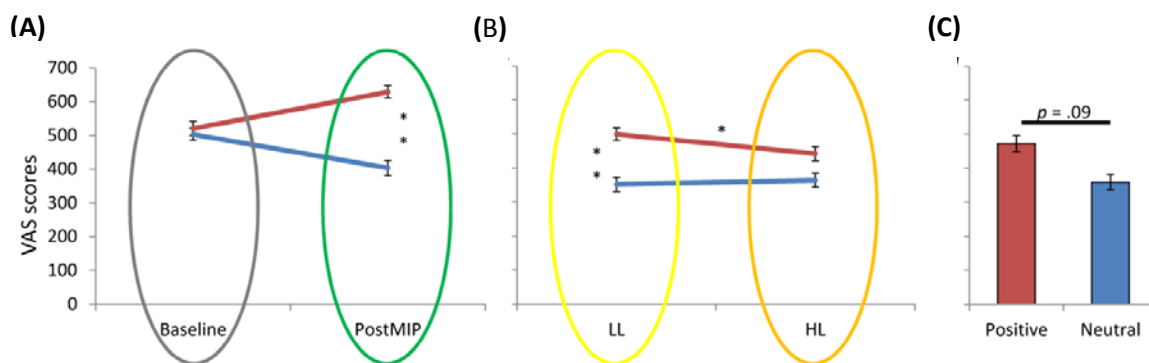


Figure 3. A) VAS scores for feelings of happiness at baseline (grey) and after the MIPs (average of the different measurements; green), for the positive (red line) and the neutral (blue line) groups. B) Average VAS scores for feelings of happiness after LL (yellow) and HL blocks (orange). C) VAS scores for feelings of happiness on the latest measurement before the localizer blocks. ** indicates $p \leq .001$ and * $p \leq .05$; error bars represent 1 S.E.M.

The Time x Mood interaction was not significant for reported levels of sadness ($F(1,36) = 0.41, p = .53$), nor arousal ($F(1,36) = 1.99, p = .17$). Together, these results showed a selective increase in positive affect after the MIP in the positive mood group.

Next, we compared the mood VASs after performing three blocks of the LL vs. the HL condition. The ANOVA showed a significant interaction between Load and Mood for feelings of happiness ($F(1,36) = 5.59, p = .024$), pleasantness ($F(1,36) = 4.23, p = .047$) and sadness ($F(1,36) = 5.09, p = .03$). In the positive mood group, a significant decrease was found after performing the HL compared to the LL condition for feelings of happiness (LL: $M = 503.67, SD = 168.27$; HL: $M = 439.31, SD = 187.13$; $t(17) = 2.32, p = .033$; see Fig. 3B) and pleasantness (LL: $M = 493.17, SD = 189.56$; HL: $M = 429.25, SD =$

195.32; $t(17) = 2.66, p = .016$), while feelings of sadness increased (LL: $M = 160.36, SD = 97.04$; HL: $M = 190.22, SD = 103.98$; $t(17) = 2.15, p = .047$). On the contrary, in the neutral mood group, feelings of happiness, pleasantness and sadness were not influenced by load (all $ps > .05$). Hence, after the LL blocks, reported mood levels still showed a significant difference for feelings of happiness ($t(36) = 2.63, p = .013$) and a marginally significant difference for feelings of pleasantness ($t(36) = 1.80, p = .08$) between groups, while no more group difference was found after performing the HL blocks for either happiness ($t(36) = 1.25, p = .22$) nor pleasantness ($t(36) = 0.65, p = .52$). In addition, we found a main effect of Load on arousal, such that arousal increased after performing the HL compared to the LL blocks (LL: $M = 318.70, SD = 151.50$; HL: $M = 336.41, SD = 174.16$; $t(17) = 5.09, p = .03$). These results suggest that HL substantially increased arousal irrespective of mood, while it lowered the level of happiness of participants in the positive mood group, compared to the LL condition, selectively.

Behavioral results.

Primary task

Participants reached high accuracy in the LL condition, while the performance decreased in the HL condition, as shown by a main effect of Load ($F(1,36) = 269.93, p < .001$). Importantly, there was a significant interaction between Load and Mood ($F(1,36) = 9.45, p = .004$), indicating that this decrease in accuracy was more pronounced in the neutral compared to the positive mood group. More precisely, both groups performed equally well in the LL condition (Positive: $M = 97.47, S.D. = 2.01$; Neutral: $M = 96.87, SD = 2.53$; $t(17) = .81, p = .43$), while the positive mood group performed significantly better in the HL condition compared to the neutral mood group (Positive: $M = 84.94, SD = 3.16$; Neutral: $M = 78.57, SD = 3.16$; $t(17) = 3.06, p = .004$; see Fig. 4C).

The ANOVA on the RTs showed that participants were significantly slower in the HL ($M = 644.26, SD = 127.59$) compared to the LL condition ($M = 573.85, SD = 73.07$; $F(1,36) = 14.96, p < .001$). Participants in the positive mood group ($M = 583.62, SD = 91.42$) were also numerically faster compared to the neutral mood group ($M = 626.76, SD = 71.40$), however this difference did not reach significance ($F(1,36) = 1.74, p = .20$; see Fig. 4D).

Secondary task

The ANOVA performed on the mean accuracy scores showed a significant main effect of Position (Close: $M = 90.51$, $SD = 11.23$; Middle: $M = 83.54$, $SD = 11.38$, Far: $M = 86.62$, $SD = 10.60$; $F(2,72) = 3.76$, $p = .028$). Post-hoc paired sample T-tests showed that accuracy was significantly higher in the close compared to the middle position, ($t(37) = 2.78$, $p = .009$), while the accuracy for the close and far position ($t(37) = 1.44$, $p = .16$) or middle and far position ($t(37) = 1.34$, $p = .19$) did not differ from each other. The main effect of Load was not significant ($F(1,36) = 2.26$, $p = .14$), nor was the main effect of Mood ($F(1,36) = 1.57$, $p = .22$). Interaction effects were not significant (all $ps > .50$). The ANOVA on the RTs for correct detections of stimuli shown at the middle position showed no significant effects (all $ps > .20$).

Additionally, we performed correlation analyses between the two tasks (using either accuracy or RTs) to assess whether any trade-off was present between them. Regarding accuracy, no relation was found, in none of the two load conditions (all $ps > .05$). For the RTs, a positive relation was found between the two tasks (LL: $r = .66$, $p < .001$; HL: $r = .48$, $p = .002$), indicating that participants who responded faster in the primary task were also faster in the secondary. However, the fact that this relation was positive ruled out the possibility of a systematic trade-off between the two tasks.

Questionnaires

Unexpectedly, we found a significant group difference on the BDI scores, indicating more elevated levels of depression in the positive ($M = 9.22$, $SD = 8.01$) compared to the neutral mood group ($M = 4.80$, $SD = 4.54$; $t(36) = 2.12$, $p = .041$), although these scores remained below the clinical cut-off for depression. Importantly, this group difference did not prevent positive mood to increase following the MIP in the positive mood group, however.

ERP results.

Primary task

P300. As predicted, the ANOVA on the P300 amplitudes showed a significant interaction between Load and Stimulus type ($F(1,36) = 40.22$, $p < .001$), indicating that Load influenced the processing of targets ($F(1,36) = 43.74$, $p < .001$) but not of standard

stimuli ($M = 4.98$, $SD = 2.64$; $F(1,36) = 0.56$, $p = .46$; see Fig. 4A and B). More specifically, the P300 to targets was decreased in the HL ($M = 11.27$, $SD = 3.26$) compared to the LL condition ($M = 14.96$, $SD = 4.09$), indicating that target detection was more effortful in the HL condition.

Importantly, we also found an interaction between Stimulus type and Mood ($F(1,36) = 5.03$, $p = .03$), showing that the P300 to targets was significantly larger in the positive ($M = 13.11$, $SD = 3.30$) compared to the neutral mood group ($M = 10.31$, $SD = 4.11$; $F(1,36) = 5.29$, $p = .027$) regardless of load, while the P300 to the standard stimuli did not differ between groups ($F(1,36) = 0.84$, $p = .37$; see Fig. 4A and B). This interaction suggested that target detection was enhanced for participants in the positive compared to the neutral mood group.

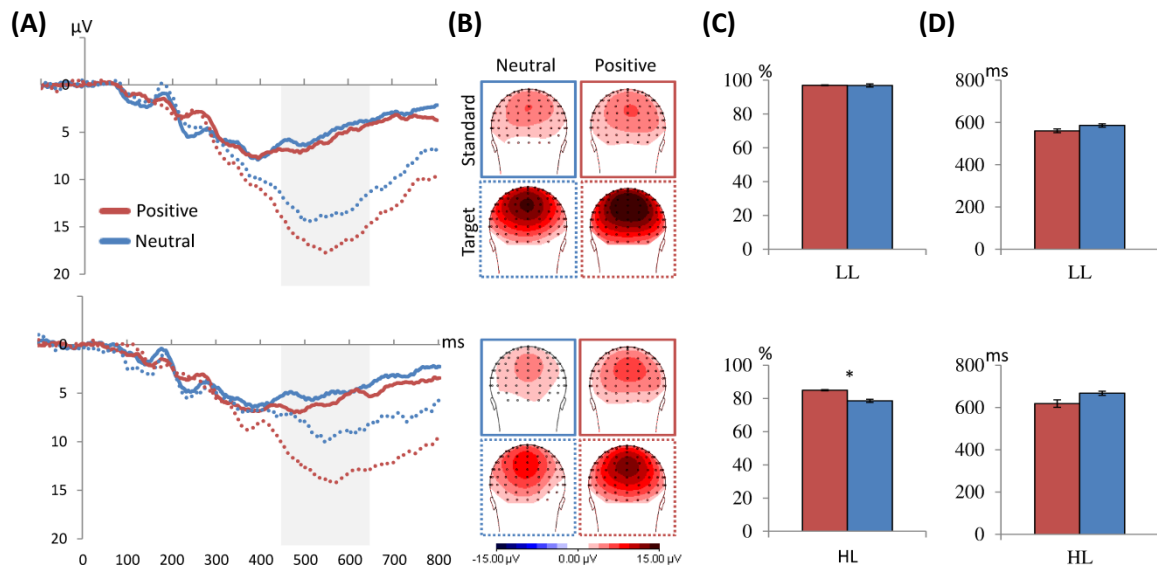


Figure 4. Results for the primary task A) Grand average ERPs to stimuli in the primary task recorded at a representative posterior parietal midline electrode (A20), for the LL (upper panel) and the HL condition (lower panel). A clear increase of the P300 component was found for oddball targets (dashed line) compared to standard stimuli (solid line), for both load conditions; and for the positive (red) compared to the neutral (blue) mood group. Negative values are plotted upwards. B) Voltage maps (back view) for the P300 component (for a time window from 450 to 650 ms post-stimulus onset; demarked by the grey frame), separately for the standard (solid line) and target stimuli (dashed line) for the positive (red) and neutral (blue) mood group, in the LL (upper panel) and the HL condition (lower panel). C) behavioral accuracy and D) RTs for LL (upper panel) and HL (lower panel) blocks. * indicates a $p \leq .05$; error bars represent 1 S.E.M.

Secondary task

ERP results

C1. As expected (see Vanlessen et al., 2013, 2014), the ANOVA on the C1 amplitudes revealed a significant main effect of Position ($F(2,72) = 16.25, p < .001$), resulting from a drop in C1 amplitude with increasing eccentricity. The C1 was larger in magnitude for peripheral stimuli shown at the close position ($M = -3.86, SD = 2.06$) relative to both the middle ($M = -2.40, SD = 1.50; t(37) = 4.38, p < .001$) and far position ($M = -1.87, SD = 1.44; t(37) = 5.19, p < .001$; see Fig. 5A and B). The C1 did not differ between the middle and far positions ($t(37) = 1.50, p = .14$). This analysis did not reveal significant main effects of Load ($F(1,36) = 0.57, p = .46$) or Mood ($F(1,36) = 1.44, p = .24$), nor did any interaction effect reach significance (all $ps > .17$).

To ensure that the earliest component recorded during the main task corresponded to a genuine C1, we compared the C1 of the main task with the localizer blocks, showing the same morphology and topography in both sessions. Importantly, for the localizer blocks, we also found a clear polarity reversal for this early striate component depending on whether the upper or the lower part of the visual field was stimulated (see Fig. 6A), indicating that this early component was a genuine C1, likely originating from V1 (Kelly, Vanegas, Schroeder, & Lalor, 2013). The ANOVA performed on the mean C1 amplitudes to the stimuli presented above fixation showed a significant main effect of Position ($F(2,74) = 4.91, p = .010$), indicating a decrease of the C1 amplitude with increasing eccentricity (close: $M = -3.54, SD = 2.78$, middle: $M = -2.09, SD = 2.15$, far: $M = -2.17, SD = 1.81$; close vs. middle: $t(37) = 2.91, p = .006$; close vs. far: $t(37) = 2.39, p = .022$; see Fig. 6B). No difference was found between the middle and the far position ($t(37) = 0.15, p = .88$).

P1. The ANOVA carried out on the P1 amplitudes showed no significant main effects of Position ($F(2,72) = 1.46, p = .24$), Load ($F(2,72) = 0.55, p = .46$) or Mood ($F(2,72) = 0.17, p = .68$). In addition, interaction effects were not significant (all $ps > .16$).

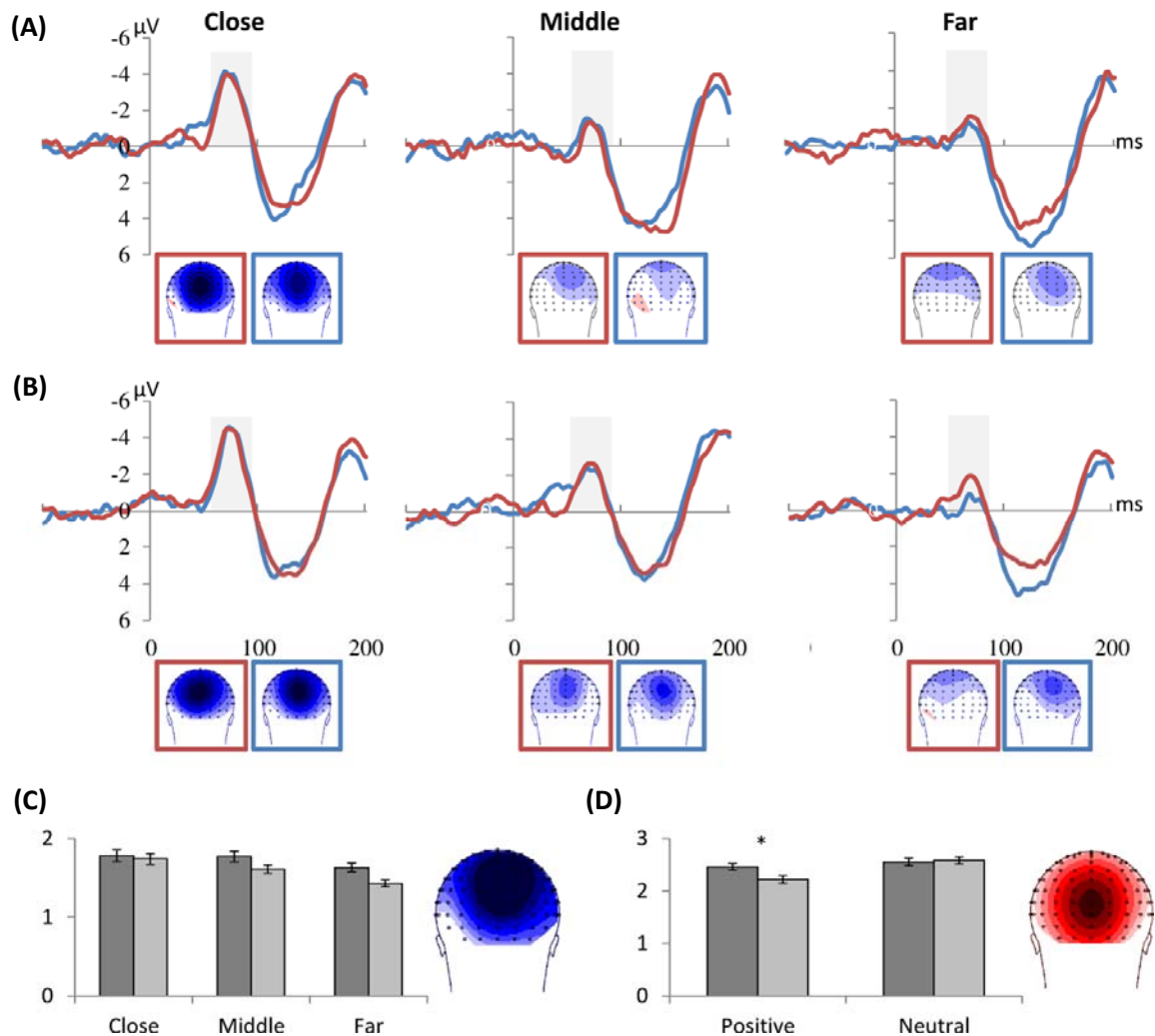


Figure 5. Grand average ERPs to peripheral textures recorded at a representative posterior parietal midline electrode position (A21/POz) for the three positions, separately for the A) LL and the B) HL condition. The amplitude of the C1 decreased with increasing eccentricity relative to fixation, regardless of load condition. No difference was found between the positive (red line) and the neutral (blue line) mood groups. The C1 was scored in individual averages as the mean VEP activity recorded during a 20 ms interval centered around the peak (demarcated by the grey frame). Negative values are plotted upwards. C) GFP values corresponding to the C1 component and the D) P1 component, separately for the LL (dark grey) and HL (light grey) conditions. Corresponding voltage maps are shown. * indicates $p \leq .05$; error bars represent 1 S.E.M.

Topographic analysis

The K-means spatial cluster analysis showed that a solution with nine dominant maps explained 91% of the variance. Among these nine map configurations, one dominant topography was found corresponding to the C1 component and one for the P1 component.

C1. The ANOVA performed on the strength (GFP) of the dominant topography found for the C1 showed significant modulations by Position as well as Load. This ANOVA showed a significant main effect of Position ($F(2,72) = 5.68, p = .005$), indicating a significant amplitude difference between Close ($M = 1.87, SD = 0.50$) and Far ($M = 1.63, SD = 0.48$; $t(37) = 2.52, p = .016$), but not between Middle ($M = 1.77, SD = 0.58$) and Far ($t(37) = 1.36, p = .18$) or Close and Middle positions ($t(37) = 0.98, p = .34$). This analysis also showed a significant main effect of Load (LL: $M = 1.76, SD = 0.53$; HL: $M = 1.59, SD = 0.31$; $F(1,36) = 9.02, p = .005$; see Fig. 5C). Hence, these results confirmed that the C1 component was reliably changed depending on both the position of the stimulus in the (upper) peripheral visual field and the load imposed at fixation (primary task). The main effect of Mood was trend significant ($F(1,36) = 3.09, p = .09$), showing a slightly larger C1 component (topography-based) for the neutral compared to the positive mood group. Note that this effect was in the opposite direction of our main prediction. No interaction effect reached significance (all $ps > .58$).

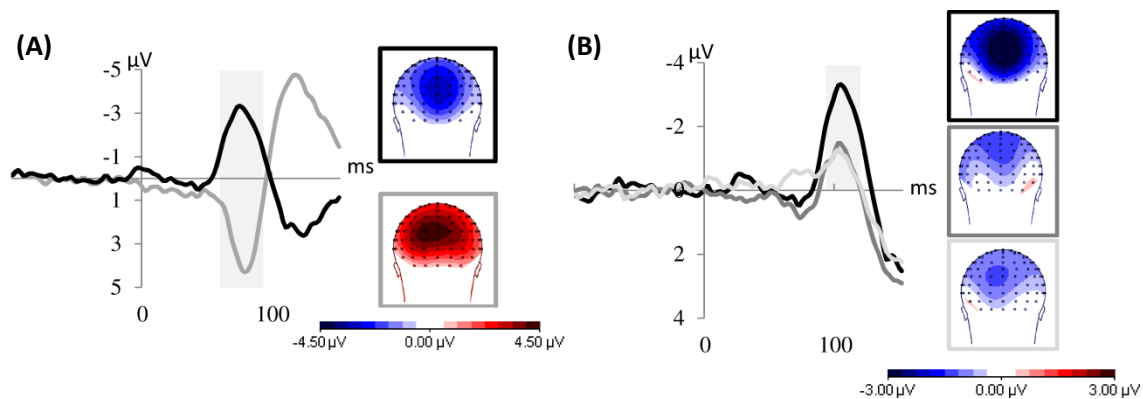


Figure 6. Localizer blocks. A) Grand average VEPs recorded at a representative posterior parietal midline electrode position (A21/POz) to peripheral stimuli presented at the close position for textures shown above (black line) and below fixation (grey line). A polarity reversal was observed for the C1 as a function of Position (i.e., negative deflections for presentations in the upper visual field and positive in the lower visual field). B) Grand average ERPs to peripheral stimuli for the position close (solid line), middle (dotted line) and far (dashed line). Corresponding voltage maps (back view) are shown.

P1. The ANOVA performed on the strength (GFP) of the dominant topography of the P1 map showed a marginally significant interaction effect between Load and Mood ($F(1,36) = 3.08, p = .088$). In the positive mood group, the GFP of the P1 map decreased for the HL ($M = 2.22, SD = 0.58$) compared to the LL ($M = 2.46, SD = 0.52, t(17) = 6.25, p = .023$).

No such load-dependent effect at the level of the P1 was found in the neutral mood group (LL: $M = 2.56$, $SD = 0.63$; HL: $M = 2.58$, $SD = 0.58$, $t(19) = 0.04$, $p = .85$, see Fig. 5D). No other effects were significant (all $ps > .15$).

DISCUSSION

The goal of this study was to test whether positive mood could hinder the early gating effect of sensory processing imposed by perceptual load. For this purpose, we focused on the earliest VEP following stimulus onset, namely the C1, which reflects the retinotopic encoding of the (peripheral) stimulus in V1 (Rauss et al., 2011). Given that load narrows attention and gates early sensory processing in V1 (Rauss et al., 2009), while positive mood creates the opposite attention-related effect in V1 (i.e., broadening, see Fredrickson, 2001, 2004; Moriya & Nittono, 2011; Vanlessen et al., 2013, 2014), we reasoned that positive mood might interact with load, and in turn shield early sensory processing from this gating effect when these two factors are manipulated concurrently. In parallel, we could also assess to which extent effects of positive mood in V1 during early sensory processing are deemed ‘automatic’, in the sense of being resistant to variable and changing task demands (see Vanlessen et al., 2014).

To investigate this question, we allocated participants to either a neutral or a positive mood condition and recorded high-density EEG while they performed a dual task. This task consisted of an oddball detection task at fixation (primary task) that could either be fairly easy (LL), or more demanding because of an increased perceptual load (HL). Concurrently, participants performed a localization task of peripheral stimuli appearing at one out of three positions in the upper visual field (secondary task). Difficulty of the secondary task was kept constant. We selected these peripheral stimuli based on earlier work (Rossi & Pourtois, 2012; Vanlessen et al., 2013, 2014) for their ability to elicit a conspicuous C1 component. Moreover, this factorial experimental design allowed us to compare the processing of the exact same physical stimuli at the electrophysiological level (i.e., peripheral stimuli shown in the upper visual field at an unpredictable time and location relative to the central stimuli) across different experimental contexts varying in load and mood, specifically. Manipulation checks and behavioral results confirmed that load and mood yielded the expected effects.

However, contrary to our main prediction, positive mood was not accompanied by a broadening of attention, with measurable effects at the level of the C1 (see Vanlessen et al., 2013, 2014). Overall, effects of load appeared to counter or outweigh effects of positive mood, consistent with the idea of a winner-take-all attention phenomenon during early stages of sensory processing in V1 (Lee, Itti, Koch, & Braun, 1999). In line with this assumption, we found that subjective levels of pleasantness and happiness in the positive mood group (which increased after the first MIP) were no longer different from the neutral mood group after the encounter with HL blocks, as if perceptual load actually depleted positive mood. Here below, we discuss the implications of these new results in greater detail.

