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Electroencephalographic insights into
affective attention

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Electroencephalographic insights into affective attention

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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3. Uusberg, A., Uibo, H., Kreegipuu, K., & Allik, J. (2013). EEG alpha and cortical inhibition in affective attention. *International Journal of Psychophysiology*, *89*(1), 26–36. doi:10.1016/j.ijpsycho.2013.04.020

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5. Uusberg, U., Uibo, H., Tiimus, R., Sarapuu, H., Kreegipuu, K., & Allik, J. (2014). Approach-avoidance activation without anterior asymmetry. *Frontiers in Emotion Science, 5*, 192. doi:10.3389/fpsyg.2014.00192

For studies I, II, III, and V the author set the aims, conducted the analyses and wrote the papers as the first author. For study IV, he was responsible for the aims, analyses and writing pertaining to the electrophysiological results. For studies I, III, IV and V he participated in designing and conducting the experiments. He also created the stimulus software for Study IV.

I. INTRODUCTION

Given its limited processing capacity, the brain needs to detect, encode and make use of the most important information in a prioritized manner. To this end, various attention mechanisms amplify some representations of internal and external reality at the expense of others (Chun, Golomb, & Turk-Browne, 2011). Vast amounts of sensed and retained information can thereby be kept at arms lengths while focussing on only the most useful bits of it. Often, this focus is captured by emotional information – a phenomenon known as affective, emotional or motivated attention (for reviews see Bradley, 2009; Compton, 2003; Mitchell & Greening, 2012; Pessoa, 2005, 2008; Pourtois, Schettino, & Vuilleumier, 2013; Tamietto & de Gelder, 2010; Vuilleumier & Huang, 2009; Vuilleumier, 2005; Yiend, 2010). Affective attention complements our abilities to concentrate at will (i.e. top-down attention) and remain vigilant for unpredicted aspects of the environment (i.e. bottom-up attention) with heightened sensitivity to threats and rewards.

Behaviourally, affective attention manifests itself in enhanced processing of inherently emotional or previously rewarded stimuli (Anderson, 2013; Yiend, 2010). Affective information seems to draw the spotlight of attention, explaining why an angry face "pops out" of a crowd (Frischen, Eastwood, & Smilek, 2008) or a sequence (e.g. Kreegipuu et al., 2013) of neutral ones. It similarly appears to retain attention to the extent that targets following an emotional distractor in a rapid stimulus stream are missed (i.e. the emotional attentional blink phenomenon; McHugo, Olatunji, & Zald, 2013). Affective content also tends to interfere with performing complex tasks such as naming the ink colour of a word instead of its meaning (Phaf & Kan, 2007). In short, behavioural responses reveal that emotional stimuli are processed in a prioritized manner.

It is currently unclear how this prioritisation emerges from the interplay between generic cognitive and specifically affective attention mechanisms. The work presented here sheds some light on this question by using electro-encephalography (EEG) to dissociate two pairs of constituent processes of affective attention. More specifically, Studies I to IV employ and extend associations between EEG dynamics and temporal stages of affective attention deployment. Studies II and III meanwhile suggest that posterior EEG power in theta and alpha frequency bands can capture, respectively, excitatory and inhibitory contributions to the relative amplification of emotional representations. Finally, these neural correlates of affective attention are demonstrated to be useful for understanding other emotional phenomena such as emotion regulation (Study II), affective time distortions (Study IV), and anterior EEG asymmetry (Study V).

1.1. Brain mechanisms of attention

The unitary experience of attending to something is produced by a number of brain mechanisms (Knudsen, 2007). In this section, I will sketch a simplified quasi-anatomical information processing model of these mechanisms (see Figure 1) based on recent reviews of cognitive (Baluch & Itti, 2011; Beck & Kastner, 2009; Katsuki & Constantinidis, 2013; Theeuwes, 2010) as well as affective visual attention research (Mitchell & Greening, 2012; Pessoa & Adolphs, 2010; Pourtois et al., 2013; Tamietto & de Gelder, 2010; Vuilleumier & Huang, 2009). The model does not attempt to explain all existing findings nor map the depicted mechanisms to actual brain regions (for a more ambitious effort in both respects see Baluch & Itti, 2011). It is also restricted to attention operating over external information captured by the visual modality. The model is intended to function as a basis for integrating the findings of this thesis as well as extrapolating them into two sets of extended hypotheses specifying (a) the emergence of two stages of attention as well as (b) manifestations of different bias signals in distinct parameters of posterior EEG dynamics.