Perceptual load narrows attention in V1

In line with previous ERP results showing an early attention gating in V1 imposed by (perceptual) load with measurable effects seen at the level of the C1 to unattended peripheral distractors (Rauss et al., 2009; Rossi & Pourtois, 2012), our new findings show that the amplitude of the C1 to attended peripheral stimuli decreased when perceptual load at fixation was high, compared to a low load condition. However, unlike these earlier studies (Rauss et al., 2009; Rossi & Pourtois, 2012), our results are not directly compatible with the main premise of the load theory of selective attention (Lavie, 1995; Lavie & Tsai, 1994), that states that distractors are processed to the extent that unused resources allocated to the primary task can spill over to them. Here, by contrast, the peripheral stimuli of interest were not distractors, but instead, they were task-relevant and to be attended, ruling out an interpretation in terms of attentional filtering or spill-over effect. In this dual task setting, we found that the accuracy for the secondary task did not differ between the LL and HL conditions. Moreover, while changes in perceptual load for the primary task were very effective (see behavioral results), they did not trade-off with the secondary task. Presumably, a mechanism that might explain these results, is the active recruitment of cognitive control mechanisms to ascertain a decent perceptual processing of the central stimuli when perceptual load is high (Linnell & Caparos, 2011, 2013). Because the spatial processing of the peripheral stimuli did not draw heavily on these top-down cognitive control mechanisms, increasing load at fixation did not induce a processing cost for them. Earlier

psychophysical results showed that perceptual load for the primary task did create a processing cost for the localization of peripheral stimuli, however only when a fine localization was required (Rossi & Pourtois, 2013). In the present case, the secondary task primarily required participants to localize large visual textures shown in the upper visual field, hence tapping into *coarse* spatial localization abilities. Interestingly, we found, using alternative topographic evoked potential mapping methods, that the C1 component (defined as a topography rather than a component measured at a few electrode positions) was smaller in amplitude during the HL, compared to the LL, though regardless of the current mood state of the participants. These auxiliary neurophysiological results suggest therefore that load can exert an early gating effect in V1 (Rauss et al., 2009), independently from changes in the affective state of the participant.

Load did not only create an early gating effect in V1 to the attended peripheral stimuli, but it also substantially influenced the processing of the central targets, in the predicted direction. The amplitude of the P300 component to targets was larger in the LL than in the HL condition, besides the classical oddball effect, occurring irrespective of load (McCarthy & Donchin, 1981; Kok, 2001; Sawaki & Katayama, 2007; Kim, et al., 2008). This neurophysiological effect suggesting a decreased target processing with increasing perceptual load paralleled the behavioral results obtained for the primary task, showing lower accuracy and slower RTs in the HL compared to the LL condition. Interestingly, we also found that regardless of load, positive mood did boost target processing, as reflected by a larger P300 component (as well as better accuracy in the HL condition) in the positive compared to the neutral mood group. Altogether, these results suggest that mood and load can each modulate target processing (P300 component), likely via different attention-related processes (i.e., oddball detection for positive mood vs. context closure for load; see Verleger, 1988).

Perceptual load as an attentional set blocks the broadening of attention with positive mood

It is important to point out that our MIP, based on self-related memories, was effective in increasing subjective feelings of happiness and pleasantness in the positive mood group, selectively. Moreover, because vivid neutral self-related memories were

retrieved from episodic memory in the neutral mood group, it is unlikely that these group differences regarding the actual mood state of the participants could be related to uncontrolled factors, besides mood. Nevertheless, contrary to our main prediction, positive mood did not broaden attention to peripheral stimuli, with visible effects at the level of the C1 component (see Vanlessen et al., 2013, 2014). If anything, positive mood did not increase the C1, but instead, reduced it (see the trend significant effect of group for the topography of the C1). Importantly, the amplitude of the C1 was clearly influenced by the stimulus position in the upper visual field, in the expected way (see also Vanlessen et al., 2013), such that the C1 was larger for the close compared to more eccentric locations in the upper visual field. In addition, independent evidence obtained from the localizer blocks in the same participants confirmed that this early component corresponded to a genuine C1 component, characterized by a polarity reversal depending on the part of the visual field being stimulated (Kelly et al., 2013). Hence, while the manipulation of the factors Position, Load and Mood was successful, positive mood did not enhance early stimulus processing in V1 (C1 effect) nonetheless. A lack of power to account for this null finding does not seem plausible in the present case. In our previous study (Vanlessen et al., 2014), we found that a similar sample size (20 participants per group vs. either 18 or 20 per group in the current study) was sufficient to give rise to a much larger effect size ($\eta p^2 = 0.135$, $f = 0.40$) and power (.98), compared with the effect size ($\eta p^2 = 0.038$, $f = 0.20$) and power (.54) gathered in the current study. An auxiliary power analysis showed that we would need to test at least 77 participants per group in order to find an effect of mood on the C1 to peripheral stimuli with the same significance and power as in our previous study (Vanlessen et al., 2014). In order to better understand the possible reasons underlying this null finding, we systematically compared the current study with this previous study, given that they share a common methodology, including the dual task setting and the MIP.

First, while the mean VAS scores for happiness showed a significant increase in the positive mood group, the gain in positive affect in the previous study was substantially larger (8.5% vs. 24.5%, when comparing mean VAS scores obtained after the MIPs compared to their respective baseline measures). In addition, in the current study, arousal was not reliably increased following the MIP in the positive compared to the neutral mood group, unlike what we found in our previous study. Possibly, the lack

of a significant arousal component accompanying the positive mood might undermine the early modulation of the C1 component by affect-related attention processes (Stolarova, Keil, & Moratti, 2006). However, bodily arousal per se appears unlikely to underlie these early gating effects in V1 (Rossi & Pourtois, 2014). In the present study, we also used a shorter SOA between the central and the peripheral stimulus than in our previous study (where it was 60 ms longer). However, this factor too appears unlikely to account for the reported effects for the C1 given that we only included in the analysis the C1 component generated in response to peripheral stimuli following central standard stimuli, which did not require any specific motor response and did not elicit any clear decision-related ERP components (see Fig. 4).

A closer look at the behavioral results obtained in these two studies for the primary task lends support to the assumption that the actual attentional or mind set adopted by the participants may have been slightly different between these two ERP studies. Presumably, this factor could account for the lack of a significant amplitude modulation of the C1 component by positive mood in the current study, although future studies are needed to confirm this prediction. As a matter of fact, in the present study, participants knew before starting the actual experimental session that easy (LL) and more difficult (HL) trials awaited them in different blocks because they were first confronted with task instructions clearly mentioning this information as well as specific practice trials. Although speculative, this foreknowledge may have biased the attentional set of the participants during the encounter of LL blocks (i.e., they ‘inadvertently’ allocated more attention to the primary task, compared to our previous study where a unique LL condition was used throughout the task and no such fine-tuning of their attentional set was possible and required). This conjecture is partly supported by the observation of a significant RT difference for the primary task when comparing the LL condition in this study ($M = 573.04$, $SD = 73.19$) to our previous study ($M = 503.54$, $SD = 79.55$; $t(76) = 4.01$, $p < .001$). Participants were actually slower to perform the primary task in the present study, compared to our previous ERP study, despite a balanced level of difficulty. Earlier studies already provided evidence for dynamic changes in early perception and attention mechanisms by alteration of the mindset, including the influence of instructions on vigilance (Lucaccini, Freedy, & Lyman, 1968), the modulation of bottom-up attention capture by top-down control

mechanisms during visual search tasks (Folk, Remington, & Johnston, 1992), the amplification or suppression of stimulus processing by the attentional set (Posner & Presti, 1987), and the transfer of a specific attentional set to a different task (Leber & Egeth, 2006). Hence, the prospect of a variable task difficulty for the primary task may have induced a specific mindset that eventually prevented participants from broadening their attention early on following (peripheral) stimulus onset after the induction of positive mood (with corresponding effects at the level of the C1), despite the use of a relatively easy task at fixation in half of the blocks. Accordingly, our new ERP results shed light on the boundaries for an early modulation of visual perception by positive affect, via the modulation of specific attention control processes. Whether an increased load at fixation directly blocks the early broadening of attention with positive mood or rather indirectly by means of the specific alteration of the mindset remains an open question for future research.

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Happy and less inhibited? Effects of positive mood on inhibitory control during an anti-saccade task

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ABSTRACT

A lowered inhibitory control has often been proposed as the underlying mechanism through which positive mood would influence higher-level cognitive functions, such as attention, reasoning or decision making. In this study, we sought to test whether positive mood could impair motor inhibition directly, as measured using a standard antisaccade task. Thirty participants were allocated either to a positive or a neutral mood induction procedure, before they completed an antisaccade task while 128-channels EEG was recorded concurrently. Results showed that positive mood did not influence motor inhibition per se, although the mood induction was successful. Instead, we found evidence for modulatory effects of positive mood on both proactive and reactive components of cognitive control during this task. Positive mood blurred proactive control (as reflected by the CNV component prior to target onset), while it sharpened reactive control (as reflected by the N2 component following target onset). Positive mood did not alter the subsequent P3 component. We interpret these new neurophysiological findings in terms of dynamic changes in the way proactive and reactive control mechanisms are timely engaged in order to resolve the antisaccade task following the induction of positive mood.

INTRODUCTION

As predicted by the broaden-and-build theory (Fredrickson, 2001, 2004) and the GLOMOsys (Forster, 2012), positive mood can influence a wide range of cognitive functions (see Ashby, Isen, & Turken, 1999 for a review). In line with this framework, positive mood has been shown to broaden the attentional focus (e.g. Moriya & Nittono, 2011; Vanlessen, Rossi, De Raedt, & Pourtois, 2013, 2014), although it remains unclear whether positive mood influences attention control mechanisms directly or rather via mediation by other cognitive processes. Previous research suggested that a decreased inhibitory control following the induction of positive mood might underlie such a broadening of (spatial) attention (Rowe, Hirsh, & Anderson, 2007). Presumably, a lower inhibition could also account for a variety of phenomena that were previously associated with positive mood, including an increased flexibility in decision-making (Isen, 2000; Isen, Rosenzweig, & Young, 1991) and creative problem solving (Estrada, Isen, & Young, 1994; Isen, Daubman, & Nowicki, 1987), a greater verbal fluency (Phillips, Bull, Adams, & Fraser, 2002), as well as a preference for a more global (as opposed to local) processing style (Basso, Schefft, Ris, & Dember, 1996; Forster, 2012). More recently, an enhanced susceptibility for distraction was found in positive mood (Biss & Hasher, 2011; Biss, Hasher, & Thomas, 2010; Dreisbach, 2006; Dreisbach & Goschke, 2004, Rowe e.a., 2007), which could be taken as evidence for a disturbance of prefrontal inhibitory control mechanisms with this mood state (Chao & Knight, 1997). However, while these earlier results indirectly suggest a link between positive mood and a reduced inhibitory control, no study to date has explored whether positive mood could exert a direct modulatory effect on inhibition and its electrophysiological correlates.

Inhibition is an utmost important cognitive process that can embrace a wide range of phenomena (Aron, 2007). It is usually defined as a central regulatory mechanism for preventing the processing of task-irrelevant information or execution of prepotent responses (Friedman & Miyake, 2004). While modulatory effects of positive mood on the suppression of irrelevant information have already been investigated in the past, much less is known about putative effects of positive mood on the inhibition of a prepotent response tendency (Mitchell & Phillips, 2007). One previous study showed that participants experiencing feelings of fun and happiness, compared to

feeling proud or neutral (induced through writing about events eliciting the respective feelings, and watching mood-congruent pictures), committed more errors in an antisaccade task (Katzir, Eyal, Meiran, & Kessler, 2010), in line with a weaker inhibitory control in this mood. Because a fronto-striatal network comprising medial and lateral prefrontal regions implicated in inhibitory control (Aron, Robbins, & Poldrack, 2014; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004) likely shares a common neurobiological ground with positive mood (Habel, Klein, Kellermann, Shah, & Schneider, 2005), this specific affective state might interfere with inhibition via modulations within this specific network, as previously put forward by several authors (Ashby et al., 1999; Mitchell & Phillips, 2007). More precisely, the induction of positive mood might influence these prefrontal inhibitory mechanisms through dopaminergic (DA) activation arising in the midbrain (Ashby et al., 1999) and affecting in turn the functioning of these prefrontal regions (Braver & Cohen, 2000; Goldman-Rakic, Muly, & Williams, 2000; Miller & Cohen, 2001).

A landmark paradigm often used in the literature to investigate frontal inhibitory control is provided by the antisaccade task (see Domagalik, Beldzik, Fafrowicz, Oginska, & Marek, 2012; Jamadar, Fielding, & Egan, 2013), besides the stop signal task or the go/nogo task (Falkenstein, Hoormann, & Hohnsbein, 1999; Logan, Van Zandt, Verbruggen, & Wagenmakers, 2014). Moreover, performance on this task is associated with changes in DA (Aron et al., 2014; Duka & Lupp, 1997; Hood et al., 2007), making it a valid method to investigate influences of positive mood on inhibition. The antisaccade task (Hallett, 1978) requires participants to execute a saccade either towards (prosaccade) or away from (antisaccade) a unilateral visual target, appearing at a peripheral spatial location following fixation. Antisaccade trials typically elicit more errors and slower reaction times (RTs) compared to prosaccades, presumably because top-down control is necessary to inhibit the execution of a reflexive saccade towards the target location and to generate a saccade in the opposite direction (for reviews, see Everling & Fischer, 1998; McDowell, Dyckman, Austin, & Clementz, 2008; Munoz & Everling, 2004). Importantly, prosaccades also require some form of cognitive control (Hutton, 2008).

In an antisaccade task, the appearance of the target gives rise to a wave of activation travelling from the retina to the occipital cortex, as well as the superior

colliculus (SC) and the (posterior) parietal cortex (McDowell et al., 2008). The parietal cortex interacts in turn with frontal motor areas, more specifically, the frontal eye fields (FEF) and supplementary eye fields. These motor-related areas report back to the SC, triggering the generation of a saccade (Pierrot-Deseilligny, Milea, & Muüri, 2004). In antisaccades, activity in these parietal and frontal motor cortices is increased compared to prosaccades, and an additional activation of the anterior cingulate cortex and the dorsolateral prefrontal cortex (DLPFC) is usually observed (Jamadar et al., 2013). Importantly, during anti-saccade trials, the activation of the DLPFC (prior to target-onset) likely reflects top-down inhibitory control mechanisms meant to hinder the generation of an (incorrect) prosaccade and to bias the oculomotor system in favor of an antisaccade (Ford, Goltz, Brown, & Everling, 2005; Jamadar et al., 2013; Munoz & Everling, 2004; Pierrot-Deseilligny et al., 2004; Pierrot-Deseilligny et al., 2003). Moreover, single-cell recordings in monkeys showed that successful antisaccades were associated with a suppressed activity of saccade neurons in the SC and FEF. These inhibitory effects could serve to prevent that the neural signal coming from the visual cortex upon perceiving the target would surpass the threshold for the generation of a reflexive prosaccade (Everling, Dorris, & Munoz, 1998; Everling & Munoz, 2000). Accordingly, inhibition during the antisaccade task appears to be a complex neural process involving coordinated changes in a distributed neural network.

At the electrophysiological level, preparatory or cue-related activity in the antisaccade task is usually captured by a negative wave ramping up prior to target onset (Klein, Heinks, Andresen, Berg, & Moritz, 2000; Reuter, Herzog, Endrass, & Kathmann, 2006) and sharing many (electrophysiological) similarities with the Contingent Negative Variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). This preparatory activity is generally more negative in anti –compared to prosaccades (Ansari & Derakshan, 2011; Klein et al., 2000), in line with the assumption of a higher inhibitory regulation in these former compared to latter trials. Interestingly, this activity was previously found to be blunted in specific groups of patients or participants characterized by break-downs in inhibitory control, such as high anxious individuals (Ansari & Derakshan, 2011) or schizophrenics (Klein et al., 2000). Event-Related Potential (ERP) activity following target-onset can also be linked to inhibitory processes. More specifically, post-target ERPs typically show an increased N2 and

decreased P3 in anti –compared to prosaccade trials, and this N2/P3 complex has been interpreted as a possible neurophysiological marker of inhibition (Müller, Swainson, & Jackson, 2009). However, while the N2 seems to provide a valid measure of response inhibition, the link between the P3 and inhibition is less clear (see Jonkman, Lansbergen, & Stauder, 2003). According to some authors, the P3 might reflect other processes than inhibition per se, including post-perceptual response monitoring (Beste, Willemsen, Saft, & Falkenstein, 2010) or decision-making processes (Nieuwenhuis, Aston-Jones, & Cohen, 2005).

In the present study, we recorded high-density EEG while healthy adult participants carried out a standard antisaccade task. These participants were allocated either to a positive or a neutral mood condition (see Vanlessen et al., 2013, 2014 for a similar procedure). In light of the literature reviewed here above, we predicted that positive (relative to neutral) mood would be associated with slower RTs, and possibly an increased error rate, in antisaccades. Second, at the electrophysiological level, we surmised that positive mood could influence inhibitory processes in antisaccade trials at multiple levels, given that this specific mood state is thought to influence prefrontal-based cognitive control systems in an undifferentiated manner through DA modulations (see Ashby et al., 1999). More specifically, we hypothesized that induced positive (compared to neutral) mood might be associated with a less efficient preparatory activity prior to target onset, as reflected by a lower CNV amplitude during antisaccade trials (in line with Ansari & Derakshan, 2011; Klein et al., 2000). Concerning the inhibitory-related ERP activities following target onset, we expected that the larger N2 and smaller P3 components in anti –compared to prosaccade trials (in line with Müller et al., 2009) would be less pronounced in the positive compared to the neutral mood group.

METHODS

Participants

Thirty students of Ghent University participated in the study (age: $M = 21$; $SD = 3$; 5 male participants). All participants reported to be right-handed, to have normal or corrected-to-normal vision and no history of psychiatric or neurological disorders. Participants gave written informed consent prior to participation and received 30 euros

compensation. One participant from the positive mood group was excluded because the reported level of feelings of happiness decreased more than 50% after the positive mood induction, relative to the baseline. Hence, the statistical analyses were performed on 14 participants in the positive and 15 in the neutral mood group.

Mood Induction Procedure (MIP)

The MIP was identical to the MIP used in our previous studies (Vanlessen et al., 2013, 2014). Participants rated their mood on three Visual Analogue Scales (VAS; see Vanlessen et al., 2013, 2014), the Positive Affect And Negative Affect Scales (PANAS; Watson, Clark, & Tellegen, 1988) and the Self-Assessment Manikin for Arousal (SAM; Bradley & Lang, 1994).

Stimuli and task

A white fixation cross (1.7° in diameter) was presented in the center of the screen and turned either green or red, indicating whether a prosaccade or an antisaccade had to be executed, respectively. The target consisted of a white asterisk (2° in diameter) presented at 10.5 visual degrees on the right or left side of the fixation cross, on the same horizontal axis. In a prosaccade trial, participants were instructed to perform a saccade towards the target. In an antisaccade trial, an eye movement was required to the horizontal mirror position of the target (see Fig. 1B). Participants were instructed to fixate the target position for the entire duration of the target presentation. All stimuli were presented against a uniform black background. The task was programmed using E-Prime Version 2 (Psychology Software Tools, Inc., 2001).

Procedure

After preparation for EEG recording, participants completed eight practice trials, followed by the first positive or neutral MIP. Next, participants completed six blocks of 40 trials each while they were seated 57 cm in front of a 19" CRT screen, with their head movements restrained by a chinrest. The MIP was shortly repeated after the first three blocks (see Fig. 1A), in order to maintain the desired mood throughout the experiment. Participants indicated their mood levels at the beginning of the experiment (baseline measure), after the MIP repetition and at the end of the experiment. After

completion of the experimental task, participants filled out three trait-related questionnaires: the Beck Depression Inventory (BDI; Beck, Steer, Ball, & Ranieri, 1996), the BIS/BAS scales (Carver & White, 1994) and the Resilience scale (Rs; Portzky, Wagnild, De Bacquer, & Audenaert, 2010).

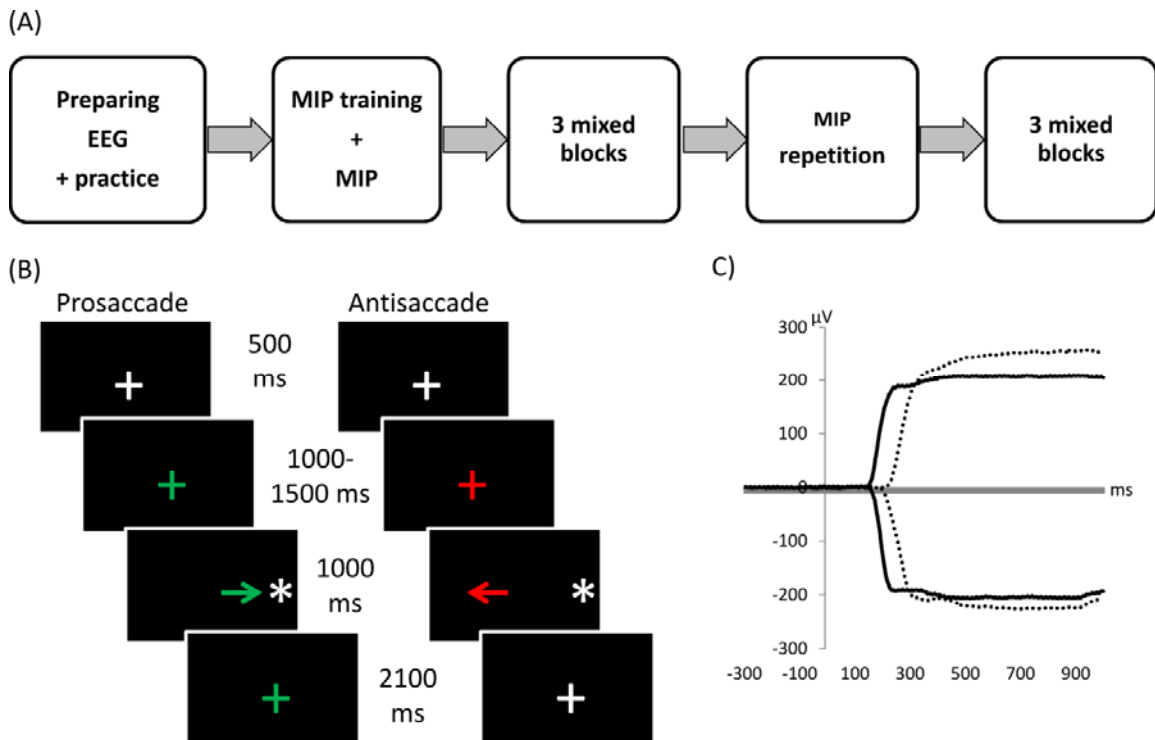


Figure 1. A) Procedure. B) Display sequence for prosaccades trials (left panel) and antisaccades trials (right panel). The color of the fixation cross (cue) indicated the trial type (green for prosaccades; red for antisaccades). The arrow indicates the correct direction of the saccade, but was not shown in the experiment. C) EOG for correct prosaccades (full lines) and antisaccades (dotted lines) to the right (positive) and left (negative) hemifield.

Each experimental block consisted of an equal number of pro –and anti-saccades (20 trials each) shown in random order. Half of the targets appeared in the left visual field and the other half in the right visual field. Each trial started with a white fixation cross presented for 500 ms, followed by either a green or a red fixation cross (for a jittered duration between 1000 and 1500 ms). Then, the unilateral target appeared for 1000 ms, with no concurrent fixation cross shown in the center of the screen. Next, the target disappeared and the white fixation cross was presented again. The inter-trial interval had an average duration of 2100 ms (randomly varying between 1000 and 3200 ms; see Fig. 1B).

Acquisition and reduction of ocular and EEG data

We recorded the EEG continuously using a Biosemi Active Two System, from 128 AgAgCl electrodes distributed evenly over the scalp and attached to an elastic cap. The signal was referenced online to the CMS-DRL ground and digitized at 512 Hz. Both vertical and horizontal oculograms were recorded through bipolar electrodes placed above and below the left eye, and on the outer canthi of both eyes, respectively. Additionally, bipolar electrodes were placed on the right and left mastoids.

Using Brain Vision Analyzer 2.0 (Brain Products GmbH, Munich, Germany), the two horizontal EOG channels were subtracted from each other to create a single monopolar channel, showing positive deflections for eye movements to the right and negative deflections for eye movements to the left (see Fig. 1C). For each trial, the accuracy and latency of the saccade (following target onset) were calculated based on this monopolar channel. More precisely, correct and incorrect trials were identified based on the polarity of the first deflection detected on this channel following target onset. The saccade reaction time (RT) was defined as the latency between target-onset and saccade-onset (defined as a sharp deflection from baseline on the EOG channel with an amplitude exceeding 70 microvolts). Mixed ANOVA's on the accuracy and RT data were performed with Saccade (pro vs. anti) as within-subjects factor and Mood (positive vs. neutral) as between-subjects factor.

Scalp EEG signals were referenced offline to the linked mastoids. We segmented the ocular and EEG data separately for components preceding target onset (from -700 ms prior to target onset until target onset) and following it (from -300 ms prior to it and until 1000 ms following its onset). The standard Gratton algorithm was applied on the EEG data to automatically correct for artifacts caused by eye blinks (Gratton, Coles, & Donchin, 1983). A spherical splines procedure was used for interpolating noisy channels. The individual epochs were baseline-corrected, using the first 50 ms of the epochs for the pre-target ERP activity and the entire pre-target interval for the post-target components. Artifacts were rejected semi-automatically using an absolute voltage criterion of $\pm 100 \mu\text{V}$. With this criterion, 87.29 % and 89.73 % of the epochs were included in the averages for the positive and the neutral mood group, respectively (with no significant difference between groups, $t(27) = 0.64$, $p = .53$). Individual averages were calculated separately for the pre –and post-target components, and

separately for the pro –and anti-saccade trials. Only correct trials were eventually included in these individual averages, before grand average ERP waveforms were calculated.

For the ERP activity preceding the target, we primarily focused on the CNV. This component was defined as the negative activity building up steadily prior to target onset, with a central scalp distribution. Based on the topographical properties of the data set, we selected five electrodes (A3, A4, A5, A19 and A32) with a centro-parietal scalp position where the CNV reached its maximum amplitude just prior to target onset. The CNV was defined as the mean ERP activity recorded at these 5 leads during the last 200ms preceding target onset. Regarding post-target ERP activities, the frontal N2 component was identified as a negative wave peaking between 140 and 190 ms following target onset at fronto-central electrodes. We selected the electrodes C21, C22, C23 (midline), as well as two parallel arrays on the right (C2, C11, C12) and left side (C24, C25, D2), resulting in 9 leads in total. The N2 was defined as the mean ERP activity recorded at these 9 electrodes during a 20 ms window around the peak. The P3 component was defined as a large positive deflection following the N2, with a clear central scalp distribution. More precisely, it was measured at electrode positions A1, A2, B1, C1, D1 and D15 and defined as the mean ERP activity computed during the 215-260 ms post-target onset interval. These electrode positions and time windows were selected based on the topographical properties of these two components (N2 and P3). For each component separately (CNV, N2 or P3), the mean amplitude values were submitted to a mixed model ANOVA with Saccade (pro vs. anti) as within-subjects factor and Mood (positive vs. neutral) as between-subjects factor.

Although this ERP analysis informed about amplitude changes occurring at a few electrode positions as a function of saccade type and mood, we also wanted to characterize more formally possible changes of the inhibition-related ERP components (in particular the N2 and P3) by these factors when taking the whole electrical field, and hence the topography, into account. To this aim, we performed a data-driven ERP topographic mapping analysis, following standard practice (see Michel & Murray, 2012; Michel, Seeck, & Landis, 1999; Murray, Brunet, & Michel, 2008; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Pourtois, De Pretto, Hauert, & Vuilleumier, 2006; Pourtois, Delplanque, Michel, & Vuilleumier, 2008; Pourtois, Thut, de Peralta,

Michel, & Vuilleumier, 2005 for the underlying principles). A K-means spatial cluster analysis was used to identify the different dominant scalp topographies during a 900 ms time window starting at target-onset and encompassing therefore the N2 and P3 components, for the pro –and the antisaccades separately. This analysis enabled us to isolate the dominant voltage maps corresponding to the N2 (125-175 ms post-target onset) and the P3 component (300-410 ms post-target onset). The two mood groups were collapsed for this analysis in order to increase the signal-to-noise ratio. The dominant maps were determined objectively, using both cross-validation (Pascual-Marqui, Michel, & Lehmann, 1995) and Krzanowski-Lai criteria (Pascual-Marqui et al., 1995; Tibshirani, Walther, & Hastie, 2001). The following parameters were used during clustering: average reference; number of random trials: 100; smoothing strength (Besag factor) of 10; smoothing half window size of 3; merging of clusters correlating above 0.92; rejection of segments less or equal to 5 time-frames; no sequentializing.

Next, these dominant N2 and P3 topographies were fitted ‘back’ to the individual ERP data using spatial fitting procedures in order to quantify their expression across subjects and conditions. We primarily focused on variations along the Global Field Power (GFP) or strength of these dominant topographies, depending on saccade type and mood group. For each topographical ERP component separately, we submitted these GFP values (resulting from the fitting) to a mixed model ANOVA with Saccade (pro vs. anti) and Map configuration (map 1 vs. map 2) as within-subjects factors, and Mood (positive vs. neutral) as between-subjects factor. Significant interaction effects were followed up by two-tailed paired or independent samples T-tests. When normality assumption was violated, corrected p-values were reported.

Analyses of behavioral data

We compared the post-MIP average scores with the baseline measure by performing a separate mixed model ANOVA for each scale separately, with Time (baseline vs. post-MIP) and Mood (positive vs. neutral) as within –and between-subjects factors, respectively. Independent samples T-tests were used to follow-up significant interactions, as well as to compare mean scores for the trait-related questionnaires between mood groups. Note that one person from the positive mood group did not

complete all arousal scores and that the questionnaire data from one person from the neutral mood group were not properly saved.

The behavioral data (accuracy and RTs) were analyzed by means of a mixed model ANOVA with Saccade (Pro vs. Anti) as within-subjects factor and Mood (Positive vs. Neutral) as between-subjects factor.

RESULTS

Changes in mood: manipulation check

The ANOVA on the VAS scores showed a significant interaction effect between Time and Mood for feelings of happiness (baseline: positive: $M = 5.75$, $SD = 2.35$, neutral: $M = 4.56$, $SD = 3.13$; post-MIP: positive: $M = 7.65$, $SD = 1.63$, neutral: $M = 4.51$, $SD = 2.68$; $F(1,27) = 13.45$, $p = .001$; see Fig. 2A), and pleasantness (baseline: positive: $M = 5.63$, $SD = 2.52$, neutral: $M = 4.97$, $SD = 2.96$; post-MIP: positive: $M = 7.54$, $SD = 1.64$, neutral: $M = 4.75$, $SD = 2.68$; $F(1,27) = 9.75$, $p = .004$; see Fig. 2B), but not for sadness (baseline: $M = 0.55$, $SD = 0.64$, post-MIP: $M = 0.41$, $SD = 0.57$, $F(1,27) = 2.61$, $p = .12$). The follow-up T-tests showed a significant difference between the positive and neutral mood group for both feelings of happiness ($t(27) = 3.78$, $p = .001$) and pleasantness ($t(27) = 3.36$, $p = .002$) following the MIP, but not for the baseline measures (all $ps > .26$). These results confirmed that positive mood increased following the MIP in the positive mood group, selectively.

The ANOVA on the PANAS scores showed a significant interaction effect between Time and Mood for the PA scales (baseline: positive: $M = 31.92$, $SD = 5.08$, neutral: $M = 29.93$, $SD = 6.50$; post-MIP: positive: $M = 32.17$, $SD = 7.36$, neutral: $M = 24.93$, $SD = 7.14$, $F(1,27) = 7.67$, $p = .01$), but not for the NA scales (baseline: $M = 12.66$, $SD = 2.02$; post-MIP: $M = 11.22$, $SD = 1.41$, $F(1,27) = 3.24$, $p = .08$). An independent samples T-test showed a significant difference between mood groups on the post-MIP PA scores ($t(27) = 2.69$, $p = .012$), while this difference was not significant at baseline ($t(27) = 0.92$, $p = .37$). These results showed that positive affect slightly increased following the MIP in the positive mood group, while it decreased in the neutral mood group.

The ANOVA on the Arousal scores showed a significant interaction effect between Time and Mood (baseline: positive: $M = 4.31$, $SD = 1.97$, neutral: $M = 3.93$, SD

= 1.58; post-MIP: positive: $M = 5.32$, $SD = 1.71$, neutral: $M = 3.47$, $SD = 1.77$, $F(1,26) = 8.62$, $p = .007$). However, the Arousal scores did not differ between groups after the MIP ($t(26) = 3827$, $p = .082$), nor at baseline ($t(26) = 0.56$, $p = .58$).

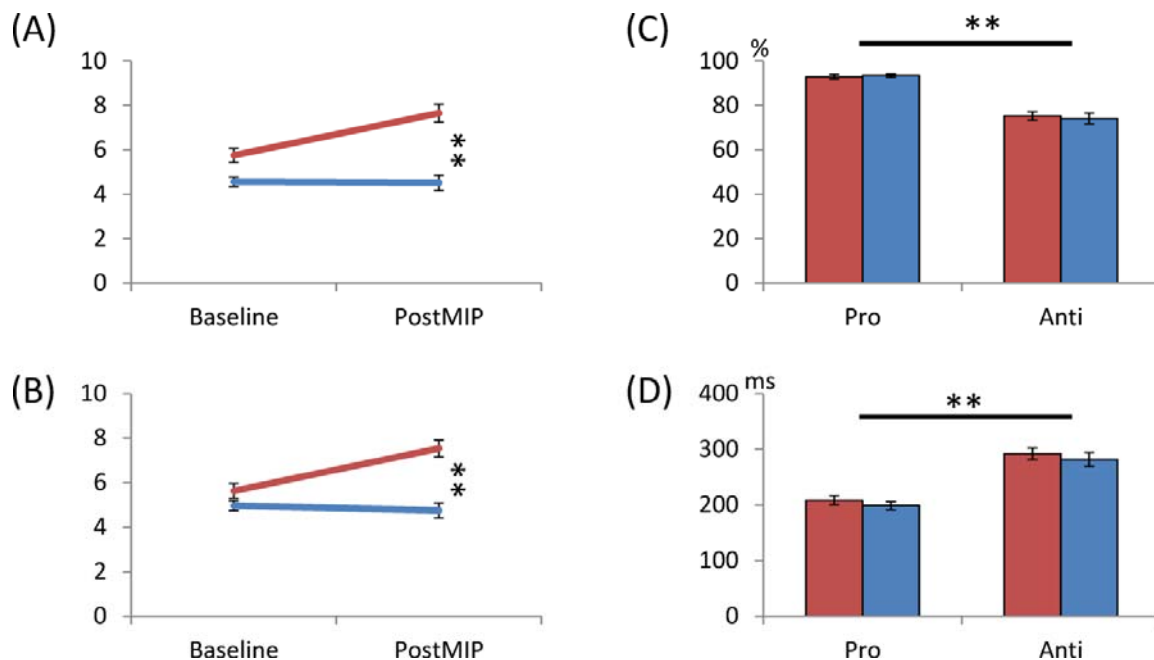


Figure 2. VAS scores for A) feelings of happiness and B) pleasantness showed a selective increase in levels of positive mood in the positive (red) but not the neutral mood group (blue). Behavioral performance showed C) decreased accuracy and D) increased RTs in anti – compared to prosaccades, in both mood groups. ** indicates $p \leq .01$

Questionnaires.

The scores on the trait-related questionnaires did not differ between groups for the BDI ($t(26) = 0.70$, $p = .49$), the BIS/BAS (BIS: $t(26) = 0.10$, $p = .92$, BAS Drive $t(26) = 1.20$, $p = .24$, BAS Fun: $t(26) = 0.80$, $p = .43$, BAS Reward: $t(26) = 0.65$, $p = .52$), nor the Rs ($t(26) = 0.32$, $p = .75$), showing that groups did not differ along these stable traits.

Behavioral results.

Participants reached high accuracy in the prosaccade condition ($M = 92.86$, $SD = 6.55$) while their performance decreased in the antisaccade condition ($M = 75.22$, $SD = 16.31$), as shown by a main effect of Saccade ($F(1,27) = 49.73$, $p < .001$; see Fig. 2C). There was no significant main effect of mood, nor a significant interaction effect between Saccade and Mood (all $ps > .48$).

The same ANOVA carried out on the RTs showed faster RTs in prosaccade ($M = 209.58$, $SD = 30.11$) compared to antisaccade trials ($M = 292.37$, $SD = 47.34$, $F(1,27) = 222.17$, $p < .001$; see Fig. 2D), while the main effect of Mood and the interaction effect between Saccade and Mood were not significant (all $ps > .46$).

ERP results.

CNV. The mixed model ANOVA showed a significant main effect of Saccade ($F(2,27) = 6.10$, $p = .02$). The amplitude of the CNV was larger for antisaccade ($M = -5.90$, $SD = 2.83$) compared to prosaccade trials ($M = -4.74$, $SD = 2.57$). In addition, a significant interaction effect was found between Saccade and Mood ($F(2,27) = 4.27$, $p = .049$; see Fig. 3A and B), showing that this differential preparatory activity was clearly evidenced in the neutral mood group (Pro: $M = -4.07$, $SD = 2.36$, Anti: $M = -6.15$, $SD = 2.69$; $t(14) = 2.74$, $p = .016$), but merely absent in the positive mood group (Pro: $M = -5.45$, $SD = 2.67$, Anti: $M = -5.64$, $SD = 3.05$; $t(13) = 0.38$, $p = .71$). Strikingly, the CNV amplitude in this latter group was as large for pro –than antisaccades.

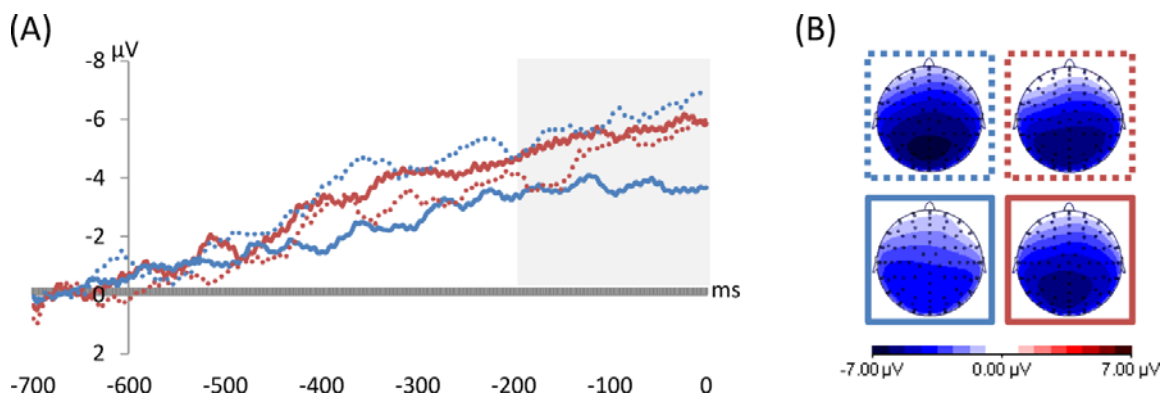


Figure 3. A) *Grand average ERPs for the preparatory activity preceding target*, recorded at a representative fronto-central midline electrode position (A1) with B) corresponding voltage maps (top view) for the positive (red lines) and neutral (blue lines) mood group, separately for prosaccades (full lines) and antisaccades (dotted lines). Negative values are plotted upwards; the gray frame indicates the window used for analyses. Note that the zero on the x-axis indicates target-onset.

N2. The mixed model ANOVA performed on the mean amplitudes showed, as expected, a larger N2 for antisaccades ($M = -5.00$, $SD = 3.03$) compared to prosaccades ($M = -1.72$, $SD = 2.96$, $F(1,27) = 36.34$, $ps < .001$; see Fig. 4A and B). However, this post-target inhibitory effect was not influenced by mood (all $ps > .41$).

P3. The mixed model ANOVA carried out on the P3 amplitudes showed, as expected, a significant main effect of Saccade ($F(1,27) = 60.66, p < .001$): the P3 was smaller for antisaccades ($M = 2.70, SD = 4.70$) than prosaccades ($M = 6.57, SD = 4.29$; see Fig. 4D and E). However, mood did not influence this effect either (all $ps > .15$).

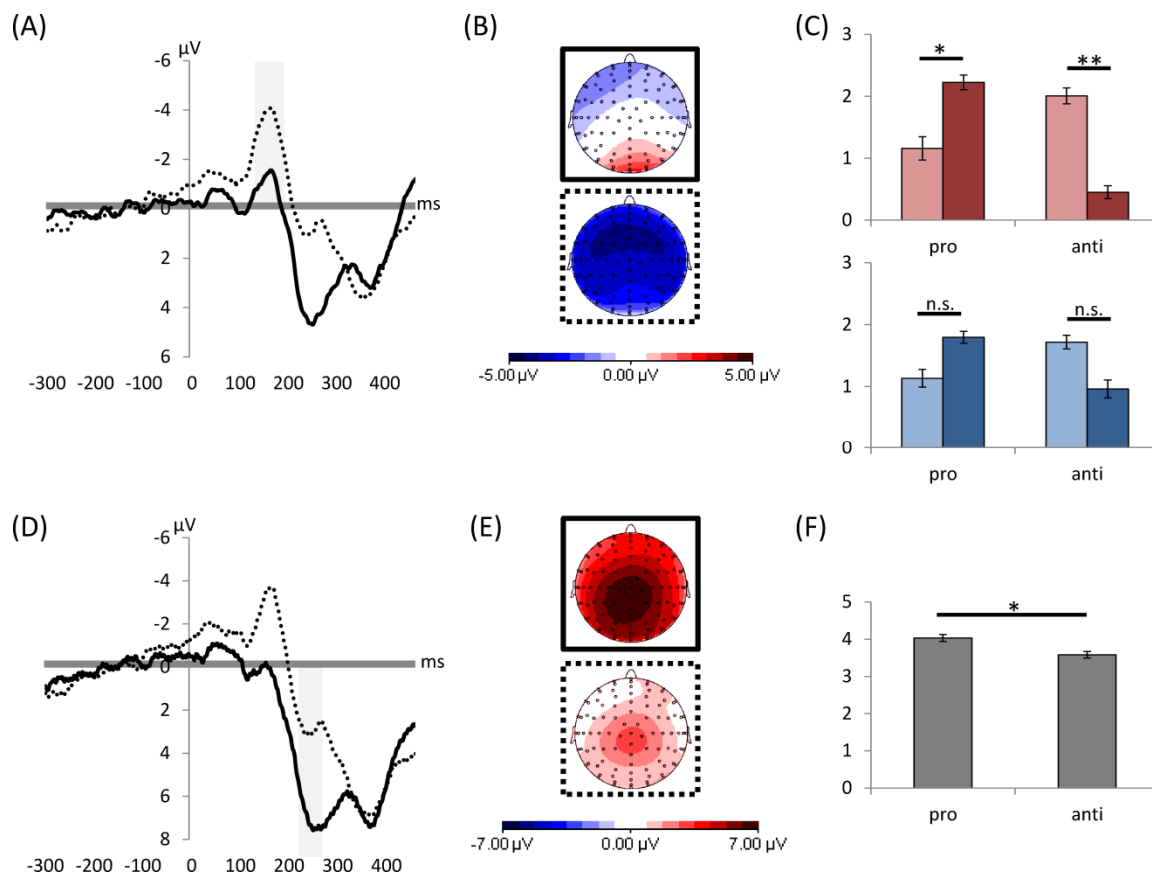


Figure 4. Grand average ERPs following target for A) the N2, recorded at a representative fronto-central midline electrode position (C22) with B) corresponding voltage maps (top view) for the positive (red lines) and neutral (blue lines) mood group, separately for prosaccades (full lines) and antisaccades (dotted lines). C) The topographic analysis identified a 'prosaccade map' (light color) and an 'antisaccade map' (dark color) for the N2 time window. GFP is shown for both maps for the positive mood group (red, upper part) and the neutral mood group (blue, lower part) separately. D) Grand average ERPs following targets for the P3, recorded at a representative fronto-central midline electrode position (A1) with E) corresponding voltage maps (top view) for the positive (red lines) and neutral (blue lines) mood group, and for prosaccades (full lines) and antisaccades (dotted lines) separately. F) The topographic analysis identified one dominant map for the P3. GFP is shown for the positive mood group (red) and the neutral mood group (blue) separately. Note that negative values are plotted upwards; the gray frame indicates the window used for analyses. * indicates $p \leq .05$; ** indicates $p \leq .01$

Topographic analysis

The K-means spatial cluster analysis showed that a solution with seven dominant maps (extracted during the first 900 ms following target onset) explained 95% of the variance (Global Explained Variance). Among these seven map configurations, two different topographies were identified for the N2 component, while a single one corresponded to the P3 component.

N2. The topographic analysis showed two different map configurations during the N2 interval, one related to prosaccade trials ('prosaccade map') and the other one to antisaccade trials ('antisaccade map'). Interestingly, we found that (positive) mood did influence the expression (i.e., strength) of these two dominant N2 topographies. The mixed ANOVA revealed a significant three-way interaction between saccade type, map configuration and group ($F(1,27) = 4.97, p = .034$). This data-driven analysis confirmed that the N2 component generated for antisaccades was not the same (at the topographical level) as the N2 component for prosaccades ($F(1,27) = 56.03, p < .001$). Follow-up ANOVAs for each group separately showed an interaction effect of Saccade Type and Maps in both mood groups, however, this interaction effect was much stronger in the positive ($F(1,13) = 41.74, p < .001$) compared to the neutral mood group ($F(1,14) = 15.66, p = .001$). In the positive mood group, follow-up t-tests confirmed that for prosaccades, the prosaccade map ($M = 2.22, SD = 0.88$) had a larger GFP than the antisaccade map ($M = 1.16, SD = 1.41; t(13) = 2.98, p = .011$). Conversely, for antisaccades, the antisaccade map ($M = 2.01, SD = 0.96$) had a larger GFP than the prosaccade map ($M = 0.45, SD = 0.78; t(13) = 3.88, p = .002$; see Fig. 4C upper panel). However, in the neutral mood group, these two effects were strongly attenuated ($t(14) = 1.63, p = .13$; and $t(14) = 1.95, p = .07$, respectively; see Fig. 4C lower panel).

P3. The topographic analysis during the P3 window showed that a single dominant map was expressed for both pro –and antisaccades. The mixed ANOVA on the GFP of this P3 topographical component showed a significant main effect of saccade type ($F(1,27) = 4.25, p = .049$; see Fig. 4F), showing a larger GFP for prosaccades ($M = 4.03, SD = 1.00$) than antisaccades ($M = 3.58, SD = 0.95$). No other effect reached significance (all $ps > .53$).

DISCUSSION

In this study, we used a standard antisaccade task to investigate whether positive mood could alter inhibitory processes, compared to a neutral condition. To test this prediction, participants were allocated to a neutral or a positive MIP. Then, they performed cue-based pro –and antisaccades in random order, while high-density EEG was recorded. Mood ratings confirmed that the MIP successfully increased positive affect in the positive mood group only. Participants were less accurate and slower for anti –compared to prosaccades, however mood did not influence these effects. Moreover, at the electrophysiological level, we found that saccade type influenced the N2/P3 complex following targets in a predictable way, showing larger N2 and smaller P3 amplitudes in anti –compared to prosaccades. Positive mood did not influence these two effects either (when the N2 and P3 were measured and scored using a standard ERP analysis; Keil et al., 2014). While these results endorse the assumption that positive mood did not alter inhibitory control, we found nevertheless that this mood state did reliably change this cognitive process (albeit without clear repercussions at the behavioral level), at two non-overlapping epochs around target onset. First, prior to target onset, we found that while the amplitude of the preparatory activity (CNV) was clearly larger in anti –compared to prosaccade trials in the neutral mood group, in line with previous findings (Ansari & Derakshan, 2011; Klein et al., 2000), this normal proactive control effect was absent in the positive mood group. Second, when characterizing the N2 component in terms of global topography rather than amplitude changes at pre-selected electrode positions, we found that positive mood led to a sharper differentiation between anti –and prosaccades than neutral mood. We discuss the implications of these new results below.