The model assumes that selection from a multitude of available stimuli is achieved by (a) *biasing* naturally occurring competition between neural representations (solid arrows on Figure 1; Beck & Kastner, 2009; Desimone & Duncan, 1995). The ultimate origins of such biases are signals arriving from (b) a *saliency map* reflecting stimulus infrequency in space or time (Theeuwes, 2010; Wolfe & Horowitz, 2004) and (c) a *relevance map* representing stimulus importance for the goals maintained in working memory (Baluch & Itti, 2011; Noudoost, Chang, Steinmetz, & Moore, 2010). These bottom-up and top-down selection filters both contribute to (d) an integrated *priority map* which sends unified bias signals to sensory brain regions (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Gottlieb & Balan, 2010; Katsuki & Constantinidis, 2013). Emotional attention involves much of the same machinery complemented by (e) an *affective* significance *map* associated with a dedicated subcortical network centred on amygdala (Pessoa & Adolphs, 2010; Pourtois et al., 2013).
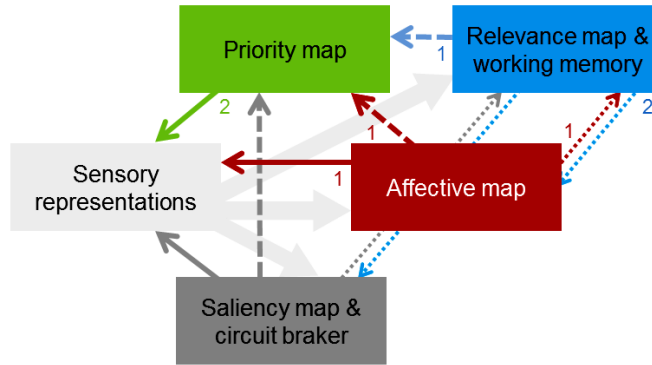
Figure 1. A simplified model of cognitive and affective attention mechanisms. Filled rightward arrows represent bottom-up flow of visual information; solid leftward arrows are the bias signals modulating recurrent sweeps in visual brain areas. Dashed arrows represent precursors to the bias signals that are integrated in the priority map. Pointed arrows are additional connections with working memory. Numbers denote the early and late stages of affective attention at which the given signals first reach their destinations. Colours represent types of selection: red – affective significance; blue – top-down goal-relevance; grey – bottom-up salience; green – integrated priority.

Selective amplification of sensory representations

According to the biased competition theory (Desimone & Duncan, 1995), selection is achieved in the brain by interfering with the natural state of competition between stimulus representations (Baluch & Itti, 2011; Beck & Kastner, 2009; Desimone & Duncan, 1995; Gilbert & Sigman, 2007; Knudsen, 2007; Noudoost et al., 2010). Without attention, simultaneously visible stimuli have been demonstrated to inhibit each other's neural manifestations on the level of single cell firing rates (e.g. Reynolds, Chelazzi, & Desimone, 1999) as well as regional brain activity (e.g. Kastner et al., 2001). Attending to one of the competing stimuli however, amplifies its representation relative to others, almost restoring the response it elicited when presented alone (Munneke, Heslenfeld, & Theeuwes, 2008; Reynolds et al., 1999). Attention can thus be said to bias the neural competition in favour of the selected stimuli. Similar attention-induced amplifications have been observed for retinotopic locations of upcoming targets (i.e. anticipatory attention; e.g. Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997) as well as neurons encoding attended stimulus attributes such as colour (i.e. feature-based attention; e.g. Bichot, Rossi, & Desimone, 2005). On a more detailed level, attentional biasing can take various forms such as enhanced or more consistent firing rates, increased neural synchrony, or altered receptive field properties; all of which serve to strengthen some neural representations relative to others (Beck & Kastner, 2009; Katsuki & Constantinidis, 2013; Womelsdorf & Fries, 2007).