Subtle modulatory effects of positive mood on inhibitory control

Previous research showing effects of positive mood on spatial attention and higher-order cognitive functions suggested that a decreased inhibitory control with this specific mood state could account for these results (Biss & Hasher, 2011; Biss et al., 2010; Phillips et al., 2002; Rowe et al., 2007; Vanlessen et al., 2013). At first sight, our results do not confirm this conjecture. Neither the behavior, nor ERP correlates of inhibition (N2 and P3) were influenced by positive mood in our study, despite the observation of

clear differences between the two saccade types at both levels, and the reliable induction and maintenance of positive affect in the positive mood group, selectively. However, we believe that the absence of evidence is not the evidence of absence in the present case. More specifically, given that inhibition is multifaceted (Aron, 2007), it is likely that positive mood does not change response inhibition as assessed by the antisaccade task, while it might influence other types of inhibition, such as the inhibition of irrelevant or distracting information (Friedman & Miyake, 2004), or the inhibition of specific emotions or memories (Aron, 2007). Moreover, it is not clear whether motor inhibition might serve as a valid model for other forms of inhibition (Aron, 2007), including inhibition at play during selective attention and memory, which could be influenced by positive mood (see Ashby, Valentin, & Turken, 2002; Vanlessen et al., 2014). Hence, we cannot exclude the possibility that positive mood influences other forms of inhibition, besides response inhibition, which appears to resist to changes brought about by this specific mood state. Possibly, positive mood might influence executive functions instead of inhibition (Martin & Kerns, 2011), or even exert opposite effects on different functions (Dreisbach, 2006; Dreisbach & Goschke, 2004), suggesting that modulatory effects of positive mood on inhibition are probably more complex than initially thought (Rowe et al., 2007). Alternatively, it is possible that positive mood can influence inhibition in the antisaccade task, but mostly on reflexive, express-latency rather than normal latency saccades we assessed in the present study, given that they might involve slightly different underlying mechanisms (Munoz & Everling, 2004). Previously, it has been shown that positive relative to neutral mood decreased the number of erroneous express-latency saccades (Van der Stigchel, Imants, & Ridderinkhof, 2011), suggesting that pre-target inhibitory processes were not different between mood groups, but rather that positive mood enabled a swift control to optimize the accuracy of these express-latency saccades once the target appeared.

Noteworthy, despite the absence of effect of positive mood on inhibition at the behavioral level, we found that this mood state did change post-target inhibition processes at the level of the N2. This result was evidenced when considering the topography of this inhibition-related ERP component. In the positive mood group, antisaccades were clearly differentiated from prosaccades at the level of the N2, as revealed by two competing topographies for this component. The fact that two

dissociable topographies were found for the N2 as a function of saccade type is compatible with the notion of non-overlapping brain networks for the generation of anti –compared to prosaccades (McDowell et al., 2008). By contrast, in the neutral mood group, this difference at the N2 level was blunted. This result is intriguing, because it suggests that positive mood does not merely impair inhibitory control as we initially surmised, but might instead sharpen it to some degree. No such modulatory effect of positive mood was evidenced for the subsequent inhibition-related P3 component.

This dissociation between the N2 and P3 components for effects of positive mood suggests that positive mood might influence inhibitory control via neural modulations within a specific neural pathway, as opposed to global undifferentiated changes in the prefrontal cortex (Ashby et al., 1999). A previous study showed that these two ERP components were likely associated with different subprocesses during response inhibition (Beste et al., 2010). More precisely, these subprocesses appeared to be regulated via different DA pathways, with the N2 reflecting (pre-)motor inhibition regulated by the nigrostriatal DA system while the P300 would correspond to activations of the mesocorticolimbic DA route during the monitoring of antisaccades. Accordingly, our new ERP findings suggest that positive mood could influence the nigrostriatal DA pathway selectively during motor inhibition, while leaving the mesocorticolimbic system unaffected. However, an older model already posited that positive mood influenced prefrontal based cognition and executive functions via modulations within this latter DA-dependent brain network (Ashby et al., 1999). Moreover, some caution is needed regarding the interpretation of the P3 in terms of inhibition, since the link between this ERP component and this specific cognitive process has been questioned (Falkenstein et al., 1999). Given that the P3 reached its maximum when the saccade was already initiated, this component might reflect the termination of the inhibition process, rather than inhibition per se (Falkenstein et al., 1999). Alternatively, it could reflect decision-related processes (Nieuwenhuis et al., 2005), or an evaluation of the inhibitory process (Roche, Garavan, Foxe, & O'Mara, 2005), which might eventually explain the involvement of the anterior cingulate cortex in the generation of this late or mid-latency ERP component (Schmajuk, Liotti, Busse, & Woldorff, 2006). In contrast, the preceding N2 component would index inhibition as

such, as compared to these other decision-making related processes that would have a later neurophysiological time-course (Jackson, Jackson, & Roberts, 1999; Jodo & Kayama, 1992; Jonkman et al., 2003; Schmajuk et al., 2006).

Does positive mood change (pro –and reactive) cognitive control rather than inhibition?

Given that antisaccades require the activation of an additional set of brain areas compared to prosaccades and rely on different underlying brain mechanisms (McDowell et al., 2008), it could be assumed that correct performance on this task requires a clear distinction between these two saccade types at some point prior to target onset (i.e., during the preparation period between cue and target), besides reactive control processes operating at the level of the N2 and P3. Moreover, post-target onset inhibitory effects are likely to be influenced by the amount of preparation occurring prior to it. For these reasons, we also explored in our study changes in the preparatory activity prior to target onset as a function of saccade type and mood.

This preparatory activity is thought to reflect frontal-lobe dependent cognitive processes, such as working memory (Klein, Rockstroh, Cohen, & Berg, 1996), motor preparation and anticipatory attention (Brunia, Hackley, van Boxtel, Kotani, & Ohgami, 2011; Brunia & van Boxtel, 2001). Within the antisaccade paradigm, this activity is thought to reflect, at least in part, inhibitory processes (Ansari & Derakshan, 2011). In accordance with this assumption, the preparatory (CNV-like) activity in our study was enhanced in anti –compared to prosaccades in the neutral mood group, while both saccade types elicited equally strong preparatory activity in the positive mood group. Such lack of differentiation preceding targets has previously been observed in groups thought to have deficient prefrontal control functions, including high trait anxious individuals (Ansari & Derakshan, 2011) and schizophrenics (Klein et al., 2000). However, while the absence of differentiation between the two saccade types in these patient groups was explained by a deficient or abnormal preparatory activity for antisaccades (Ansari & Derakshan, 2011; Klein et al., 2000), in our study, by contrast, we found that this preparatory activity (consistent with the CNV) was increased for prosaccades in the positive, compared to the neutral mood group. Hence, we found that positive mood

influenced proactive control processes during this antisaccade task, prior to target onset (Braver, 2012).

Accordingly, it is tempting to hypothesize that positive mood changes cognitive control processes, rather than inhibition per se, which might eventually explain why the two groups did not differ from each other at the behavioral level. In this scenario, positive mood would influence cognitive resource allocation during the antisaccade task, instead of simply lowering inhibition. Consistent with this interpretation, we found that positive mood seems to influence the CNV (proactive control) and the N2 (reactive component) in opposite ways. Because the differentiation between the two saccade types was less clearly expressed during the preparation phase in the positive mood group (CNV), this differentiation was sharpened later, at the level of the N2. By comparison, in the neutral mood group, a stronger proactive effect was evidenced at the level of the CNV, while reactive inhibition was less expressed (N2). Consistent with such trade-off between pro –and reactive control mechanisms (Braver, 2012), an additional correlation analysis (when collapsing the ERP data across the two groups) showed a trend-significant positive association between the CNV component on the one hand and the N2 component on the other hand, of similar magnitude for prosaccades ($r = 0.37$; $p = .05$) and antisaccades ($r = 0.32$, $p = .088$). In a previous ERP study using a continuous performance task, positive mood influenced reactive control selectively (indexed by the N2 following targets), but not proactive control (reflected by the P3 and the CNV following cues; van Wouwe, Band, & Ridderinkhof, 2011). Our new ERP results add to these earlier findings by showing for the first time that positive mood can also exert modulatory influences on proactive control mechanisms.

An enhanced reactive control might be associated with higher cognitive flexibility, in line with previous findings showing that participants become more flexible after the induction of positive mood (Dreisbach, 2006; Dreisbach & Goschke, 2004; van Wouwe et al., 2011). In these earlier studies, the results were interpreted as reflecting neuromodulatory changes in DA activation after the induction of positive mood, modulating phasic DA increases either in the PFC (Dreisbach & Goschke, 2004) or the striatum (van Wouwe et al., 2011). Similarly, the ERP results of our study, showing a modulation of the CNV and the N2 concurrently, might be explained by changes in DA activation in these brain structures, in line with the tenets of an older neuro-anatomical

model accounting for effects of positive affect on prefrontal-based cognition (Ashby et al., 1999). However, additional pharmacological and neurophysiological studies are needed to corroborate the existence of a link between these amplitude variations at the level of these scalp ERP components (CNV and N2) as a function of positive mood, and intracerebral neuromodulatory effects influencing these dopaminergic-dependent neural pathways.

Conclusions

The results of this study show that positive mood does not simply lower inhibition, as measured using a standard antisaccade task. Instead, it is associated with subtle changes in the way pro –and reactive control mechanisms dynamically come into play during the preparation and execution of saccadic eye movements. Relative to neutral mood, positive mood blurs the differentiation between pro –and antisaccades during the preparation phase (CNV), prior to target onset. Following target onset, it sharpens inhibitory control at the level of the N2 component, though without influencing the subsequent P3 component. Accordingly, positive mood appears to influence the way through which cognitive resources are timely made available during the task in order to resolve it, as opposed to merely impairing motor inhibition in a global manner. We speculate that these effects could arise due to changes in DA-dependent neural pathways, connecting midbrain structures to the prefrontal cortex. Because these neurophysiological effects depending on positive mood were evidenced in the absence of a clear change in the (inhibition of) behavior, future studies are needed to assess whether some of these effects might reflect an active compensatory process or not.

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We probably do not live one moment without being in some kind of mood. These affective states continuously influence our cognition and behavior, although little is known about the actual nature and direction of this interaction effect. The main goal of this dissertation was to delineate the influence of mild mood changes, and specifically positive mood, on visual perception as well as inhibitory control and creative thinking. To investigate these questions, we first validated a new mood induction procedure (MIP) based on guided imagery (**chapter 1**). Next, using this MIP, we induced either a positive or a neutral mood in healthy adult participants and compared the behavioral performance and/or psychophysiological responses in tasks measuring creative thinking (**chapter 1**), early perceptual visual processes and attention (**chapters 2-4**), or inhibitory control (**chapter 5**). In the first section of this General Discussion, we perform an in-depth assessment of the MIP used throughout the studies presented in this dissertation. While the induction of positive mood with our MIP showed clear increases in happiness and pleasantness based on subjective self-reports, we did not find a transfer to creative thinking skills assumed to benefit from positive mood, nor did we find changes at the psychophysiological level (either facial EMG or blink rate). In the second part, we discuss the results of our main line of research, focused on effects of positive mood on early visual perception and attention control processes. These studies showed that positive mood reliably modulates (early) visual perception and attention, at an early latency following stimulus onset and in a relatively 'automatic' way (**chapters 2-4**). In general, these results are in accordance with the broaden-and-build theory (Fredrickson, 2001, 2004), although the broadening effect resulting from the induction of positive mood appears to be bound to certain requisites and limitations, which we also outline in this section. In the third section, we discuss our new results suggesting that positive mood might influence inhibitory control (**chapter 5**). However, while positive mood influences different components of cognitive control during inhibition (**chapter 5**), it remains unclear whether these effects might explain or mediate effects of positive mood on (early) visual perception and attention (**chapters 2-4**). Finally, we outline several mechanisms that likely explain the influences of positive mood on attention and early visual perception. In this closing part, we emphasize that the dominant broaden-and-build theory, although valuable and useful to generate

predictions, cannot account for the variety of subtle changes in attention control brought about by the transient experience of positive mood in healthy adults.

1. GUIDED IMAGERY AS AN EFFICIENT MEANS TO INDUCE POSITIVE MOOD

In **chapter 1**, we assessed the efficiency of our MIP to selectively induce positive mood by means of subjective self-reports, as well as electromyographic and eye blinks recordings. In addition, we assessed the transferability of the induced mood to tasks measuring two dissociable aspects of creative processes, namely divergent vs. convergent thinking, which are classically shown to be influenced by positive mood (see Isen, 2000). However, we did not find evidence supporting effects of positive mood on either measure of creative thinking. These null-findings might be ascribed to the nature of the standard tasks used to assess either convergent or divergent thinking, namely the RAT (Chermahini, Hickendorff, & Hommel, 2012) and the AUT (Guilford, 1967), respectively. These tasks likely encompass many mental processes (see Baas, De Dreu, & Nijstad, 2011; De Dreu, Baas, & Nijstad, 2008; Forster & Dannenberg, 2010; Hennessey & Amabile, 2010) that can each be influenced by mood in different ways and to different extents. Hence, these tasks might be insufficiently sensitive to capture influences of mood on creative thinking as such. Altogether, our results add to an increasing number of studies showing inconsistent effects of positive affect on creative processes (see Baas, De Dreu, & Nijstad, 2008; Hennessey & Amabile, 2010), suggesting that the link between positive mood and creative thinking is not transparent. While an increased creative capacity following the induction of positive mood or affect lies at the foundation of the broaden-and-build theory (Fredrickson, 2001, 2004), here we did not find evidence for this conjecture for reasons that are not entirely clear yet (**chapter 1**).

1.1. Psychophysiological correlates of positive mood

Besides assessing the transfer of positive mood on creative thinking, we also recorded psychophysiological data concurrently to gauge the propensity of our MIP to influence well-known markers of affect processing. For this purpose, we measured facial electromyography (focusing on the corrugator supercilii involved in frowning the eyebrows and the zygomaticus major involved in smiling) as well as the spontaneous

eye blink rate. However, we did not find systematic amplitude variations in these psychophysiological measures as a function of positive mood.

The eye blink rate was measured to estimate endogenous brain levels of dopamine (DA; Chermahini & Hommel, 2012; van Bochove, Van der Haegen, Notebaert, & Verguts, 2013) given the presumed role of this neurotransmitter in positive affect (Ashby, Isen, & Turken, 1999; Helie, Paul, & Ashby, 2012). Hence, we hypothesized that an increase in positive mood would give rise to an increased blink rate. However, our data did not confirm this prediction, and several reasons might potentially account for this null-finding. First of all, there is no direct evidence for the link between the eye blink rate and DA in transient positive affect (see Chermahini & Hommel, 2010). More specifically, the relation between brain DA and blink rate is mostly based on research focused on individuals with certain DA polymorphisms (Dreisbach, et al., 2005; Müller, et al., 2007) or patient populations with a dysfunctional DA system (Colzato, van den Wildenberg, & Hommel, 2008; Deuschl & Goddemeier, 1998; Freed, 1980). Hence, to use the spontaneous blink rate as a measure to quantify the presumed increase in DA accompanying positive mood requires additional empirical validation. Moreover, one study specifically aimed at evaluating eye blink rate as a correlate of DA activity did not find a modulation of this measure after the administration of DA antagonist or agonist drugs (Van der Post, De Waal, De Kam, Cohen, & van Gerven, 2004). In addition, the link between DA and positive mood remains elusive (Dreisbach, 2006; Young & Leyton, 2002; Liggins, Pihl, Benkelfat, & Leyton, 2012).

Concerning the facial electromyographic activity, several methodological issues might explain the absence of a systematic modulation of the corrugator supercilii and the zygomaticus major by mood, even though we note that it remains difficult to interpret null findings. First, the electromyographic recording took place after and not during the mood induction, when the task was already initiated, as opposed to rest. Hence, it is possible that these conditions were not optimal to capture enhanced activity for the zygomaticus major and/or decreased activity for the corrugator supercilii. Second, the absence of changes in facial muscle activity by mood might be related to the nature of the MIP based on guided imagery. Facial muscles are thought to show specific activations associated with specific emotions, in accordance with changes in the underlying motivational systems (Ekman, Sorenson, & Friesen, 1969; Susskind, et

al., 2008). However, compared to receiving a bar of chocolate or other gifts (i.e. the use of reward as MIP), remembering, sharing and mentally reliving a positive experience might engage higher order cognitive functions that preclude a simple expression of the mood change in terms of facial EMG. Hence, it is conceivable, although speculative, that we did not find systematic mood effects on facial muscle activations because our MIP was not associated with a strong motivational drive. Third, emotions carry a strong communicative value (Darwin, 1872), as reflected in the automatic (Dimberg, Thunberg, & Grunedal, 2002) mimicking or mirroring of emotional expressions of others (Achaibou, Pourtois, Schwartz, & Vuilleumier, 2008), starting at a very young age (Field, Woodson, Greenberg, & Cohen, 1983; Reissland, 1988). Moods, on the other hand, might rather inform a person about the own inner state (Morris, 1992) and thus be less strongly associated with prototypical facial expressions compared to emotions. Moreover, given the task setup we used, with the participant facing the computer screen and the researcher sitting behind him/her in a dimly lit room (hence, not being able to see each other's faces), the occurrence of facial muscle activity with positive mood might not have arisen because the communicative value was virtually nonexistent, in line with research showing weaker mimicry effects when someone is alone compared to social situations (Chapman, 1974). A final point concerns the nature of the stimulations that classically elicit facial EMG activities. Most studies finding a clear activation of facial muscles in relation to affect use static (Dimberg & Thunberg, 2007; Larsen, Norris, & Cacioppo, 2003) or dynamic (Achaibou, et al., 2008) emotional facial expressions, scenes (Cacioppo, Petty, Losch, & Kim, 1986; Lang, Greenwald, Bradley, & Hamm, 1993), words (Larsen, et al., 2003) or sounds (Bradley & Lang, 2000; Larsen, et al., 2003). By contrast, with respect to facial muscle activation to the induction of positive affective *states*, little is actually known. Moreover, previous research mostly investigated negative rather than positive affect. In addition, activation of the corrugator supercilii to negative stimuli is generally stronger than the activation of the zygomaticus major to pleasant stimuli (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Cacioppo, et al., 1986; Lang, et al., 1993; Larsen, et al., 2003), while the latter activity reflects positive affect and was the main focus of our EMG recordings in **chapter 1**. Altogether, it appears plausible that a lack of systematic changes in facial EMG following the induction of positive mood may be imputed either to

methodological factors, or the fact that positive mood does not trigger clear facial EMG effects, unlike emotions for example.

1.2. Subjective ratings of happiness

The subjective mood reports we used throughout the empirical chapters, including Visual Analogue Scales (VAS) for feelings of happiness, pleasantness and sadness, the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988) and the Self-Assessment Manikin (SAM; Bradley & Lang, 1994) or VAS for arousal consistently showed that the elected MIP was successful to induce and maintain positive affect (compared to an active control, neutral condition). Across the five chapters of this dissertation, the VASs for feelings of happiness and pleasantness showed increased scores in the positive compared to the neutral mood group after the MIP. On the contrary, the VAS for feelings of sadness never showed any change over time in either group, suggesting that our MIP led to a valence-specific effect.

Although less clear than the VASs, the scores on the PA of the PANAS also showed a systematic change after the MIP, while the NA was overall not influenced by the MIP. For the PA scores, this interaction was mostly due to a decreased level of positive affect in the neutral mood group, rather than a genuine increase in positive affect following the MIP in the positive mood group. Hence, the change in mood following the MIP was expressed differently for the VASs and the PANAS. This might be explained by differential sensitivities of these two instruments to capture changes in positive affect (Rossi & Pourtois, 2011). While the VASs encompass various positive affective states regardless of their origin and nature, the PA scales seem to grasp a more specific kind of positive affect, characterized by positive emotions high in activation and alertness (Crawford & Henry, 2004; Russell & Carroll, 1999; Watson, Clark, & Tellegen, 1988; Watson, Wiese, Vaidya, & Tellegen, 1999). Hence, based on the PA scores, it appears that the positive MIP somehow shielded participants from fatigue or boredom possibly arising during task performance compared to the neutral MIP.

After the induction of positive mood, self-reported levels of arousal generally increased compared to the baseline and the neutral mood group, although we did not encourage participants to select arousing memories for the MIP. These results show that besides positive affect, arousal was also enhanced in the positive compared to the

neutral mood group across the different studies. Usually, concurrent changes in motivation may indirectly explain variations in both valence and arousal, following a specific experimental manipulation, such as a MIP. For example, moods characterized by high levels of approach or avoidance motivation are usually also highly activating. This is probably the case for MIPs using gifts or funny videos (e.g., Isen & Daubman, 1984; Isen, Daubman, & Nowicki, 1987; Isen, Rosenzweig, & Young, 1991; Van Steenbergen, Band, & Hommel, 2009). By comparison, while in our MIP, based on the use of person-specific imagery and episodic memory, reward-related activity might initially be triggered alike, this is followed by a complex feeling involving positive valence, rather than arousal per se, given the lack of a clear motivational drive. Moreover, participants were never told that we actually aimed at inducing positive mood or that the maintenance of a certain mood state would be beneficial for the task or rewarded during or at the end of the experimental session. At any rate, the added value of our MIP was to limit the contribution of motivation as the key factor accounting for the changes in the positive, compared to the neutral mood group.

2. BROADENING OF ATTENTION WITH POSITIVE MOOD, AND ITS LIMITATIONS

The broaden hypothesis of the broaden-and-build theory, stating that the scope of attention expands in positive relative to neutral or negative affective states (Fredrickson, 2001), has received ample support over the years (e.g., Isen, 2000; Moriya & Nittono, 2011; Rowe, Hirsh, & Anderson, 2007). Our new ERP findings presented in **chapters 2-4** add to this existing literature, but also go beyond it by showing effects of positive mood both on bottom-up sensory processing guided by low level stimulus features (Egeth & Yantis, 1997; Wolfe & Horowitz, 2004) and top-down attention control factors sensible to the goals and the actual mind set (Buschman & Miller, 2007; Corbetta & Shulman, 2002; Marois & Ivanoff, 2005; Theeuwes, 2010), however under certain conditions.

To unravel these complex interaction effects between the current mood state of the participant on the one hand, and attention control processes activated at a given moment on the other hand, we developed a dual task setting enabling us to assess, primarily at the electrophysiological level, changes in bottom-up and top-down attention processes following the induction of positive mood. The task consisted of a

demanding oddball detection task at fixation, meant to lock voluntary attention and foveal vision at this location, and the presentation of stimuli in the upper visual field. Importantly, all visual stimuli used in this task were neutral (non-emotional). Hence, the extent to which these stimuli were processed was not attributable to their biological meaning, nor were they directly motivationally relevant or significant for the participants. Rather, changes in how these stimuli were processed were imputed to the current internal state of the participant, being either in a happy or neutral mood. Using this task, we studied early sensory processing of the peripheral stimuli as well as target processing at fixation, depending both on the specific mood of the participant and specific attentional manipulations, enabling us to delimit the possible boundaries of a broadening of attention following the induction of positive mood. In particular, throughout the three studies (**chapters 2-4**), we systematically manipulated the task-relevance and instructions for the peripheral stimuli, as well as the task load at fixation. Using visual ERPs, we could then track, using a millisecond time-resolution, changes in the electrical brain activity elicited by either the central or peripheral stimuli, and assess at which stage of processing positive mood exerted a reliable modulatory effect. We discuss the results of this series of studies in detail below. First, we outline and discuss the main findings concerning the putative broadening of attention by positive mood and hence we focus on the processing of peripheral visual stimuli. Next, we review the main results obtained regarding target-processing at fixation and how this top-down attention control process is shaped by positive mood too.

2.1. Positive mood effects on early sensory processing in V1

2.1.1. Competition between mood and attention control

Our results showed that positive mood can alter the earliest stage of stimulus processing taking place in V1 rapidly following stimulus onset (i.e., C1 component; Rauss, Schwartz, & Pourtois, 2011), although this modulatory effect seems to be tied to certain boundaries. More precisely, in **chapter 2**, we assessed influences of positive mood on bottom-up capture by task-irrelevant peripheral stimuli shown at different eccentricities in the upper visual field. In this study, we found that the position of the stimuli clearly altered the amplitude and the topography of the C1, in accordance with its retinotopic properties (Clark, Fan, & Hillyard, 1995). Remarkably, while in the neutral

mood group a clear reduction of the C1 with increasing eccentricity of the stimulus was observed, no such effect was seen in the positive mood group, where the C1 remained unchanged regardless of the eccentricity of the peripheral stimulus, as if spatial attention was spread over a larger portion of the upper visual field with this specific mood state (consistent with an early broadening of attention), relative to a neutral mood. In this study (**chapter 2**), the peripheral stimuli were fully task-irrelevant. Hence, we ran another study (**chapter 3**) to assess to which extent this early broadening as a function of positive mood was automatic. For this purpose, we adapted the paradigm by making the peripheral stimuli task-related to investigate if the broadening effect would occur regardless of the relevance of these stimuli. Under these specific conditions, the C1 varied again depending on the position of the stimulus in the upper visual field, as expected, and importantly, this early striate component was enhanced in the positive compared to the neutral mood group. We interpreted these ERP results for the C1 as reflecting a broadening of attention rapidly following stimulus onset, after the induction of positive mood. These findings suggested that positive mood may be associated with a 'diffuse mental (or attentional) state (or set)', characterized by a broader scope of attention over the attended portion of the visual field, instead of a focused or local mode of processing. Olivers and Nieuwenhuis (2006) previously hypothesized that positive affect can elicit such diffuse mental state, preventing 'over-processing' of information and as such reducing distractor interference. Our new ERP results are compatible with the assumption of a more uniform distribution of attentional resources in positive compared to neutral mood (**chapter 2**), and a beneficial effect of such distribution in terms of a stronger processing of task-relevant peripheral stimuli rapidly following stimulus onset (**chapter 3**; in contrast to Dhinakaran, et al., 2013). However, we did not find that such diffuse mental state, operating early on following stimulus onset at the level of the C1, was associated with a reduced distractor processing (Olivers & Nieuwenhuis, 2006), but rather, with an equal enhanced neural processing in V1 of all distractors regardless of their actual spatial location.