Saliency map – bottom-up infrequency detection
As can be seen on Figure 1, sensory representations can be biased by several mechanisms. The most apparent distinction among these sources of attention involves bottom-up (also exogenous, automatic) and top-down (also endogenous, controlled) selection, represented on Figure 1 by the saliency and relevance maps, respectively. Exogenous attention results in a largely involuntary prioritization of stimuli that are infrequent in space (e.g. salient) or time (e.g. novel; Knudsen, 2007). For instance, it is hard not to notice an abrupt onset of motion such as a bird taking off from a stationary flock. Saliency is a function of spatial discontinuity along simple dimensions such as colour, orientation, size, or motion (Theeuwes, 2010; Wolfe & Horowitz, 2004). Meanwhile, the attentional pull of novelty can be observed in response to stimulus changes (Wolfe & Horowitz, 2004) and rare events (Näätänen, 1990). As a system dedicated to infrequency, bottom-up attention assures prompt processing of unpredicted aspects of the environment with higher-than-average informational value (Gottlieb & Balan, 2010). Neural computations of saliency occur first of all within the visual brain areas themselves. For instance, even low-level mechanisms such as lateral inhibition and temporal adaptation serve to amplify infrequency in space and time, respectively (Knudsen, 2007). Meanwhile, more complex integration of local infrequency into a global saliency map seems to require activity in subcortical regions such as the superior colliculus (SC) and the substantia nigra as well as a dorsal frontoparietal cortical network comprising of regions such as the frontal eye fields (FEF) and the lateral intraparietal area (LIP; Baluch & Itti, 2011; Corbetta & Shulman, 2002; Katsuki & Constantinidis, 2013). Finally, a "circuit-breaking" function of exogenous attention, whereby on-going endogenous concentration is intercepted, has been associated with a ventral frontoparietal network encompassing the temporoparietal junction as well as the ventral prefrontal cortex (PFC; Corbetta & Shulman, 2002; Shomstein, 2012).

Relevance map – top-down goal-congruence
Complementing the vigilance provided by bottom-up attention, top-down selection mechanisms assure that goal-relevant information is prioritized irrespective of its saliency. For instance, drivers can concentrate on a changing traffic light while ignoring equally salient events such as someone opening a colourful umbrella on the sidewalk. Endogenous attention can be conceptualised as a relevance map maintained in working memory (WM) where each spatial location and/or perceptual feature receives a value based on its significance for current goals. For instance, an arrow cue in a typical attention task increases the relevance of one visual hemifield over the other, based on task structure ("cues generally predict stimulus locations") and active goals ("I need to respond to stimulus onsets"; collectively also called an attention set) represented in working memory (Baluch & Itti, 2011; Corbetta & Shulman, 2002; Soto, Hodsoll, Rotshtein, & Humphreys, 2008). In addition to maintaining the attention set, working memory constantly updates the representations of internal

states and external reality with the help of different attention mechanisms (Knudsen, 2007). Conceptually, attention and working memory therefore overlap to some extent – a view also supported by their shared capacity limitations, frontoparietal substrate and reliance on biasing of sensory representations (Chun, 2011; Corbetta & Shulman, 2002; Gazzaley & Nobre, 2012; Knudsen, 2007; Postle, 2006). In the brain, working memory involvement implicates the PFC as the distal source of top-down biasing (Baluch & Itti, 2011; Knudsen, 2007). From the PFC onwards however, the relevance signals seem to be relayed via the same dorsal frontoparietal network implicated in salience mapping (Baluch & Itti, 2011; Corbetta & Shulman, 2002; Katsuki & Constantinidis, 2013; Noudoost et al., 2010).

Priority map – integrated salience and relevance
The dichotomy between bottom-up and top-down mechanisms captures the dual purpose of attention – to filter out goal-irrelevant information while retaining vigilance for significant bits of it. Think of concentrating to what your friend is saying in a crowded café until someone you know is mentioned at the neighbouring table. In many ways however, the distinction between endogenous and exogenous attention is far from clear-cut (Baluch & Itti, 2011; Katsuki & Constantinidis, 2013; Rauschenberger, 2010). On one hand, as expressed in models such as the contingent capture theory (Folk, Remington, & Wright, 1994), bottom-up stimulus selection is constrained by top-down attention control settings (Egeth, Leonard, & Leber, 2010; de Fockert, 2010; Nordfang & Bundesen, 2010). For instance, the pop-out effect characteristic of bottom-up attention is facilitated when salient stimuli are also task-relevant (Anderson, 2013; Eimer & Kiss, 2008; Wolfe, 1994). On the other hand, exogenously captured information can swiftly enter working memory, be judged as goal-relevant and thereby become targeted by endogenous attention as well (Knudsen, 2007). In short, a realistic sketch of attention mechanisms should consider exogenous and endogenous selection as integrated and recurrent processes (Rauschenberger, 2010).

One way to account for the simultaneous inter- and independence of ascending and descending attention is to imagine an intermediate priority map that pools exogenous saliency and endogenous relevance into a unitary representation of what is important which is then used to guide sensory amplification (Baluch & Itti, 2011; Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Serences & Yantis, 2007; Wolfe, 1994). On the neural level, this fourth mechanism of attention may be the best conceptualisation for the role of the brain regions that have been implicated in both bottom-up and top-down tasks (Baluch & Itti, 2011; Fecteau & Munoz, 2006; Knudsen, 2007). In particular, the priority map has been associated with the LIP (Bisley & Goldberg, 2010), the FEF (Thompson & Bichot, 2005) and/or the SC (Baluch & Itti, 2011). In top-down selection the FEF possibly drives the LIP while in bottom-up tasks information initially flows in the opposite direction (Katsuki & Constantinidis, 2013). Notably, these brain regions are also involved in generating eye-move-

ments. For instance, while weak stimulation of the FEF moves the focus of attention, stronger input also initiates a saccade to the attended location (Moore & Fallah, 2004). This observation converges with a premotor theory which considers attention to be a covert predecessor of overt eye-movements. According to this view, both mechanisms enhance the quality of neural representations with the respective help of foveal vision and sensory biasing (Nobre, Gitelman, Dias, & Mesulam, 2000; Rizzolatti, Riggio, Dascola, & Umiltá, 1987).

A simplified model of the brain mechanisms of cognitive attention has thus emerged (see Figure 1, ignoring the affective significance map for now). The end result of all selection mechanisms is modulated activity in sensory brain regions. The bias signals inducing these modulations originate from a priority map which in turn integrates the saliency of stimuli detected in bottom-up manner with their relevance assessed in working-memory. Given the involvement of visual brain areas in computing the former, the saliency map on Figure 1 also has a direct input to sensory representations while its' circuit-breaking function is depicted as a connection with WM. Finally, top-down attention involves a relevance map that weighs visual input in light of current goals and communicates the results to the priority as well as saliency maps. Taken together, the four components introduced up to now represent the machinery involved in visual cognitive attention. The next section explains how the same components interact with an affect-specific network in emotional attention.

Affective significance map
Affective attention is usually differentiated from the rest of selection phenomena by its target – information with some emotional significance, stemming from evolutionary past, reinforcement history or appraisals linking stimuli to the goals of the perceiver. In the brain however, selection of emotional stimuli does not employ a completely separate set of mechanisms. First of all, it is reasonable to assume that all stimuli, affective or otherwise, become prioritised via biased neural competition. Indeed, emotional stimuli consistently enhance the activity in visual brain areas (Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012; Sabatinelli et al., 2011; Tamietto & de Gelder, 2010). As the next paragraphs will explain, the sources of such modulations can lay both within the cognitive (or generic) attention mechanisms outlined above as well as a dedicated ventral affective loop. This intertwined architecture sets the stage for the central question of this thesis – how to disentangle contributions from different attention mechanisms using EEG correlates of inhibitory and excitatory as well as fast and slow selection processes.

The involvement of cognitive mechanisms in affective attention is evident already on conceptual grounds. Given that emotions are reactions to stimuli that are somehow relevant for the goals of the perceiver (Frijda & Scherer, 2009), any information that induces emotions should by definition also attract top-

down attention[1]. Many empirical findings also implicate cognitive attention mechanisms in affective attention phenomena (Baluch & Itti, 2011; Mohanty & Sussman, 2013). For instance, emotional stimuli routinely activate the fronto-parietal attention networks (Lindquist et al., 2012). Meanwhile, occupying top-down attention with a demanding task can disrupt prioritised processing of task-irrelevant emotional stimuli suggesting that affective attention requires endo-genous resources to some extent (Pessoa, 2005). Although emotional stimuli can sometimes also be salient (e.g. the shape of eye-brows in an angry face; Larson, Aronoff, Sarinopoulos, & Zhu, 2008), this is probably not a primary mechanism of affective attention. In summary, affective attention relies in part on the frontoparietal mechanisms implicated in top-down attention (Lindquist et al., 2012; Mohanty & Sussman, 2013; Pessoa & Adolphs, 2010; Pourtois et al., 2013).