Crucially, we only observed these early broadening effects of positive mood on early sensory processing when attention resources were not depleted by a high load task. In **chapter 4**, we kept the peripheral stimuli task relevant, as in **chapter 3**, but we

also introduced two levels of perceptual load (low vs. high load) by varying the difficulty of the oddball detection task at fixation (primary task). This way, we could investigate if positive mood could still modulate early sensory processing of the peripheral stimuli at the level of the C1, despite the use of a high load task at fixation in half of the blocks. In these conditions (**chapter 4**), we no longer found a boost of the C1 component by positive mood. Surprisingly however at first sight, we did not find evidence for a broadening of attention at the level of the C1 when participants had a low load task at fixation either, unlike what we found in **chapter 3**. To account for this discrepancy, we reasoned that the specific mindset or attentional set adopted by the participants in **chapter 4** may have hindered an early broadening of attention with positive mood. Hence, the lack of modulation of the C1 component by positive mood under low load reported in **chapter 4** might be explained by a mechanism whereby central attention resources are somehow hijacked or monopolized to deal efficiently with changing task demands occurring with the primary task, eventually leaving very little or no room for an additional modulation of the early sensory processing of the peripheral stimuli by positive mood. More generally, the new results reported in **chapter 4** point to a hierarchy in different attention control processes, where modulatory effects of positive mood on early sensory processing appear to be subordinated or dependent upon other or higher attention control processes (e.g., perceptual load and top-down factors; analogously to reward, see Krebs, Boehler, Roberts, Song, & Woldorff, 2012). In this framework, the enhanced perceptual load therefore undoes the broadening of attention with positive mood. Accordingly, these new findings also suggest that the broadening of attention occurring rapidly following stimulus onset in V1, and following the induction of positive mood is not fully automatic, in the sense that it depends on the availability of central processing resources or capacities (see Marois & Ivanoff, 2005; Moors & De Houwer, 2006).

2.1.2. Early and selective effects of mood on early sensory processing in V1

Strikingly, we found that the effects of positive mood on early sensory processing of the attended (**chapter 2**) and unattended peripheral stimuli (**chapter 3**) selectively modulated the C1, but not the subsequent P1 or N1 components. In other words, positive mood boosted the early spatial encoding of the peripheral stimuli in the

primary visual cortex before classical top-down attention control mechanisms exerted their gating effects in the extrastriate visual cortex, regardless of positive mood. This component-specific effect of positive mood might be explained by the fact that we used a spatial localization task with the peripheral stimuli (**chapters 4-5**), even though the C1 has been shown to be resistant to attention or task manipulations (see Rauss, et al., 2011). Hence, it remains to establish whether other task demands requiring to process the content rather than the position of these peripheral stimuli might lead to amplitude modulations of ERP components subsequent to the C1, including the P1 or N1 thought to index visual detection or discrimination processes (see Moriya & Nittono, 2011).

More generally, our new ERP results (**chapters 2-4**) add to the increasing evidence in the literature showing that the C1 component, and thus the earliest sweep of activation in V1 following stimulus onset, can be modulated by higher-order cognitive or emotional factors, besides purely bottom-up stimulus properties (see Rauss, et al., 2011). However, as already mentioned in the **General Introduction** of this dissertation, despite converging evidence (Clark, et al., 1995; Jeffreys & Axford, 1972), a unique generator in V1 for the C1 is still a matter of debate in the literature (e.g. Ales, Yates, & Norcia, 2010). This discrepancy might in part be accounted for by the wide range of methodologies used to study the C1 (Rauss, et al., 2011), as well as the large inter-individual differences in the shape and size of V1 and the calcarine fissure (Amunts, Malikovic, Mohlberg, Schormann, & Zilles, 2000; Dougherty, et al., 2003). Recently, Ales et al. (2010) argued and demonstrated that the polarity reversal obtained for the C1 depending on the part (either lower or upper) of the visual field being stimulated was also consistent with generators in V2 and V3, besides V1. Hence, they challenged the use of this distinctive electrophysiological property to establish a V1 source for the C1. Moreover, given that V1 and V2/V3 are located close to each other, it is difficult to disentangle activity originating from these two regions using source localization techniques (Vanni, et al., 2004). However, Kelly and colleagues (Kelly, Vanegas, Schroeder, & Lalor, 2013) argued that while polarity reversals are indeed also expected for V2 and V3, they should be opposite to the polarities of the C1, such that stimulation of the upper visual field gives rise to a positive deflection (while it is negative for the C1) and vice versa for stimuli shown in the lower visual field. They concluded that the V1 contribution to the C1 prevails over the contributions of V2 and V3. Other authors

suggested that only the first phase of the C1 has ‘exclusive’ sources in the striate cortex, followed by a fast propagation of activity to other brain areas and a subsequent C1 phase to which other sources contribute, such as frontal and parietal areas providing feedback information into V1 (Foxe & Simpson, 2002). However, even if other cortical regions besides V1 also contribute to the C1, it is not challenged that the C1 is the earliest scalp VEP following stimulus onset, with a main generator in V1. Hence, our new ERP findings clearly show that positive mood can gate or change the earliest VEP elicited by a peripheral stimulus selectively, in a way resembling an early broadening effect of attention (see **chapters 2-3**).

2.1.3. Behavioral effects of positive mood on early visual processing: costs or benefits?

In addition to changing the earliest VEP following stimulus onset and its likely spatial encoding in V1, positive mood can also influence behavioral responding to these peripheral stimuli. In our studies (see **chapters 2-3**), we found both beneficial and detrimental effects of positive mood on the processing of the peripheral stimuli at the behavioral level. This discrepancy can be understood by scrutinizing the kind of task that was performed by the participants: while we found a (RT) advantage for positive compared to neutral mood when localizing a large peripheral texture in the upper visual field (**chapter 3**), we found that participants in the positive mood group performed significantly worse than in the neutral mood group when asked to discriminate fine-grained details of these peripheral textures (**chapter 2**). Interestingly, although maybe counterintuitive at first sight, *both* results are in line with a broadened attentional scope consecutive to the induction of positive mood. Given the existence of a trade-off between the size of the attentional focus and the resolution of visual processing (Castiello & Umiltà, 1990, 1992; Eriksen & Yeh, 1985; Ivry & Robertson, 1998; Müller, Bartelt, Donner, Villringer, & Brandt, 2003), a lowered capacity to discriminate small differences can be expected with a broader focus of attention. According to the biased competition account of attention (Desimone & Duncan, 1995), spatial selection of a part of the visual field implies no more competition between separate elements within that zone. In other words, separate elements within the selected part are no longer subject to mechanisms of enhancement or suppression of sensory processing (gain

control effects). Hence, the selection of a larger part of the visual field in positive vs. neutral mood renders it impossible to single out one element, necessary to precisely discriminate it. This might result in the processing of the stimulus as one texture instead of a pattern made up out of several smaller elements, explaining why a broad focus in positive mood was associated with an impaired identification of local details (see behavioral results in **chapter 2**). However, if the task requires to rapidly localize the entire texture in the upper visual field as a whole, then positive mood is associated with a behavioral gain compared to neutral mood, given the putative broader attention focus elicited in this specific mood state (see behavioral results in **chapter 3**). Accordingly, positive mood might lead to opposite behavioral effects, depending on the specific task demands.

2.1.4. Interim conclusions

Our ERP results are in accordance with a broadening of attention following the induction of positive mood, with an early electrophysiological effect. However, this broadening effect is not fully automatic. As our new ERP results clearly show, enhancing perceptual load at fixation undoes it, revealing clear boundaries in the way early visual perception is shaped by the current internal state of the participant (see **chapter 4**). Thus, positive mood does not ‘magically’ broaden attention, but rather, it competes for resource allocation with other ‘structural’ attention factors (e.g., task set), eventually revealing a hierarchical organization in attention control mechanisms, with mood likely occupying a lower position relative to top-down endogenous mechanisms. Moreover, this early broadening of attention can be accompanied by changes in task performance at the behavioral level, which is either improved or impaired relative to a neutral mood condition depending on the specific demands imposed by the task at hand.

2.2. Facilitated top-down post-perceptual processing in positive mood

The attention tasks we used in **chapters 2-4** resemble many everyday life situations, where attention is focused on a primary task while other stimuli that may or may not be important appear outside the focus of attention. Hence, an important question concerns the distribution of resources available over both target-related processes (primary task), and the processing of either attended or unattended peripheral stimuli

(secondary task) concurrently. When a single task was used at fixation (**chapter 2**), the C1 to peripheral stimuli was influenced by positive mood, while the P300 component to central target stimuli in the primary task was not (see also Moriya & Nittono, 2011; Rossi & Pourtois, 2012, 2014). Hence, this first study suggested that the early broadening of attention with positive mood occurred without any concurrent change of top-down attention control processes (primary task). However, when a dual task setting was used and hence the peripheral stimuli became task-relevant too (**chapters 3 and 4**), the amplitude of the target-related P300 component was augmented in the positive compared to the neutral mood group (see also Shackman, Maxwell, McMenemy, Greischar, & Davidson, 2011), and this effect was independent from load-related modulations (see **chapter 4**). These results suggested that positive mood was likely associated with an enhanced target processing during the primary task (see Polich, 2007), although the two mood groups showed comparable behavioral performance (see **chapters 2-4**). The discrepancy between the absence of a clear positive mood-related modulation of the P300 in **chapter 2** and a larger target-related P300 in the positive compared to the neutral mood group in **chapters 3-4** could potentially be explained by methodological differences between these studies. More precisely, because we used a counting task for the primary task in **chapter 2**, our offline ERP data analysis may have included some 'noisy' trials in the averages (i.e., missed targets or false alarms for the standard stimuli), thereby overshadowing possible group differences for the P300 component. However, in all studies (**chapters 2-4**), we note that the number of errors was relatively small and equal in both groups. Importantly, across all these studies, we could also demonstrate the lack of a systematic trade-off between the processing of these central vs. peripheral stimuli, suggesting that the broadening of attention with positive mood (C1; see **chapters 2-3**) could not be explained simply by changes in top-down attention control mechanisms (P300) with this specific mood state.

Alternatively, this dissociation for the P300 might reflect a more fundamental aspect related to the modulation of positive mood on target-related processing in the primary task. More precisely, our new ERP results suggest the existence of a double dissociation between the processes involved either in the primary task or the concurrent processing of peripheral stimuli: while positive mood appears to influence

the processing of peripheral stimuli (broadening of attention) when processing capacity is still available, it is only beneficial for target processing at fixation when this processing capacity is 'challenged'. Interestingly, we only found a clear modulation of target processing by positive mood when using a dual task setting, requiring participants to attend two locations in the visual field concurrently (i.e. foveal and peripheral vision), instead of focusing attention on one spatial location exclusively (Carrasco, 2011). More generally, these results therefore emphasize that positive mood can exert dissociable attention-related effects on the central and peripheral stimuli. While increasing task demands abolish the early broadening of attention by positive mood, it did facilitate or enhance target processing at fixation, despite the fact that processing resources are heavily taxed in this situation.

Noteworthy, our new ERP findings contradict the assumption of an increased distractibility in positive mood (see also **chapter 5**; with opposite results compared to Dreisbach, 2006; Dreisbach & Goschke, 2004). Here, we found an enhanced discrimination of targets from standard stimuli at fixation, with effects measurable at the level of the P300 component (see **chapters 3-4**). Accordingly, these data do not support the view of a deficient shielding of the primary task in a dual task context under positive mood (Zwosta, Hommel, Goschke, & Fischer, 2013). If anything, positive mood appears to protect the primary task from interference, in line with the assumption that emotion/mood may modulate perception with the aim to sharpen resource allocation (Zadra & Clore, 2011). Further, our P300 results even suggest that positive mood somehow led to a prioritization of the primary task at fixation: in case not all resources were depleted by a high load task, our results showed enhanced processing of both central and peripheral stimuli (see **chapter 3**). On the other hand, when processing resources were taxed by a high load task, effects of positive mood were still visible for the primary task (i.e. enhanced target processing at the level of the P300), but the broadening of attention disappeared (see **chapter 4**).

2.3. Does positive mood influence attention control via concurrent changes in arousal ?

Although our MIP was aimed at eliciting a mild positive mood colored by joy and happiness, it increased arousal as well. It is always difficult to tease the respective

contributions of valence and arousal apart in emotion research (Ashby, et al., 1999; Gable & Harmon-Jones, 2013). Given that previous ERP research linked amplitude changes of the P300 (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich & Kok, 1995) and to a lesser degree also the C1 to arousal (Stolarova, Keil, & Moratti, 2006), it may be that our new findings for this post-perceptual component (see **chapters 3-4**) were somehow inflated by a concurrent change in arousal in the positive mood group.

2.3.1. Arousal influences on the post-perceptual P300 component

Previous ERP studies showed that the P300 is associated with noradrenaline (NE) and the locus coeruleus (LC), and is sensitive to variations in arousal (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich, 2007), besides dopaminergic inputs (Pogarell, et al., 2011). More precisely, the P300 reflects both phasic and tonic activity of the LC-NE system (Howells, Stein, & Russell, 2012) and thus also arousal ‘indirectly’ (Polich, 2012). Whereas phasic arousal reflects a brief reaction to a specific stimulus or response, the induction of a positive mood would presumably elicit a tonic change in arousal. Effects of arousal on the P300 would reflect a greater availability of attentional resources and the engagement of working memory processes (Polich, 2012). However, NE might influence the P300 only indirectly, by modulating glutamate and cholinergic neurotransmitters (Frodl-Bauch, Bottlender, & Hegerl, 1999). Moreover, recent ERP studies found that (bodily) arousal (at the tonic level) was accompanied by a decreased P300 (Shackman, Maxwell, et al., 2011; Rossi & Pourtois, 2014), challenging the idea that amplitude-modulations of the P300 found in our studies would reflect arousal exclusively. Moreover, we did not find any significant correlation between changes in subjective levels of arousal following the MIP and the amplitude of the P300 to target stimuli in the primary task in our studies.

2.3.2. Arousal contributions to the broadening of attention at the level of the C1

Arousal might also have contributed partly to the broadening effects in early visual processing at the level of the C1 in our studies (**chapters 2 and 3**), although this seems unlikely. Previous studies demonstrated that arousal can influence visual processing areas via regions involved in top-down attentional control (Foucher, Otzenberger, & Gounot, 2004). Moreover, the arousal-related NE-LC system plays an important role in

attention and vigilance (Sara & Bouret, 2012). A previous ERP study showed that affective arousal was associated with an increased C1 amplitude, comparing conditioned threat-related (CS+) to neutral (CS-) stimuli (Stolarova, et al., 2006). However, an earlier fMRI study found interaction effects between arousal and attention in the thalamus, but other (task-related) cortical activations were mainly influenced by attention, and not by arousal, nor did arousal alone (without attention) influence attentional performance in this task (Portas, et al., 1998). Another MEG study found that the earliest striate activity (in V1) did not vary with arousal and/or attention (Poghosyan, Shibata, & Ioannides, 2005). In addition, other ERP studies using a very similar paradigm as used in **chapters 2-4** found that arousal and negative affect resulting from a psychosocial stressor led to a smaller C1 to peripheral stimuli than a neutral condition with lower arousal (Rossi & Pourtois, 2012, 2014). Hence, amplitude modulations of the C1 found in our ERP studies (see **chapters 2-3**) and in previous studies with mood manipulations cannot be explained easily by arousal alone. Moreover, at a conceptual level, it appears difficult to explain why arousal, given its tonic or increased vigilance effect, would enhance the C1 component selectively, while leaving the subsequent P1 and N1 unchanged.

2.4. Interim conclusions

Altogether, we found a facilitation of the early spatial encoding of peripheral stimuli with positive mood, either expressed as a broadening of the attentional focus (**chapter 2**) or an enhanced processing of peripheral attended stimuli uniformly across the upper visual field (**chapter 3**), showing the dynamic nature of modulatory effects of positive mood on early visual perception. Importantly, however, these effects are bound to certain conditions or restrictions (**chapter 4**), and thus they cannot be considered fully automatic.

While we focused on what effects positive mood could have on perception and attention in **chapters 2-4**, we did not investigate *how* these effects occur. A prevalent hypothesis concerning the mechanisms underlying these attentional effects is that positive mood influences sensory processing in V1 indirectly by influencing inhibitory control (Wang, et al., 2011). In this view, under positive mood, early sensory processing and attention gain control effects taking place in V1 are shaped ‘remotely’ by prefrontal

control mechanisms (see also Rossi & Pourtois, 2012), thanks to long-distance anatomical projections connecting these non-overlapping brain regions (Van Essen, Anderson, & Felleman, 1992). In **chapter 5**, we put the prediction that positive mood might influence inhibition, besides attention, to the test. In the next section, we review the behavioral and psychophysiological results obtained in this chapter that did not however confirm this prediction, but suggested instead subtle and indirect effects of positive mood on two complementing aspects of cognitive control.

3. NO DIRECT INFLUENCE OF POSITIVE MOOD ON (MOTOR) INHIBITION

In **chapter 5**, we assessed if positive mood was associated with a decreased inhibitory control that could possibly account for mood effects on spatial attention, as suggested by our ERP results (**chapters 2-3**) and independence evidence in the literature (Biss & Hasher, 2011; Biss, Hasher, & Thomas, 2010; Phillips, Bull, Adams, & Fraser, 2002; Rowe, et al., 2007). We hypothesized that through its presumed influences on DA activity (Ashby, et al., 1999; Dreisbach & Goschke, 2004), positive mood would affect inhibitory control, in line with research showing modulations of positive affect on higher-level cognitive functions (Braver & Cohen, 2000; Cohen, Braver, & Brown, 2002; Dreisbach & Fischer, 2012; Goldman-Rakic, Muly, & Williams, 2000; Müller, et al., 2007; Müller, et al., 2005; O'Reilly, 2006). However, our results did not show an interference effect of positive mood on inhibitory control, as tested with a standard antisaccade task (Hallett, 1978). More precisely, while we found the expected modulation of behavioral and electrophysiological measures by saccade type (i.e., lower accuracy and slower RTs as well as larger N2 and smaller P3 amplitudes for anti –compared to prosaccades), these processes were not affected by mood. However, these results did not imply that positive mood cannot influence inhibitory or other forms of cognitive control, but rather suggest that positive affect can have distinct effects on different aspects of control (Dreisbach & Goschke, 2004; Martin & Kerns, 2011). In line with this assumption, earlier research on depression showed effects of this mood only on one specific aspect of control, while no general impairment was observed (Saunders & Jentsch, 2013). For instance, it is conceivable that positive mood might influence the inhibition of task-irrelevant distractor processing, rather than response inhibition per se (Yuan, et al., 2011).

Supporting a more subtle and nuanced effect of positive mood on cognitive processes, we found mood-related changes at the electrophysiological level at two non-overlapping time points during the antisaccade task. First, during the preparation phase prior to target onset, the amplitude of the preparatory activity (CNV component) was clearly larger in anti –compared to prosaccade trials in the neutral mood group, in line with previous findings (Ansari & Derakshan, 2011; Klein, Heinks, Andresen, Berg, & Moritz, 2000). However, in the positive mood group, an equal, intermediate CNV activity was observed for these two trial types, implying that positive mood interfered with the normal preparation for an anti –compared to a prosaccade. Other studies already reported such lack of differentiation during the preparation phase prior to target onset in high anxious individuals (Ansari, Derakshan, & Richards, 2008) and schizophrenia (Klein, Rockstroh, Cohen, & Berg, 1996). However, unlike our results, these previous studies reported a decreased activity in anticipation of different targets eventually causing an undifferentiated (CNV) activity, in line with other studies focusing on the effects of negative mood and depression on preparatory activity (Ashton, et al., 1988; West, Choi, & Travers, 2010). By contrast, in our study, the CNV component was not dampened in antisaccade trials, but of similar amplitude in both saccade types, as if an increased preparatory activity was also present when the trial did not require strong control (i.e., prosaccade). Furthermore, our data showed that this lack of differentiation between the two trial types during the preparation phase was compensated at a later time point: following target onset, the global topography of the N2 component showed a sharper differentiation between anti –and prosaccades in the positive compared to the neutral mood group. Given that both activities (CNV and N2) have been linked to inhibitory control in the antisaccade paradigm (see Ansari & Derakshan, 2011; Müller, Swainson, & Jackson, 2009), these results suggested that the locus of control likely shifted to a later point in time in the positive compared to the neutral mood group.

We referred to the framework of proactive and reactive control to interpret these results, with the first reflecting the maintenance of goal-relevant information in prefrontal cortex (PFC) to *prevent* interference, and the latter engaging a wide network of (non-overlapping) frontal areas to reactivate goals and *solve* interference (Braver, 2012; De Pisapia & Braver, 2006). The dual mechanism of control proposes that successful conflict resolution depends on the interplay between pro –and reactive

control, which can be biased by various factors, including mood (Braver, 2012). Our results suggested that the normal proactive control was disturbed in the positive mood group, in line with previous research showing that positive affect low in arousal diminished reliance on informative cues preceding targets (Fröber & Dreisbach, 2012) and the coasting hypothesis predicting that positive affect prompts people to ‘take it easy’ (Carver, 2003). However, our results showed that this altered early control was compensated with a stronger reactive control. Hence, positive mood might influence the distribution of pro –and reactive control processes, tipping the balance to reactive control and possibly impairing proactive control. Unlike our results, Fröber and Dreisbach (2012) did not report changes in reactive control. One reason for this discrepancy might be the use of behavioral measures only in this latter study, as opposed to the use of both behavioral and EEG measurements in our study (**chapter 5**). Previous research showed that neurophysiological measures may be more sensitive to capture variations in cognitive control as a function of affect, while the concurrent behavioral measures might remain blind to them (Chiu & Deldin, 2007; Vanderhasselt & De Raedt, 2009; West, et al., 2010).

Interestingly, the two kinds of cognitive control are thought to rely on DA activity to different degrees, with a role for phasic DA in the maintenance of selected information in PFC enabling proactive control (Braver & Cohen, 2000), while the implication of DA in reactive control remains uncertain (see van Wouwe, Band, & Ridderinkhof, 2011). However, the link between DA and positive mood is not clearly understood and several recent studies pointed out that positive affect and reward, which are both related to DA activity, may have different effects on cognitive control (see Chiew & Braver, 2011, 2014; Dreisbach & Fischer, 2012; Fröber & Dreisbach, 2014). A recent study showed that both positive affect and performance-non-contingent reward reduced proactive control, as our new data also suggest, while performance-contingent reward stimulated a shift toward increased proactive control (Fröber & Dreisbach, 2014). Together, these and our results suggest that while cognitive control and reward can have similar effects on cognitive control, they cannot be reduced to one another. However, an important limitation of these recent studies is their reliance on positively valenced pictures to induce positive affect, given that other MIPs (including guided imagery) may produce other effects on cognitive control (Chiew & Braver, 2011).

For example, the modulatory effects of positive affect on cognitive control found in these recent studies might actually reflect enhanced attentional capture or other processes linked to the visual processing of external emotional information, rather than a real change in the current mood state of the participant. To conclude, our new results (see also **chapter 1** on creative thinking) did not confirm the hypothesis that positive mood merely impaired inhibition, eventually resulting in poorer performance in the antisaccade task, relative to a neutral mood condition. However, we did find evidence for a modulatory role of positive mood on cognitive control during this task, as shown by a lowered proactive but increased reactive control.

4. NO EVIDENCE FOR GENERAL BROADENING OF ATTENTION IN POSITIVE MOOD

Taken together, our new findings do not support the view of a general broadening effect of positive mood on attention, as entailed by the broaden-and-build theory (Fredrickson, 2001, 2004). Rather, they show that positive mood can influence attention and early visual perception in a context-specific way. Across the different empirical chapters, we found evidence for a change in the way resources available for task performance are (re)distributed during the experience of positive mood, as opposed to clear-cut gains or impairments at the behavioral level for example. Our studies on attention and early visual perception (see section 2) clearly delineated boundaries for an early broadening of attention with positive mood. For example, increasing task load at fixation strongly reduced this broadening effect (**chapter 4**), which speaks against a general effect of positive mood on attention and cognition. Furthermore, target-related processing (and presumably top-down endogenous attention) was facilitated in dual task settings under positive mood (see **chapters 3-4**), although the broaden-and-build theory did not make clear predictions on the fate of stimuli that are actually attended. Moreover, the lack of a beneficial effect of positive mood on creative thinking (**chapter 1**), does not support the ‘broadened cognition’ assumed to arise from positive mood. In addition, our findings showing that positive mood did not impair inhibitory control as such (**chapter 5**) are difficult to reconcile with a mere broadening of attention and cognition resulting from the experience of positive affect (Fredrickson, 2001), given that decreased inhibition is sometimes taken as evidence for a less selective and thus broader attention mode (Rowe, et al., 2007). Together, our new results uncover effects

of positive mood on attention and cognition that appear more subtle and complex than initially proposed in the broaden-and-build theory.

While the broaden-and-build theory has been very influential and valuable, it also appears too general to explain the richness of phenomena resulting from the complex interplay between (positive) mood and attention/cognition, a situation which might have led to several discrepancies in the field. Using various tasks, many other studies have already reported results that are difficult to integrate with the broaden hypothesis, for both positive and negative moods. First of all, using interference tasks and the global-local paradigm, studies have reported no effects (Bruyneel, et al., 2013; Finucane, Whiteman, & Power, 2010) or narrowing effects (Gable & Harmon-Jones, 2008a) of positive mood on attention. Second, studies reporting indications of a broadened attention found that this effect was dependent on the specific stimulus content, showing a broadening of attention towards rewarding, positive stimuli only (Tamir & Robinson, 2007) or self-related information (Grol, Koster, Bruyneel, & De Raedt, 2013), rather than a general broadening effect per se. Third, the same tasks used to investigate the narrowing hypothesis of negative mood did often not yield the expected results, when tested for sadness (Gable & Harmon-Jones, 2010b; Rowe, et al., 2007) and fear (Susskind, et al., 2008; Weymar, Keil, & Hamm, 2013). Some researchers even showed a broadened attentional focus with negative affect (von Hecker & Meiser, 2005; Weymar, et al., 2013), in line with arousal-biased competition models predicting enhanced information processing whether stimuli fall in the fovea or at a peripheral location (Mather & Sutherland, 2011). Fourth, using similar tasks, others have found a greater predictability of the dynamic changes of the attentional focus based on approach or avoidance motivational states, rather than valence (Friedman & Forster, 2005; Gable & Harmon-Jones, 2008b, 2010a, 2010c). Furthermore, we and others have found differential and even opposite effects of affect on the electrophysiological time course of early visual information processing (Rossi & Pourtois, 2012; Shackman, Maxwell, et al., 2011; Vanlessen, Rossi, De Raedt, & Pourtois, 2013, 2014), as opposed to a general influence.

Noteworthy, findings contradicting the tenets of the broaden-and-build theory are also found for so-called higher level cognitive functions, showing broad cognitive sets in negative mood (Martin Deseilles, Chang, Piguet, Bertschy, & Dayer, 2012),

narrow cognition in positive mood (George & Zhou, 2002; Kaufmann & Vosburg, 1997) or no effect of mood states at all (see Baas, et al., 2008). Moreover, while the broaden-and-build theory implicitly assumes that positive mood has overall beneficial effects on attention (Fredrickson, 2001; Fredrickson & Branigan, 2005), several studies actually reported drawbacks of positive mood, such as a higher distractibility (Biss & Hasher, 2011; Biss, et al., 2010; Dreisbach, 2006; Dreisbach & Goschke, 2004). Hence, while positive mood can dynamically influence attention and cognitive control to some extent, the modulatory effects are more complex than a general ‘broadening’ of these mental processes, and therefore, these influences should be deemed context-sensitive. In the next section, we aim at pinpointing several aspects or core components that may tentatively better explain the scope of influences exerted by positive mood on attention and early visual perception, than assuming an unspecific broadening effect.

5. TOWARDS ALTERNATIVE MECHANISMS FOR INFLUENCES OF POSITIVE MOOD ON ATTENTION AND EARLY VISUAL PERCEPTION

In comparison with negative emotions and affective states, few models have been proposed to explain how positive affect influences perception and what the underlying mechanisms are. Moreover, existing emotion or affect models are mostly based on the processing of emotional *information* (e.g., Brosch, Pourtois, Sander, & Vuilleumier, 2011; Markovic, Anderson, & Todd, 2014; Mohanty & Sussman, 2013; Pessoa & Adolphs, 2010; 2013), rather than the affective *state* of the perceiver. However, as argued by others before, it appears important to distinguish between these two realms (Kaspar & König, 2012).

A previous model did already propose some mechanisms accounting for a wide range of cognitive changes associated with positive mood. This model put forward that positive mood is closely related to reward, and that variations in DA activity might mediate effects of positive mood on cognition, given the role of this neurotransmitter in reward processing (Ashby, et al., 1999). However, DA is not uniquely related to reward (Salamone, Correa, Mingote, & Weber, 2005), but can also alter the firing rates of neurons to communicate the saliency of an object or event for example (Berridge, 2007; Ungless, 2004; Winton-Brown, Fusar-Poli, Ungless, & Howes, 2014). In addition, phasic and tonic changes in DA are known to elicit different influences on different aspects of

cognitive functioning (e.g., Braver & Cohen, 2000). Moreover, it is difficult to conceive how all cognitive changes associated with positive mood may depend on the activity of DA alone (Dreisbach, 2006), as was already noticed by Ashby and colleagues (1999) themselves. The effects of positive affect on cognition are also likely supported by other neurotransmitter systems besides DA, such as NE (Dreisbach, 2006), with phasic increases in LC activity linked to selective attention (and/or arousal), and tonic increases in flexibility (Aston-Jones & Cohen, 2005; Aston-Jones, Rajkowski, & Cohen, 1999). In addition, serotonin (Young & Leyton, 2002) and other neurotransmitters (see Liggins, et al., 2012) are thought to be implicated in positive affect as well. Hence, although the neuropsychological theory of positive affect (Ashby et al., 1999) has been useful to stimulate research on effects of positive mood on cognition, the putative link between DA and positive affect is probably too simplistic and this model does not allow to generate specific predictions regarding the nature and extent of positive mood influences on attention and cognition. Moreover, empirical evidence supporting this model is rather scant, and more recent studies testing the implication of DA in positive mood actually suggested that this specific neurotransmitter might not play an important role in positive affect (Liggins, et al., 2012), in line with the proposition that the experience of positive affect might be associated with liking (relying on several neurotransmitters, such as opioids), without wanting (relying on DA primarily), or a co-activation of both systems (Kringelbach & Berridge, 2009). Hence, a gap in the literature exists when it comes to models enabling clear predictions for positive mood effects on attention, and the possible underlying (cognitive and/or neural) mechanisms.

Ideally, such model should incorporate a wide range of variables able to account for various phenomena, including a broadening of attention with positive mood. Affective influences on visual perception are complex and probably associated with multiple underlying mechanisms (Zadra & Clore, 2011). Hence, given that we only tested a small range of attentional processes in this dissertation and that this project was not aimed at assessing the possible underlying brain mechanisms extensively, it is obviously impossible for us to provide an alternative model able to capture this complexity. Instead, we outline here below several hypotheses about how positive mood might change visual information processing at multiple levels via changes in specific attention control processes. We start out by discussing the actual position of

positive mood in the dominant attention framework classically delimited by top-down vs. bottom-up processes, followed by the broad distinction between internal vs. external attention. Next, we offer an alternative account and list specific neuropsychological mechanisms through which positive mood could dynamically influence perception and attention, integrating knowledge from these classical frameworks in attention research.

5.1. Positive mood as a third and separate source of influence on attention, besides top-down and bottom-up factors?

Attention selection is governed by both external stimuli (bottom-up) and internal processes (top-down; Corbetta & Shulman, 2002; Desimone & Duncan, 1995). Previously, it has been shown that the bottom-up attentional capture by specific stimuli can be modulated by top-down processes as well as (negative) affective factors (Pessoa & Adolphs, 2010; Pessoa & Engelmann, 2010; Pourtois, et al., 2013; Rossi & Pourtois, 2012, 2014). Mechanisms explaining affective influences on attention in terms of top-down and bottom-up control usually propose that affect depends on either mechanism, or rather constitutes a separate pathway influencing attention (Pourtois, et al., 2013).

Top-down mechanisms for affective influences on perception have been put forward by accounts of arousal-biased (Mather & Sutherland, 2011) and affect-biased competition (Todd, Cunningham, Anderson, & Thompson, 2012). In these frameworks, (affective) arousal guides the allocation of attention in a top-down manner, based on an 'affective control setting', the individual's history of what is motivationally relevant at a given moment in time (Todd, Cunningham, et al., 2012). In this model, affective saliency can tune the visual system based on the predisposition of the person to prioritize certain information via 'top-down templates' (Todd, Cunningham, et al., 2012) or 'top-down salience maps' (Mohanty & Sussman, 2013). Moods can also be conceptualized as driving attention in a top-down manner because it comes from within the perceiver (Kaspar & König, 2012), biasing attention towards important information in the environment (Mather & Sutherland, 2011).

However, these theories are based on the processing of emotional stimuli (Markovic, et al., 2014; Mather & Sutherland, 2011; Todd, Cunningham, et al., 2012) and predict that such top-down modulation of affective arousal accentuate the

dissociation between relevant vs. irrelevant stimuli in terms of processing, or in other words, potentiate the enhancement of attended and the suppression of unattended stimuli (Phelps, Ling, & Carrasco, 2006). On the other hand, our new results did not show an amplification of ‘normal’ attentional processing in positive mood, which also encompasses the suppression of irrelevant information (Hillyard & Anillo-Vento, 1998; Hillyard, Vogel, & Luck, 1998). Rather, a positive internal state seemed to enhance the processing of all stimuli, regardless of their relevance or low-level features. For instance, in **chapter 2**, we showed a clear C1 for unattended stimuli, regardless of their position, in positive but not neutral mood, and in **chapter 3** we showed an enhanced C1 to all peripheral stimuli, also the ones presented at task-irrelevant positions. Moreover, in this scenario, we would also expect reliable influences of positive mood on the classical electrophysiological correlates of selective attention, namely the P1 and N1 components. However, this is not what we found (see **chapters 2-4**).

Our results suggest that positive mood does not only modulate bottom-up capture of attention in some kind of top-down way, but can also modulate these top-down processes themselves, in line with previous research (Rossi & Pourtois, 2012, 2014). More precisely, our data resonate more with a separate system allowing for influence of both bottom-up and top-down attention modulation concurrently (Brosch, et al., 2011; Pourtois, et al., 2013), at least partly dissociable from these two processes and their respective neural substrates (Markovic, et al., 2014), in line with a distinct pathway of ‘emotional attention’ (Vuilleumier, 2005). The induction of positive mood seems to influence bottom-up and top-down pathways concurrently, or one of them only, depending on the specific task demands. For instance, the C1 to unattended peripheral distractors was more strongly expressed, reflecting enhanced bottom-up capture of attention by these stimuli in positive compared to neutral mood (**chapter 2**). The C1 was also enhanced in the positive mood group when these stimuli were task-relevant and to be attended (**chapter 3**). In addition, post-perceptual processing in the primary task (reflected by the P300) was also enhanced in the positive compared to the neutral mood group (**chapters 3 and 4**). These two results reflect influences of positive mood on top-down attention processes. However, based on our results presented in **chapter 4**, showing that mood effects were overruled by load, it appears that not all factors have an equal contribution to the modulation of attention. Rather, in conditions

of increased task-difficulty, positive mood effects are cancelled out by the likely prioritization of attention resources to resolve the task, unlike the processing of emotional stimuli that can elicit prioritized processing even when resources are limited (Anderson, 2005). In other words, positive mood did not exert any modulatory effect on peripheral stimulus processing when attention control mechanisms were actively recruited to efficiently deal with a high perceptual load task heavily taxing (central) processing resources (i.e., in **chapter 4**; Linnell & Caparos, 2011, 2013). Hence, task demands (and/or processing resources) appear to be an important parameter to take into account for a better understanding of interaction effects between positive mood and attention.

More generally, the involvement of cognitive control seems to define to what extent different task-related processes and information processing are eventually influenced by positive mood. When only a low or moderate involvement of cognitive control is necessary, ‘bottom-up’ processes are modulated by positive mood, while top-down processes might be influenced or not. On the other hand, when cognitive control processes are actively engaged by a demanding (high load) task (Linnell & Caparos, 2011, 2013), the facilitatory effect for target processing at fixation with positive mood ‘survives’, while the broadening of attention by positive mood in the (upper) peripheral field is no longer visible (**chapter 4**). Together, both bottom-up and top-down processes can be influenced by positive mood, however under certain conditions defined by the need to exert ‘acute’ or intense cognitive control.

5.2. From the inside out: does positive mood enhance external attention?

We showed that positive mood can enhance processing both at fixation (P300) and in the upper visual field (C1). Strikingly, the enhancement of one process by positive mood is not compensated by a drop or impairment of the other. In other words, based on our results, it looks like positive mood is somehow able to generate *more* resources compared to neutral mood, as opposed to creating tradeoff effects. However, this account goes against the well-established notion of a ‘restricted amount’ of resources (capacity limits), probably suggesting the involvement of mechanisms beyond the classical attentional top-down or bottom-up processes in positive mood. Hence, given that we and others have argued that our results can hardly be explained by an increase

in arousal only, the mobilization of these extra resources must come from ‘somewhere else’. Perhaps, positive affect can prompt people to use attention resources differently, rather than merely mobilizing more resources (Todd, Talmi, Schmitz, Susskind, & Anderson, 2012).

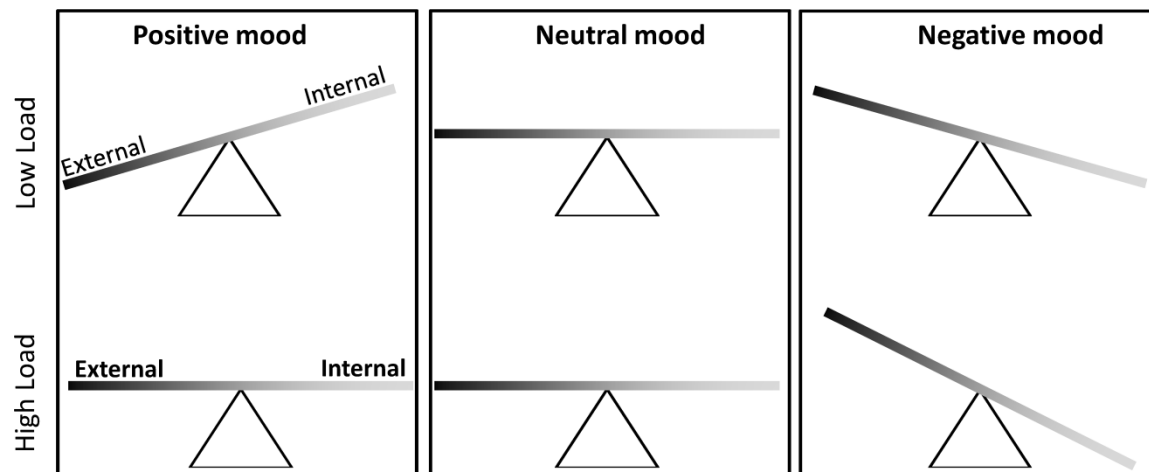


Figure 1. *Positive mood (left panel) might tip the balance in favor of external rather than internal attention, in the case of low load/ task difficulty (upper row; see also Chun et al., 2011). On the other hand, when a high load/ task difficulty is imposed (lower row), positive mood does not influence this scale. In neutral mood (middle panel), available resources are presumably equally distributed to internal and external attention, while attention might be oriented more towards inward than outward information in negative mood (right panel), associated with thinking styles characterized by worry and rumination.*

At the broadest level, our new results are compatible with a change in the balance between external and internal attention (Chun, Golomb, & Turk-Browne, 2011), possibly in favor of the former (see Fig. 1). More precisely, it is possible that positive mood stimulates a mobilization of resources towards external attentional processing, instead of internal attention. Such mechanism is in line with the initial cognitive and behavioral adaptive effects associated with positive mood, as proposed in the broaden-and-build theory: to broaden attention in order to learn from the environment and to foster its exploration (Fredrickson, 2001, 2004). On the other hand, negative affective states are associated with processes reflecting a focus on internal information rather than the external environment, such as enhanced interoception (Paulus & Stein, 2010; Vanden Bogaerde, Derom, & De Raedt, 2011) and rumination (Nolen-Hoeksema, 2000; Whitmer & Gotlib, 2012). Along the same lines, it has been shown that depressive

moods can be alleviated by distracting information (Joormann, Siemer, & Gotlib, 2007; Van Dillen & Koole, 2007) or decentered thinking elicited by mindfulness practice (Teasdale, et al., 2002), or in other words, by tipping the balance towards external instead of internal information.

5.3. Broaden-and-build theory revised

Above we described how positive mood could exert influence on early visual perception and attention departing from the classical dichotomy between bottom-up and top-down attention control mechanisms (or external vs. internal attention). However, our goal is also to try to move beyond this taxonomy, and integrate this with the main premises of the broaden-and-build theory, such as to generate more specific and testable predictions regarding the way positive mood shapes and transforms selective attention. In the original broaden-and-build theory, a general broadening of attention was proposed, while the possible limitations of this effect and underlying mechanisms remained largely underspecified (Fredrickson, 2001, 2004). Although our data are in line with such broadening, they reveal a less general effect of positive mood on attention.

We would argue that the name of the broaden-and-build theory is somewhat misleading, given that a broadening of attention can only occur in very specific situations, namely when a substantial part of the visual field is not attended. Our results show that positive mood can also influence the processing of stimuli that fall into the focus of attention, and therefore are by definition not subject to a broadening of attention. Rather, we would argue that positive mood creates opportunities to encounter interesting information, either by broadening the attentional focus when the focus is limited or narrow, or by processing attended stimuli to a larger extent when the attentional focus is already stretched over a larger part of the visual field. Hence, positive mood seems to sensitize the visual system for information, or enhances the propensity of the visual system to use an attentive mode of exploration. Remarkably, we found these effects of positive mood in the absence of any emotional or rewarding stimulus shown in the environment (see **chapters 2-4**), confirming that these effects were not bound to uncontrolled changes in motivation, but rather to an alteration of the internal state of the participant dynamically changing the guidance of attention in his/her proximal visual environment.

5.3.1. *The role of cognitive control in broadened attention by positive mood*

In this alternative model, cognitive control is thought to play a pivotal role in the dynamic interplay between positive mood on the one hand and perception and attention on the other (see section 2.4.). Positive mood might influence cognitive control functions in such a way that the latter plays the role of a 'switch'. More precisely, when task load/difficulty is low, positive mood can broaden attention and allow for the processing of additional information, in line with a loose cognitive control, while cognitive control is not influenced when task load/difficulty increases and the perceived intensity of the mood is diminished (see **chapter 4**). Our data suggest that positive mood enhances both bottom-up and top-down attention effects when the task is easy, while in a difficult task context, only top-down processes are 'gated' by this affective state. This is compatible with the dual-control model of selective attention (Caparos & Linnell, 2010), proposing that both bottom-up ('perceptual control') and top-down processes ('cognitive control') influence selective attention, while post-perceptual selection is only modulated by the latter. Translated to our results, this means that the increased C1 amplitudes in positive mood (broadening of attention) might stem from both enhanced bottom-up and top-down processes, while changes in target processing by positive mood at the level of the P300 component are confined to top-down attention modulations. Hence, this model helps understanding the differential mood effects on the C1 and the P300 components respectively: when task demands are low, both processes are somehow facilitated by positive mood, allowing mood effects on the C1 and the P300 concurrently (see Fig. 2). On the other hand, when task demands are high and processing resources temporarily depleted to some extent, positive mood might only influence top-down processes, resulting in an increased P300 for central targets, but not change the C1 to peripheral stimuli and hence no broadening of attention (see Fig. 2). One could speculate that certain negative affective states, such as anxiety, might influence these processes in the exact opposite direction compared to positive mood, even though this idea requires direct empirical validation. For instance, it has recently been shown that (perceptual) load and (state) anxiety influence attention in a seemingly comparable way, by narrowing attention in both cases (Rossi & Pourtois, 2012, 2014).

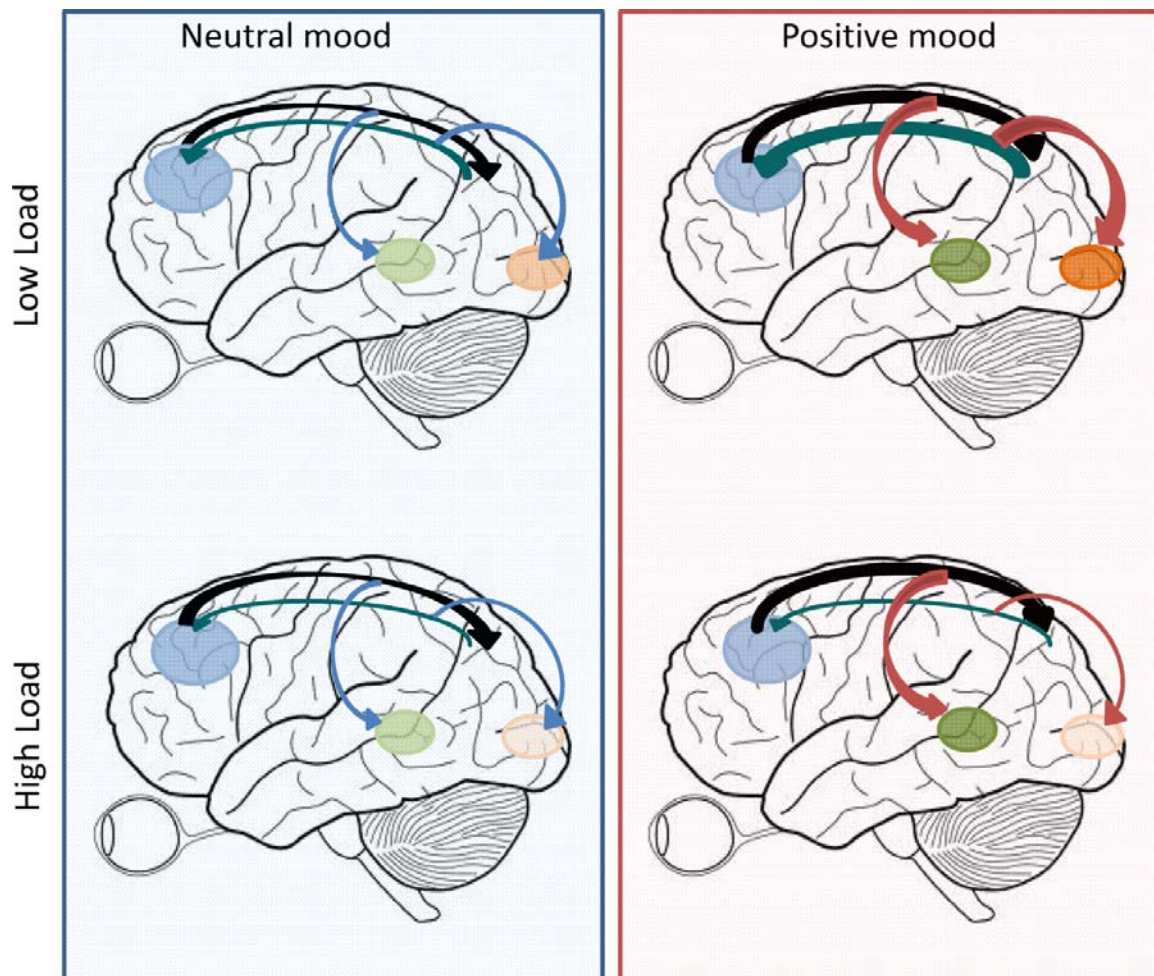


Figure 2. Schematic presentation of synergistic effects of mood and load on top-down (black arrow) and bottom-up (green arrow) attention control brain mechanisms for neutral (blue frame) and positive (red frame) mood. Positive mood enhances both bottom-up and top-down attention effects when the task is easy (low load), resulting in a stronger activation in V1 (C1 component) to peripheral stimuli (orange circle) and larger decision-related P300 component for central targets (green circle). In a difficult task context, only these latter top-down attention processes are presumably boosted by positive mood. Possibly, the dorsal ACC (blue circle) coordinates these mood-related changes acting on these non-overlapping bottom-up (broadening of attention in V1) and top-down (enhanced post-perceptual target processing) attention networks.

Together, we propose that cognitive control sets priorities and ‘monitors’ whether positive mood can impinge on attention (such as to foster a broadening effect) or not. One way cognitive control could exert this function, is by reorienting resources towards internal information (see Chun, et al., 2011) when task load is high, counteracting thereby the tendency to orient towards external information and broaden attention in positive mood, as we speculated in section 5.2. On the other hand,

allocating the flow of resources to external information in positive mood is not obstructed when task load is low to moderate.

5.3.2. *Possible neuro-anatomical underpinnings*

Our results suggest that positive mood might make specific neural systems or networks more receptive for external information and induces openness and interest towards the outside world, in line with the broaden and-build-theory (Fredrickson, 2001, 2004). However, the underlying mechanisms accounting for such influences are still poorly understood. As discussed above (section 5.1.), our data show that both bottom-up and top-down processes can be enhanced by positive mood, depending on the specific task context. Distributed and non-overlapping fronto-parietal networks underlie bottom-up and top-down attention processes (Buschman & Miller, 2007; Corbetta & Shulman, 2002). Additionally, prefrontal regions are involved in cognitive control (Miller & Buschman, 2013; Miller & Cohen, 2001). On the other hand, positive mood is thought to depend upon the integrity of numerous brain structures and wide-spread neural networks. Kringelbach and Berridge (2010) proposed that pleasure, as a precursor of positive mood, is represented at two levels in the brain. At a subcortical level, the nucleus accumbens, ventral pallidum and the brainstem have been pinpointed as possible ‘hedonic hotspots’. At the cortical level, these authors listed the orbitofrontal, cingulate, medial prefrontal and insular cortices as candidate areas. Thus, several limbic structures are proposed to be involved in positive mood, and earlier research already showed reciprocal projections between these areas and the visual cortex, including the primary visual cortex (Amaral, Behniea, & Kelly, 2003), possibly accounting for affective influences on early sensory processing and biased competition for stimulus selection (Anderson, Siegel, & Barrett, 2011; Pessoa & Adolphs, 2010; Pourtois, et al., 2013).

Based on these independent lines of research, we propose that positive affect may influence the fronto-parietal networks involved in top-down and bottom-up attention processes via modulations of prefrontal cognitive control regions, possibly via DA or other neurotransmitter systems, which are released ‘endogenously’ upon the induction of positive mood. Continuing the metaphor of cognitive control as a switch, positive mood might prompt cognitive control to ‘open the valve’, making visual cortices more receptive to bottom-up sensory processing when the task load is low to

moderate. This would in turn lead to a broadening of attention (C1), as well as increased target processing at fixation (P300). On the other hand, when task difficulty is high, it is possible that these long-distance projections to the visual cortex may be partly inhibited or suppressed, especially those responsible for the early bottom-up gating in V1, while leaving top-down attention processes unaffected.

A candidate brain area involved in these dynamic interaction effects between positive mood, cognitive control and attention is the anterior cingulate cortex (ACC; see Shackman, Salomons, et al., 2011). The ACC is known to play an important role in both affective (rostral ACC) and cognitive (dorsal and posterior ACC) processes. Interestingly, the rostral part of the ACC has, among others, connections with the nucleus accumbens and the orbitofrontal cortex, two of the 'hedonic hotspots' identified by Kringelbach and Berridge (2010), as well as with the amygdala, involved in affective processes (Anderson, et al., 2011; Pessoa & Adolphs, 2010; Pourtois, et al., 2013) and the modulation, remotely, of the primary visual cortex (Amaral, et al., 2003). This part of the ACC also plays a role in assessing emotional information and emotion regulation (see Bush, Luu, & Posner, 2000). The 'cognitive' part of the ACC on the other hand is involved in executive attention (Posner, 1990) and allocation of (attention) control (Banich, et al., 2000). Moreover, this part is thought to modulate sensory and response selection and to monitor competition (see Bush, et al., 2000). Additionally, the ACC is also involved in the anticipation of challenging tasks and the evaluation of task performance, and hence in an ideal position to monitor if sufficient resources are allocated to perform the task at hand. Moreover, the cognitive part of the ACC is thought to detect conflicts or worse than expected events, signaling the need for enhanced cognitive control (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter, Botvinick, & Cohen, 1999). Additional cortical areas (lateral prefrontal cortex) are then engaged to resolve this conflict by means of higher attention control and the enhancement of task-related, as well as the suppression of distracting information.

5.4. Functional meaning of positive mood effects on perception and attention

At the perceptual level, the proposed influences of positive mood on top-down/bottom-up and internal/external attention could be translated as a biased threshold. In this framework, perception is conceptualized as a decision, and perceiving

or not perceiving as responses (Lynn, Zhang, & Barrett, 2012). Hence, positive mood seems to bias the system in favor of responding, as opposed to depressive affective states for example. An interesting framework for understanding the influence of mood on perception was proposed by Nettle and Bateson (2012), who argued that moods can be conceptualized as ‘detectors’, aimed at assisting the organism in defining the threshold for detection. The optimal threshold depends on a trade-off between the probability to encounter a certain event and the relative costs of responding. Positive moods might signal that the environment is safe, implying little costs for false alarms and an optimistic set about the occurrence of a wanted event, thereby lowering the threshold for detecting information. An anxious mood, on the other hand, is also characterized by a low detection threshold, because a false negative is more costly than a false positive and the occurrence of negative events is deemed likely. Indeed, our results showed enhanced C1 to stimuli in positive mood, while a similar early ‘hypervigilance’ was found in an anxious affective state (Weymar, et al., 2013). However, our data suggest a plausible distinction between the sensitivity to capture information between the two moods. While in positive mood, this stronger early processing of peripheral stimuli was not accompanied by a cost for a concurrent task, it is conceivable that such trade-off would be found for negative moods (Rossi & Pourtois, 2012; Vanden Bogaerde, et al., 2011). As argued above, this could be explained by a stronger representation of the external environment compared to internal information in positive mood, if we assume that this specific mood state biases attentional resources allocation between external and internal attention (Chun, et al., 2011).

5.4.1. Can positive mood influence perception by influencing perceived saliency?

Generally, the framework put forward by Nettle and Bateson (2012) implies that the saliency of stimuli is altered by mood. Both bottom-up and top-down attention control mechanisms can be boosted by saliency, which also plays a crucial role in capturing attention during exposure to emotional stimuli (Markovic, et al., 2014; Mather & Sutherland, 2011; Todd, Cunningham, et al., 2012). The concept of ‘core affect’ offers an explanation for the influence of inner affective states on the saliency of stimuli, suggesting that affect is fundamentally bound to perception and attention (Barrett & Bliss-Moreau, 2009; Duncan & Barrett, 2007). Research showed that the emotional

saliency of a stimulus ‘fuses’ with the subjective experience of the perceiver, making a certain stimulus salient to that person (Todd, Talmi, et al., 2012). Hence, it is possible that, in positive mood, neutral information is treated the same way as emotional information, because the inner state of the perceiver ‘spills over’ to the environment and ‘contaminates’ the stimuli, making them salient. For instance, it has been shown that positive affect can increase the subjective vividness of stimuli, even if they are neutral, similarly to the experience of a stronger vividness of emotional stimuli, paired with a higher activation of the visual cortex (Todd, Talmi, et al., 2012). Speculatively, positive mood might enhance baseline activation of the visual cortex, diminishing the extent to which stimuli have to elicit cortical activation in order to surpass the threshold for being processed by the visual system.

5.4.2. The rewarding nature of perception

The adaptive function of positive emotions might help to understand specific perceptual changes with positive mood (Stefanucci, Gagnon, & Lessard, 2011; Shiota, et al., 2014). The notion that perceptual learning and curiosity are inherently pleasant for humans, and therefore stimulating people to look for information (Biederman & Vessel, 2006; Perlovsky, Bonniot-Cabanac, & Cabanac, 2010) can further elucidate the effects of positive mood on attention. When people are in a safe environment, they might engage in this so-called ‘infore’ behavior (Biederman & Vessel, 2006), that based on our results may be characterized by a higher readiness to perceive stimuli. Hence, detecting information and acquiring knowledge is inherently rewarding and thus congruent with positive mood. Interestingly, this behavior only occurs when no other motivations prevail (Biederman & Vessel, 2006), in line with our ERP findings showing that high task load cancelled the broadening effect created by positive mood in the peripheral visual field. The increased task difficulty might have induced stress in participants (Baeken, et al., 2014), or have diminished the rewarding value of otherwise pleasant events (Ivanov, et al., 2012). Together, sensory processing ‘may “gate” hedonic or reward based responses’ to stimuli, while positive mood states might alter perception and in turn influence this gating (Fitzgerald, 2013). Hence, positive mood might facilitate this gating by enhancing perceptual processing.

Our results further suggest that when task load is low or moderate, the inhibitory or filtering aspect of attention (i.e., the bottleneck) occurs later in time (**chapters 2-3**), in line with our finding that positive mood might enhance reactive rather than proactive control (**chapter 5**). As mentioned in section 5.3.2., given that positive mood specifically altered the C1 but not later VEPs (P1 or N1), this emphasis on reactive control might explain an initially increased processing of peripheral stimuli, while control mechanisms kick in only after the C1, 'normalizing' filtering at the level of the P1 and beyond. One question that remains unanswered by our studies is if this normalization would also take place if the stimuli would not be neutral, but rather of (biological) relevance for the individual. It is possible that the initial broadening we observed under mild to moderate task load serves as an exploring mechanism, scanning the environment for possible interesting information, keeping in mind the hypothesis that perceiving new information and learning is intrinsically rewarding and pleasant for people (Biederman & Vessel, 2006). Such process supports the affect-as-input hypothesis and the broaden-and-build theory in the sense that if positive mood broadens attention initially and a positive stimulus would be encountered, the person would be rewarded for her/his positive mood and might continue this behavior (Clore, Schwarz, & Conway, 1994). In line with this idea are findings showing that positive mood broadens attention towards rewarding information (Tamir & Robinson, 2007) and that happy faces become dominant in a binocular rivalry task when participants experience a positive mood (Anderson, et al., 2011). On the other hand, it is also possible that in positive mood, the person is more open to the external environment because of an alertness towards negative signals, prompting the individual to search for information of the opposite valence in order to regulate his/her mood (Schwager & Rothermund, 2013a, 2013b), or allocating attention to other areas where more processing resources are needed because unexpected opportunities appeared (Carver, 2003). Hence, the broadening of attention might indeed serve adaptive goals, however in a less rigid way as proposed by the broaden hypothesis. Positive mood might prompt an initial broadening of attention to increase the probability to encounter information that is either rewarding or important for survival, enabling the system to decide if positive affect and a broad cognitive style are adaptive, or rather they should be extinguished.

6. CONCLUSIONS

6.1. Implications and recommendations

Several implications can be drawn from the studies presented in this dissertation, both at the research and clinical levels. As a first caveat, we would recommend to systematically take into account and measure the current mood of participants, also in research not aimed at assessing affective processes. In this dissertation, we have shown that positive mood, the most prevalent affective state of healthy adults (Diener & Diener, 1996), has an extensive and significant impact on attention and early visual processes involved in the processing of neutral and simple visual stimuli, as well as on higher order cognitive functions. We have shown that a mild positive mood, as naturally occurring in everyday life, can broaden attention and enhance the processing of both relevant and irrelevant information, as well as sharpen reactive control. Hence, it cannot just be assumed, as is however often the case in experimental designs in psychology or neuroscience, that participants are in a neutral affective state and effects of mood on attention and early visual perception do not exist (Kaspar & König, 2012). For instance, in the case of positive mood, attention might be biased towards external information, while the research question might focus on internal mental processes.

Second, we also showed that effects of positive mood on attention and early visual perception are not ubiquitous, but they critically depend on the actual operationalization of these mental processes and thus the specific tasks and experimental paradigms selected to explore them. Given the complexity of interaction effects between mood and cognition, it appears important to avoid tasks that actually reflect an amalgam of different cognitive functions, such as the AUT and the RAT (see **chapter 1**). With regard to attention specifically, we have shown that task load or difficulty can be either a requisite or a limitation for observing modulatory effects of positive mood on this cognitive process. More precisely, mood effects might remain invisible because the task is too easy to utilize mood to coordinate the redistribution of cognitive or attentional resources, or on the contrary, the task is too difficult and brain circuits other than those involved in mood take over and erase possible effects of mood. Hence, fine-tuning, manipulating and systematically comparing a restricted number of task factors (such as perceptual load) may provide a promising avenue for experimental research in affective neurosciences, as it contributes to a better

understanding of the *modus operandi* through which positive mood shapes attention and early visual perception. In addition, our results emphasize that the choice of the methods used to investigate subtle effects of positive mood on cognitive functions is essential. In particular, behavioral methods might often be blind to the variety and subtlety of changes in attention or early visual perception arising after the induction of positive mood. In this context, the use of scalp ERP methods gave us some critical insights into these complex interaction effects between the internal state of the participant and attention, that behavioral measures alone were unable to unravel.

Finally, at the clinical level, our new studies may be relevant for a better understanding of the specific anomalies during information processing typically observed in the most prevalent psychopathological condition in western countries, namely depression. Depression is characterized by anhedonia (Pizzagalli, 2014), which can be considered the exact opposite affective state of happiness and pleasantness. Complementing our data showing an early broadening of attention with positive mood, (early) visual perception is altered in depression, probably because of upstream impairments in attention control processes leading to a narrow mode of functioning and exploration of the environment (de Fockert & Cooper, 2013). Additionally, such narrowing in perception can also contribute to mood changes (Fitzgerald, 2013). Hence, it is conceivable that positive mood might protect people against depression because it can 'undo' its narrowing effects (Bar, 2009), creating more opportunities to gain sensory information, which has been shown to be inherently rewarding and pleasant (Biederman & Vessel, 2006; Perlovsky, et al., 2010). Hence, if positive mood motivates people to broaden their attention and gives rise to stronger perceptual processing, this might counteract the loss of interest associated with depression and enhance the opportunities to elicit pleasurable responses associated with sensory perception in healthy people. Hence, clinical interventions aimed at both inducing positive affect as well as a broader attentional scope might support recovery from depression (or prevent relapse), especially when (external) attention towards positive information is actively trained (Grafton, Ang, & MacLeod, 2012). At a theoretical level, these results raise the possibility that depression can be understood, at least partly, as a perceptual disorder, given that negative mood and depression can already influence early visual perception

as early as in V1 (Desseilles, et al., 2009), or even earlier (i.e., at the level of the retina; see Fitzgerald, 2013).

6.2. Limitations and future perspectives

Several limitations of the presented studies should be mentioned. First of all, we have concentrated on the effects of positive compared to neutral affective states. In particular, we investigated the effects of positive mood low in arousal on attention and specific cognitive functions (inhibition and creative thinking). However, natural emotional states unfolding in real life are often characterized by fluctuations in arousal too, while we only explored a positive affect with low levels of arousal. Accordingly, future studies are needed to disentangle effects of positive affect vs. arousal during state-dependent changes of attention and perception. Moreover, another important limitation of this research is that we never included negative effect, which would have allowed not only to contrast the effects of positive to negative valence, but also delineate the specific contribution of arousal to the observed findings. Along the same line, we acknowledge that we did not differentiate between different kinds of positive mood (e.g., the contrast between relief vs. euphoria), reflecting factors such as reward and motivational intensity in different extents and associated with specific responses. In our studies, we did not investigate how these different mood aspects might have influenced our findings. Hence, it appears important in future research to break down the construct of positive affect or mood (Griskevicius, Shiota, & Nowlis, 2010; Shiota, et al., 2014) and start looking into the diversity of positive affective states with the aim to better delineate to what extent they involve reward, motivation and arousal, and eventually define which of these factors are critically involved in the modulation of attention and perception by ‘mood’ reported in this dissertation.

A related limitation is that we did not find ‘objective’ correlates of the increases in positive mood reported by the participants after the induction of positive mood (hence defined by means of subjective reports mainly). Although we used a cover story to mitigate social desirability effects (Westermann, Spies, Stahl, & Hesse, 1996), we cannot formally exclude the possibility that some of the effects reported in our studies were related to this factor, at least partly. Hence, additional research is needed to develop and validate more objective measures (e.g., psychophysiology) able to capture

changes in the mood state of the participants, without relying on subjective reports and introspection exclusively.

Concerning the interpretation of our ERP results in terms of a broadening of attention under positive mood, it is important to note that we could only draw this conclusion indirectly. Although we reported several results that are in agreement with an attentional broadening in positive mood, none of our paradigms was suited to test the actual size and likely expansion of the focus of attention. Hence, we could only indirectly deduce a broadened attentional scope after the induction of positive mood. In order to test this hypothesis more formally and directly, psychophysics should be used in combination with EEG methods. Further, our tasks primarily focused on spatial attention, while many other forms of attention (e.g., temporal attention) could possibly be influenced by positive mood alike (see Olivers & Nieuwenhuis, 2006). Hence, including the study of temporal attention might eventually provide a better picture of how positive mood interacts and shapes attention and (early) vision.

Another limitation of our research is that only healthy adults selected from a student population participated in our studies. Early visual processing could also be altered in patients suffering from depression, or from impairments related to DA depletion, such as Parkinson's disease, in opposite ways compared to positive mood. In the future, several research lines could be interesting and valuable in this framework, such as validating the MIP for the induction of positive affect in these populations, the measurement of the 'default' attentional scope without any mood manipulation, as well as the causal relationship between the induction of a broad attentional scope and an increase in feelings of happiness, and vice versa.

6.3. General summary and conclusions

"The appearance of things change according to the emotions and thus we see magic and beauty in them, while the magic and beauty are really in ourselves (Kahlil Gibran). " This quote nicely captures how positive mood experienced by the perceiver can alter early perception and attention in a dynamic and versatile way. Moreover, it emphasizes that our internal states continuously and actively shape the way we see and perceive the outside or external world, often without us even noticing. The results reported in this dissertation show that positive mood can enhance visual perception dynamically

and at multiple levels, through changes in multiple attention control processes in the human brain. While this broadening effect is not fully automatic or devoid of restrictions, we found that it influences the earliest stage of visual information processing in V1, as well as post-perceptual endogenous attention processes. In other words, positive mood can boost both bottom-up and top-down attention processes. Tentatively, we put forward the idea that positive mood might bring about these modulatory effects on perception through biasing the attention system towards the exploration and processing of external, as opposed to internal, information. Crucially, we showed that these effects depend on the amount of resources available at a given moment. As a matter of fact, several theoretical frameworks, besides the dominant broaden-and-build theory, provide plausible accounts to explain our new empirical results, including the internal vs. external attention taxonomy (Chun, et al., 2011), the dissociation between bottom-up and top-down attention control mechanisms (Corbetta & Shulman, 2002), or the metaphor of detection thresholds in perception (Nettle & Bateson, 2012). However, none of them alone appears able to account for the diversity of effects of positive mood on cognition reported in this work, and earlier studies available in the literature. Accordingly, additional empirical and theoretical work is absolutely needed in order to better appraise what positive mood is exactly, and why/how it can influence perception and attention so profoundly and diversely. These efforts may also be valuable for a better understanding of specific break-downs in positive affect, such as anxiety or depression. Because our new empirical results suggest that positive mood dynamically shapes visual perception and attention such as to foster the exploration of the visual environment and eventually likely maximize the encounter of new opportunities, we believe that research on positive mood, which is still in its infancy, definitely deserves more attention. We hope that the present dissertation might help promote and develop further this interest and curiosity in the field.

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**Invloed van positieve emotie op aandachtsbreedte:
een experimentele benadering**

INLEIDING

Hoe je de wereld ziet heeft invloed op hoe je je voelt, en verschillende therapeutische technieken zoals cognitieve reappraisal en mindfulness oefeningen zijn hierop gebaseerd. Echter, je gemoed bepaalt ook actief hoe je de wereld ziet. In dit doctoraatsproject onderzochten we hoe een positieve gemoedstoestand invloed kan uitoefenen op de manier waarop mensen specifieke visuele informatie selecteren of juist onderdrukken, en hoe dit hun denkstijl kan beïnvloeden. Zulke fundamentele veranderingen in perceptie liggen mogelijk aan de basis van invloeden op algemeen cognitief functioneren en welzijn van positief gemoed. Inzicht verwerven in deze modulerende effecten van positief gemoed op cognitieve functies is belangrijk in het veld van affectieve neurowetenschappen, waar nog steeds een focus op negatief affect overheerst, alsook voor het verwerven van kennis over het behoud en verbetering van mentale gezondheid en de preventie van affectieve stoornissen. In wat volgt bespreken we eerst positief gemoed, hoe deze interne affectieve toestand selectieve aandacht en cognitie in het algemeen kan beïnvloeden, en ten slotte focussen we op verschillende aandachtsprocessen en hoe deze gemeten kunnen worden.

Gemoed kan onderscheiden worden van 'affect' en 'emotie', hoewel deze termen vaak gebruikt worden om hetzelfde aan te duiden. In navolging van Larsen (2000), gebruiken we de term 'affect' om te verwijzen naar het ervaren, evaluatieve gevoel van gemoed en emoties. Gemoed verwijst naar meer diffuse affectieve toestanden die lager in intensiteit zijn en langer duren dan emoties (Beedie, Terry, & Lane, 2005; Gross, 1998; R. J. Larsen, 2000; Russell, 2003). De affectieve inhoud van gemoed en emotie kan beschreven worden aan hand van de dimensies 'valentie' (van positief tot negatief) en 'arousal' (van slaperig tot zeer actief; Barrett, 1998; Russell, Weiss, & Mendelsohn, 1989). Een derde dimensie die vaak gebruikt wordt om gemoed/emotie te beschrijven is motivatie om bepaalde mensen, objecten of situaties te 'benaderen' of 'vermijden' (Cacioppo & Gardner, 1999; Lang & Bradley, 2010; Lang, Bradley, & Cuthbert, 1998). Emotionele en motivationele circuits zijn nauw met elkaar verbonden, onder meer doordat ze gedeeltelijk dezelfde onderliggende mechanismen zouden delen (Ashby, Isen, & Turken, 1999; Kringelbach & Berridge, 2010), waardoor het moeilijk is om een duidelijk onderscheid te maken tussen beloning ('reward') en positief affect. Dit zou vooral te wijten zijn aan de belangrijke rol die de neurotransmitter dopamine zou spelen in beide processen (Ashby, Isen, & Turken, 1999). De inductie van positief gemoed zorgt mogelijks voor vrijlating van dopamine in de middenhersenen, die

betrokken zijn bij beloning, waarna deze dopaminerge activiteit verder wordt verspreid naar prefrontale regio's en op die manier verschillende cognitieve functies kan beïnvloeden. Echter, positief gemoed is niet te herleiden tot enkel beloning, gezien het ook een bewuste subjectieve ervaring omvat (Barrett, Mesquita, Ochsner, & Gross, 2007; Kringelbach, 2005). Bovendien spelen ook andere neurotransmitters naast dopamine een rol in zowel positief affect en beloning (Berridge & Kringelbach, 2013; Berridge, Robinson, & Aldridge, 2009; Biederman & Vessel, 2006; Koeppe et al., 2009) en toonden neurobeeldvormingsstudies aan dat verschillende neurale systemen betrokken zijn bij de twee respectieve processen (Berridge, 1996; Berridge, Kringelbach, & Valentin, 2008; Berridge et al., 2009). Tenslotte verschillen de effecten van beloning en positief gemoed op cognitieve functies vaak (Chiew & Braver, 2011).

De meest invloedrijke theorie over de effecten van positief gemoed op cognitie is de 'broaden-and-build' theorie (Fredrickson, 2001, 2004). De 'broaden' hypothese van deze theorie stelt dat positieve emoties aanleiding geven tot een verbrede cognitie, door mentaal 'uit te zoeken' en aandacht te besteden aan de globaliteit van concepten, situaties en objecten. Op het niveau van aandacht, dat centraal staat in deze dissertatie, wordt 'verbreding' gedefinieerd als een aandachtsfocus die een groot deel van het visuele veld omvat, en de verwerking van globale eerder dan gedetailleerde aspecten van objecten (Basso, Schefft, Ris, & Dember, 1996; Moriya & Nittono, 2011; Rowe, Hirsh, & Anderson, 2007). In hogere-orde cognitieve taken, zoals denken en redeneren, kan een brede cognitieve stijl gedefinieerd worden als een flexibele en integratieve denkstijl, het gebruik van brede semantische categorieën en grotere creativiteit (zie Chermahini & Hommel, 2012; Dreisbach, 2006; Dreisbach & Goschke, 2004; Estrada, Isen, & Young, 1997; Isen & Daubman, 1984; Isen, Daubman, & Nowicki, 1987; Isen, Rosenzweig, & Young, 1991). Echter, de broaden-and-build theorie laat niet toe om specifieke hypothesen te maken over cognitief functioneren en gedrag, en de definitie van een 'brede cognitie' blijft vaag. Bovendien vonden vele studies geen ondersteuning voor een bredere aandacht en cognitie in positief gemoed (zie Bruyneel et al., 2013; Gable & Harmon-Jones, 2008; Huntsinger, Clore, & Bar-Anan, 2010; Kaufmann & Vosburg, 1997). In deze dissertatie focusten we op de invloed van een positieve gemoedstoestand laag in motivatie en arousal, geassocieerd met een verbrede aandachtsfocus. Om dit verder te onderzoeken, bespreken we eerst verschillende componenten van aandachtscontrole die beïnvloed kunnen worden door affect.

De hoeveelheid informatie waarmee we geconfronteerd worden is veel groter dan onze hersen kunnen verwerken, waardoor een selectie van informatie cruciaal is. Aandachtscontroleprocessen voeren deze rol uit door het selecteren van relevante informatie en het onderdrukken van de verwerking van irrelevante of afleidende informatie (Marois & Ivanoff, 2005). Vele metaforen zijn gebruikt geweest om selectieve aandacht te beschrijven, zoals de schijnwerper ('spotlight'; Broadbent, 1982), de zoomlens (Eriksen & St-James, 1986) en een gradiënt van aandacht (Mangun & Hillyard, 1988). Al deze modellen benadrukken het belang van spatiële aandacht, de selectie van en focus op een specifieke locatie in het visueel veld. Op neurofysiologisch niveau vertaalt selectieve aandacht zich in een versterkte verwerking van stimuli die in de focus vallen, vergeleken met stimuli die buiten de focus vallen en onderdrukt worden (Hillyard, Vogel, & Luck, 1998; Kastner & Ungerleider, 2000). Deze selectie kan zowel vroeg of laat in de stroom van informatieverwerking plaatsvinden, afhankelijk van de cognitieve en perceptuele last van de taak (Lavie, 1995, 2001, 2005). Het uitfilteren van irrelevante informatie kan dus plaatsvinden op alle niveaus van visuele cortex, vanaf de primaire visuele cortex (V1; Rauss, Schwartz, & Pourtois, 2011). Zowel externe stimuli (zoals een plotse lichtflits) als interne processen (zoals specifieke doelen) bepalen welke informatie geselecteerd wordt (Corbetta & Shulman, 2002; Desimone & Duncan, 1995). Het bewust richten van aandacht op een bepaalde taak die relevant is voor onze doelen wordt 'top-down' aandacht genoemd (zie Hopfinger, Buonocore, & Mangun, 2000; Müller, Geyer, Zehetleitner, & Krummenacher, 2009), en steunt op prefrontale processen (Miller & Cohen, 2001). Echter, je aandacht kan ook snel en 'automatisch' getrokken worden door nieuwe, bewegende of onverwachte stimuli, en dit type van aandachtsoriëntering wordt 'bottom-up' genoemd (zie Hickey, McDonald, & Theeuwes, 2006; Ranganath & Rainer, 2003; Wolfe & Horowitz, 2004). Deze twee processen interageren met elkaar op een dynamische manier, waardoor de selectie van informatie voor verdere verwerking het resultaat is van zowel bottom-up als top-down factoren (Connor, Egeth, & Yantis, 2004; Egeth & Yantis, 1997; Schneider, Beste, & Wascher, 2012). Deze aandachtscontroleprocessen vinden plaats in een fronto-pariëtaal netwerk dat sensorische verwerking in de visuele cortex regelt, met een ventraal netwerk betrokken in stimulus-gestuurde aandacht en een meer dorsaal netwerk voor doelgerichte selectie van sensorische informatie (Corbetta & Shulman, 2002). Op een breder niveau kan aandacht ook

worden ingedeeld in interne processen (zoals geheugen en plannen) en externe informatie (Chun, Golomb, & Turk-Browne, 2011).

Verschillende neurofysiologische correlaten kunnen gebruikt worden voor de studie van aandacht en perceptie. Een precies onderzoek van de temporele structuur van aandachthinvoeden op verschillende niveaus van visuele verwerking is mogelijk dankzij de hoge temporele resolutie van EEG (elektro-encefalogram). Nadat een stimulus verschijnt in het visuele veld worden verschillende opeenvolgende elektrische potentialen gegenereerd in de (visuele) cortex die het tijdsverloop van visuele informatieverwerking weergeven met een millisecondeprecisie, zogenaamde Event-Related Potentialen (ERP). Spatiële aandachtsmechanismen moduleren stimulusverwerking in de visuele cortex, waardoor verschillende visuele ERPs onderscheiden kunnen worden. Klassiek worden de P1 en N1 componenten beschouwd als de eerste visuele ERPs na stimulus-onset. De P1 is een positieve golf die piekt tussen 80 en 130 ms na stimulus-onset en wordt gegenereerd in de extrastriate visuele cortex (Clark, Fan, & Hillyard, 1995; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002; Gomez, Clark, Fan, Luck, & Hillyard, 1994). De N1 is een negatieve component die piekt tussen 120 en 180 ms en verschillende neurale bronnen heeft (Clark et al., 1995; Di Russo et al., 2002). Beide componenten zijn gevoelig voor selectieve aandacht: de P1 en N1 zijn groter voor stimuli waar aandacht aan gegeven wordt, vergeleken met genegeerde stimuli (Hillyard & Anllo-Vento, 1998; Luck, Woodman, & Vogel, 2000). Echter, recent heeft men ook aangetoond dat een nog vroegere component beïnvloed kan worden door top-down aandachtsmodulaties, namelijk de C1 component, hoewel lang gedacht werd dat de C1 enkel door bottom-up modulaties kon beïnvloed worden (see Ales, Yates, & Norcia, 2013 vs. Kelly, Vanegas, Schroeder, & Lalor, 2013 en Ding, Martinez, Qu, & Hillyard, 2013 vs. Rauss, Pourtois, Vuilleumier, & Schwartz, 2009). De C1 piekt tussen 60 and 100 ms na stimulus-onset en heeft een bron in V1 (Clark et al., 1995; Di Russo et al., 2002; Jeffreys & Axford, 1972; Rauss et al., 2011). Terwijl de P1 en N1 vooral op inhoud van de stimulus reageren, varieert de polariteit en de amplitude van de C1 met de positie van de stimulus in het visueel veld. Interessant is dat de C1 ook door affectieve processen beïnvloed kan worden (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Rossi & Pourtois, 2012, 2014; Stolarova, Keil, & Moratti, 2006; Weymar, Keil, & Hamm, 2013). Samengevat toonden deze studies aan dat de C1 niet enkel vroege aandachtsgerelateerde effecten in V1 reflecteert, maar ook beïnvloed kan worden door de motivationele betekenis van stimuli of de interne

gemoedstoestand van de observator. Deze bevindingen motiveerden deze dissertatie, waarin we ons focusten op mogelijke invloeden van positief gemoed op deze vroege visuele component.

Meer algemeen is dit doctoraatsproject geïnspireerd door de algemene stijgende interesse in de functies en mechanismen van positief gemoed sinds de publicatie van de broaden-and-build theorie (Fredrickson, 2001, 2004). De basisassumptie van deze theorie is dat een verbreding van aandacht aan de basis ligt van de effecten van positief gemoed op welzijn en gezondheid. Echter, ondersteuning voor een échte verbreding van aandacht door positief gemoed is beperkt in de bestaande literatuur en de huidige bevindingen blijven onduidelijk (Bruyneel et al., 2013; Huntsinger, 2013). Dus, het hoofddoel van deze dissertatie is het onderzoeken of positief gemoed aandacht kan verbreden.

BEKNOPT OVERZICHT VAN DE BELANGRIJKSTE BEVINDINGEN

In **hoofdstuk 1** onderzochten we de efficiëntie van een nieuw ontwikkelde methode om een positieve gemoedstoestand te induceren bij de deelnemers. Eén groep deelnemers onderging de positieve gemoedsinductieprocedure (GIP), en de andere groep de neutrale GIP. Deze GIP bestond uit het begeleid mentaal visualiseren van positieve (positieve gemoedsgroep) of neutrale (neutrale gemoedsgroep) herinneringen. Meer specifiek, deelnemers werden gevraagd om een herinnering te zoeken in het episodische geheugen en vervolgens zich zo levendig en zo precies mogelijk in te beelden deze gebeurtenis opnieuw te beleven (gebaseerd op Holmes, 2006; Holmes & Mathews, 2005). Ze werden geïnstrueerd de situatie in te beelden vanuit het eigen perspectief, en niet vanuit het perspectief van een observator, gezien dit de levendigheid en emotionele doorleving van de inbeelding versterkt. Met deze GIP wilden we een gemoed induceren in gezonde volwassen deelnemers dat gekarakteriseerd is door geluk met een laag motivationeel niveau, en onafhankelijk van de taak. Tijdens de GIP en de daaropvolgende taak werd muziek gespeeld zodat de muzik de deelnemer impliciet zou herinneren aan het opgeroepen gemoed.

Hoofdstuk 1 was dus gericht op het valideren van deze GIP in twee verschillende studies. In de eerste studie werd nagegaan of deze GIP effecten zou hebben op creatieve vaardigheden. Om dit te testen werd gebruikt gemaakt van twee taken die verschillende componenten van creativiteit meten: de Alternate Uses Test (AUT) voor divergent denken en de Remote Associates Test (RAT) voor convergent denken. Er werd ook onderzocht of de GIP

efficiënt was in het uitlokken van een positief gemoed. Dit werd nagegaan door het meten van psychofysiologische activiteit (activatie van gezichtsspieren, studie 1), het tempo van oogknipperen (studie 2) en het afnemen van vragenlijsten voor en na de GIP (studie 1 en 2). De zelf-gerapporteerde niveaus van positief affect werden voornamelijk gemeten door Visuele Analogie Schalen (VAS). VAS zijn horizontale lijnen van tien centimeter met labels aan beide uiteinden, zodat deelnemers intuïtief op de lijn kunnen aanduiden hoe ze zich voelen. De VAS droegen het label 'neutraal' aan het linker uiteinde en het label 'zo blij/aangenaam/verdrietig als je kan indenken' aan het andere uiteinde. Voor de psychofysiologische metingen werd de activatie van de *currogator supercillii* (de spier betrokken bij het fronsen van de wenkbrauwen) en de *majeure zygomaticus* (de spier betrokken bij het glimlachen) gemeten met elektroden op het voorhoofd en de wang aan de linkerzijde van het gezicht. Vorig onderzoek heeft aangetoond dat activatie van de *currogator supercillii* geassocieerd is met het verwerken van negatieve informatie en negatief affect, terwijl de activatie van de *majeure zygomaticus* betrokken is bij positieve informatie en positief affect (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Korb, Grandjean, & Scherer, 2010; J. T. Larsen, Norris, & Cacioppo, 2003). Oogknipperingen werden gemeten omdat vorig onderzoek een link aantoonde met dopamine, een neurotransmitter die mogelijks een belangrijke rol speelt in positief gemoed (Chermahini & Hommel, 2010, 2012). Onze resultaten toonden een duidelijke verbetering van het gemoed in de positieve gemoedsgroep na de GIP vergeleken met een baseline meting, terwijl het gemoed niet veranderde in de neutrale gemoedsgroep, aan de hand van zelf-rapportage. Echter, positief gemoed had geen effect op de gedragsresultaten op de AUT of de RAT. Dit is mogelijks te wijten aan de complexiteit van deze taken en de samenloop van verschillende processen die mogelijks op tegengestelde wijzen beïnvloed worden door positief gemoed. Het is mogelijk dat positief gemoed enkel specifieke componenten van creativiteit beïnvloedt, zoals associatief denken. We vonden ook geen effect van gemoed op de psychofysiologische metingen en het oogknippertempo. Dit is mogelijks te wijten aan de suboptimale experimentele setup voor deze metingen, hoewel dit onduidelijk blijft.

In **hoofdstuk 2-4** gingen we de effecten na van positief gemoed op aandacht en vroege perceptuele processen. Hiertoe ontwikkelden we een dubbele taak die bestond uit een oddball detectie taak op fixatie om de aandacht en de ogen van de deelnemers hier te vestigen, en de presentatie van texturen in het bovenste visuele veld. Op deze manier

konden we elektrofysiologische activiteit meten voor zowel de vroege sensorische verwerking van perifere stimuli als de verwerking van doelstimuli op fixatie, en nagaan of deze maten beïnvloed zouden worden door de specifieke gemoedstoestand van de deelnemer en specifieke aandachtsmanipulaties om de grenzen van aandachtsverbredende effecten van positief gemoed te exploreren. Alle stimuli waren neutraal, en dus veranderingen in de verwerking van deze stimuli zijn te wijten aan de invloed van de interne affectieve toestand van de deelnemer. Doorheen de studies beschreven in **hoofdstukken 2-4** hebben we de taakrelevantie en de instructies voor de perifere stimuli systematisch gemanipuleerd, alsook de taaklast op fixatie. Gebruikmakend van visuele ERPs konden de veranderingen in de elektrische hersenactiviteit nagaan met een millisecondeprecisie van de stimuli op fixatie en in de periferie, en onderzoeken welke fase van informatieverwerking door gemoed zou worden beïnvloed.

In **hoofdstuk 2** testten we de hypothese dat de inductie van positief gemoed aandachtsallocatie dynamisch kan beïnvloeden, met effecten op vroege stimulusverwerking in V1, gemeten aan de hand van de C1 component. Deelnemers ondergingen een (neutrale of positieve) gemoedsinductie en kregen vervolgens de taak bestaande uit de oddball detectie op fixatie en de presentatie van taak-irrelevante perifere stimuli. Deze stimuli konden dichtbij fixatie, op midden afstand of ver van fixatie worden aangeboden. De resultaten toonden dat de topografie van de vroegste visuele component na stimulus-onset (C1) sterk varieerde in functie van de positie van de perifere distractoren. Echter, dit effect was enkel zichtbaar voor deelnemers in een neutrale gemoedstoestand. In de positieve gemoedsgroep werd geen modulatie van deze vroege component waargenomen naargelang positie. Deze resultaten toonden aan dat ongeacht waar de stimulus in het perifere visuele veld verscheen, de stimuli even sterk verwerkt werden in de positieve gemoedsgroep. Latere componenten (P1 en N1) die klassiek als correlaten van selectieve aandacht worden beschouwd, werden niet beïnvloed door gemoed. Belangrijk, ook de P300 component voor stimuli in de oddball taak op fixatie verschilde niet tussen gemoedsgroepen, hoewel een duidelijk verschil te zien was tussen de component voor standaard –en doelstimuli. We voerden ook een controle gedragsexperiment uit, waarin we deelnemers vroegen om de inhoud van twee perifere texturen te onderscheiden. We vonden dat de juistheid van discriminatie daalde in de positieve vergeleken met de neutrale gemoedsgroep. Samen zijn deze resultaten in lijn met een verbreding van aandacht, waarbij de aandacht over een

breder deel van het visueel veld wordt verspreid en de spatiële resolutie daalt. Bovendien tonen deze resultaten aan dat de positie-specifieke codering van stimuli in de V1 getuned kan worden door gemoed, snel na stimulus-onset.

In **hoofdstuk 3** bouwden we verder op deze studie door dezelfde taak te gebruiken, met één aanpassing: de perifere stimuli werden nu taakrelevant en de deelnemers moesten aangeven wanneer een stimulus verscheen op de middelste van de drie (dichtbij, midden, ver) posities. Opnieuw werden deelnemers toegewezen aan de positieve of neutrale gemoedsgroep en werden ERPs opgenomen tijdens het uitvoeren van de taak. We vonden dat deelnemers in de positieve gemoedsgroep sneller waren in het lokaliseren van de perifere stimuli en dat de amplitude van de C1 groter was in vergelijking met de neutrale gemoedsgroep. Specifieker, positief gemoed versterkte de vroege spatiële codering van stimuli in V1. Samen met de resultaten van **hoofdstuk 2** suggereerden deze bevindingen dat het verbredende effect van positief gemoed op aandacht automatisch is, gezien de C1 beïnvloed werd door gemoed ongeacht van de taakrelevantie van de perifere stimuli en vóór het optreden van klassieke top-down effecten van aandachtscontrole op de volgende P1 component. Positief gemoed versterkte ook de post-perceptuele P300 voor doelstimuli op fixatie, terwijl de P300 voor standaardstimuli niet beïnvloed werd door gemoed. Deze resultaten suggereren dus dat positief gemoed de spatiële codering van perifere stimuli automatisch kan boosten vroeg na stimulus-onset.

We onderzochten deze verbredende effecten van positief gemoed op aandacht en visuele perceptie verder in **hoofdstuk 4**. In dit hoofdstuk onderzochten we de interactie van perceptuele last (op fixatie) en positief gemoed. Vroeger onderzoek toonde aan dat beide factoren selectieve aandacht en vroege visuele perceptie kunnen beïnvloeden, in tegengestelde richting (nl. vernauwing van aandacht door perceptuele last en verbreding door positief gemoed). Meer specifiek onderzochten we of deze factoren zouden competieren met elkaar voor de beïnvloeding van visuele aandacht wanneer deze gecombineerd worden in hetzelfde experimentele design. Deelnemers ondergingen een positieve of neutrale gemoedsinductie waarna ze de dubbele taak uitvoerden, terwijl EEG werd opgenomen. De dubbele taak van **hoofdstuk 3** werd aangepast zodat de lokalisatietaak van de perifere stimuli gelijk bleef, maar de taak op fixatie werd aangepast. Meer precies, de perceptuele last van deze taak werd aangepast door de moeilijkheid van de oddball detectie te veranderen, zodat deze ofwel hoog ofwel laag (zelfde niveau als in **hoofdstukken 2 en 3**)

was. De ERP resultaten toonden dat de C1 kleiner was in de conditie met een lage last op fixatie vergeleken met een hoge last. Echter, positief gemoed had geen enkele invloed op de uitdrukking van de C1. De P300 voor doelstimuli op fixatie was wel vergroot in de positieve vergeleken met de neutrale gemoedsgroep. Deze resultaten suggereerden dat de vernauwende effecten van taaklast de verbredende effecten van positief gemoed teniet deden en dat de effecten van gemoed dus hiërarchisch lager staan dan andere processen van aandachtscontrole die een effect hebben op V1. Een specifieke mentale toestand die gepaard gaat met een grotere taakmoeilijkheid kan mogelijk het verschil tussen de bevindingen van **hoofdstukken 2 en 3** waarin we duidelijke verbredende effecten van positief gemoed op V1 vonden enerzijds, en deze laatste studie anderzijds, verklaren. Deze resultaten geven aan dat de verbreding van aandacht in V1, als weergegeven door de C1 component, na de inductie van positief gemoed niet volledig automatisch is, maar afhankelijk van de beschikbaarheid van centrale verwerkingsresources (see Marois & Ivanoff, 2005; Moors & De Houwer, 2006).

Eén mechanisme dat in de literatuur is aangehaald om verbredende effecten van positief gemoed op aandacht te verklaren is een gebrek aan of een vermindering van inhibitoire controle. In **hoofdstuk 5** exploreerden we deze mogelijkheid door na gaan of de inductie van een positief gemoed (motorische) inhibitie kan verslechteren. Om dit te onderzoeken ondergingen de deelnemers eerst de neutrale of positieve GIP, gevolgd door een standaard antisaccadetaak (Hallett, 1978), terwijl EEG opgenomen werd. Resultaten toonden dat deelnemers in de positieve gemoedsgroep geen moeilijkheden vertoonden op gedragsniveau om prosaccades (naar de stimulus) tegen te houden en een antisaccade (weg van de stimulus) te initiëren, hoewel de GIP succesvol was. Ook ERP componenten die beschouwd worden als correlaten van inhibitoire processen, de N2 en de P300, vertoonden het typische patroon van een vergrootte N2 en een verkleinde P300 component in anti – vergeleken met prosaccades (Mueller, Swainson, & Jackson, 2009). Echter, we vonden wel ondersteuning voor een modulatie door positief gemoed van proactieve en reactieve componenten van cognitieve controle in deze taak. Om dit te onderzoeken vergeleken we de activiteit tussen de neutrale en de positieve gemoedsgroep voor activiteit in afwachting van het verschijnen van de doelstimulus (CNV), en tijdens de vroege verwerking ervan (N2). Bij gezonde volwassenen vindt men klassiek een duidelijk verschil in voorbereidende activiteit

voor makkelijke trials die weinig inhibitie vereisen (prosaccades) en moeilijke trials die veel inhibitie vereisen (antisaccades; zie Klein, Rockstroh, Cohen, & Berg, 1996). Terwijl dit onderscheid zichtbaar aanwezig was in de neutrale gemoedsgroep, was de anticipatieve activiteit in de positieve gemoedsgroep even sterk voor beide trialsoorten. Echter, na het verschijnen van de doelstimulus op het scherm, werd een sterk onderscheid gemaakt tussen beide trialsoorten ter hoogte van de N2 in de positieve gemoedsgroep, terwijl geen verschil werd gevonden op dit niveau voor de neutrale gemoedsgroep. Deze resultaten suggereren dat er een shift plaatsvond in de locus van controle, waarbij de proactieve controle minder sterk (CNV component) en de reactieve controle sterker (N2) was in de positieve vergeleken met de neutrale gemoedsgroep. We interpreteerden deze bevindingen als dynamische veranderingen in de manier waarop proactieve en reactieve controlemechanismen tijdelijk betrokken worden om de antisaccadetaak op te lossen na de inductie van positief gemoed.

DISCUSSIE

We verkeren waarschijnlijk elk wakker moment van ons leven in een bepaald gemoed. Deze affectieve toestanden beïnvloeden onze cognitie en ons gedrag voortdurend, hoewel weinig geweten is over de werkelijke aard en richting van deze effecten. Het hoofddoel van deze dissertatie was de invloed van milde gemoedsveranderingen, en vooral positief gemoed, op visuele perceptie alsook op inhibitiecontrole en creatief denken na te gaan. De resultaten gerapporteerd in deze dissertatie tonen dat positief gemoed visuele perceptie dynamisch en op verschillende niveaus kan beïnvloeden. Terwijl het verbredende effect van positief gemoed niet automatisch is, maar eerder aan beperkingen onderwerpen, vonden we dat positief gemoed de vroegste fase van visuele informatieverwerking kan beïnvloeden in V1, alsook latere post-perceptuele aandachtsprocessen. Concreet kan positief gemoed zowel bottom-up en top-down aandachtsprocessen versterken. Wij schuiven hier de hypothese naar voren dat positief gemoed deze effecten op perceptie kan uitoefenen door het aandachtssysteem te richten op de verwerking en exploratie van externe (i.p.v. interne) informatie, afhankelijk van de beschikbare resources op een bepaald moment. Verschillende theoretische kaders, zoals de onderverdeling in interne vs. externe aandacht (Chun et al., 2011), de dissociatie tussen bottom-up en top-down attention controlemechanismen (Corbetta & Shulman, 2002) of de conceptualisatie perceptie in termen van detectiedrempels (Nettle & Bateson, 2012) beschrijven aspecten van deze interactie. Echter,

geen van deze theorieën alleen kan de diversiteit van de effecten van positief gemoed op cognitie, zoals beschreven in onze en vroegere studies, omvatten. Samenvattend is meer onderzoek nodig om beter te begrijpen wat positief gemoed exact is, en waarom en hoe het perceptie en aandacht op zulke diverse wijzen kan beïnvloeden. Dit zou tevens bijdragen aan een beter begrip van specifieke defecten in positief gemoed, zoals in angst –en gemoedsstoornissen.

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