In addition however, emotional attention can also tap into a separate re-source. For instance, even stimuli that are task-irrelevant and non-salient can attract attention if they share an attribute with previously rewarded stimuli (re-markably, even months after and without explicit recollection of reward learning; Anderson, 2013; c.f. Brosch, Pourtois, Sander, & Vuilleumier, 2011). In the brain, such affect-specific selection is associated with a ventral network comprising of the amygdala, orbitofrontal and anterior cingulate cortices as well as other regions (Mitchell & Greening, 2012; Pessoa & Adolphs, 2010; Pourtois et al., 2013; Tamietto & de Gelder, 2010). Amygdala in particular is well-suited for affective significance detection given its bidirectional connectivity with visual, medial temporal as well as prefrontal regions (Kim et al., 2011). It re-ceives rapid low-resolution visual input from the thalamus via the SC and pulvinar (Tamietto & de Gelder, 2010) and/or from the ventral visual cortical pathway (Pessoa & Adolphs, 2010). It can also bias sensory representations via direct excitatory projections to visual areas (Freese & Amaral, 2006) as well as its connectivity with the frontoparietal attention network (e.g. Lim, Padmala, & Pessoa, 2009; for reviews see Anderson, 2013; Mohanty & Sussman, 2013; Jacobs, Renken, Aleman, & Cornelissen, 2012). Based on these arguments, the model on Figure 1 construes an affective significance map that biases sensory representation both directly as well as indirectly via the priority map.

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[1]   Although the opposite – that all events attracting attention must be emotional – is not true, the laboratory study of cognitive attention often in fact involves affective processes. Experimental study of attention usually requires particular responses (e.g. react to an onset) that are encouraged by explicit (e.g. a squirt of juice to an animal) or implicit (e.g. gratitude of the experimenter) rewards, thus rendering task-relevant stimuli also reward-relevant.

1.2. Aims and hypotheses

In summary, the existing literature suggests that affective attention involves amplification of emotional representations by ventral (i.e. subcortical, affective) as well as dorsal (i.e. cortical, cognitive, top-down) attention systems (Mitchell & Greening, 2012; Pessoa & Adolphs, 2010; Pourtois et al., 2013; Tamietto & de Gelder, 2010; Vuilleumier & Huang, 2009). An overarching aim of this thesis is to better understand how these mechanisms interact. To this end, the studies presented here deploy as well as develop EEG correlates of specific aspects of affective attention such as early and late processing stages and excitatory and inhibitory gain control. Using this strategy, the individual publications reveal (a) that affective attention is more automatic on early than later processing stages (Studies I to III); (b) that affective attention may make different use of excitatory and inhibitory biasing (Studies II and III); and (c) that EEG correlates of affective attention benefit the investigation of broader emotional phenomena (Studies II, IV and V).

Beyond these contributions, the findings from Studies I to III are also used to construct extended hypotheses for future research. These specify (a) how the ventral and dorsal bias signals may be differentiated using EEG dynamics, and (b) how distinct processing stages may emerge from the mechanisms depicted on Figure 1.

Individual publications
Studies I to IV help to differentiate stages of affective attention. Specifically, activity between 150 and 350 ms was linked to initial large-capacity scanning of stimulus representations for motivational significance (the first stage) while subsequent dynamics were associated with capacity-limited elaboration of selected stimuli, presumably in WM (the second stage; Codispoti, Ferrari, & Bradley, 2007; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Often, a further dissociation between processes occurring before and after 500 ms within the second stage was also observed. These distinctions support, explicitly in Study I and more implicitly in others, the hypothesis that affective attention is more automatic on the first than the second processing stage (c.f. Pessoa, 2010; Pourtois et al., 2013). Several studies also suggest that during the second stage, the dorsal and ventral attention signals become gradually more and more integrated. These findings have implications for emotion regulation (Study II) as well as affective time distortions research (Study IV).

Meanwhile, Studies II and III indicated that excitatory and inhibitory signals may serve different functions in affective attention. In principle, sensory competition can be biased both by amplifying the representations of targets as well as inhibiting those of distractors (e.g. Luck et al., 1997; Moran & Desimone, 1985; Reynolds et al., 1999). While the former mechanism is often implicated in affective attention, the role of inhibition is relatively less appreciated in affective compared to cognitive attention literature (e.g. Foxe & Snyder, 2011). Building on relevant advances in cognitive neuroscience (Klimesch, Sauseng, &

Hanslmayr, 2007), Study III suggests that emotionally elicited posterior power dynamics in EEG upper alpha frequency band may reflect inhibitory biasing of visual representations by affective attention. Adoption of this framework is argued to explain a seemingly unexpected correlation between alpha power and emotional arousal as well as generate intriguing hypothesis for the study of concurrent task demands and affective tuning phenomena. The need to re-think the meaning of alpha oscillations in affective neuroscience is further illustrated in Study V. Meanwhile, Study II conceptualises occipital theta power in terms of excitatory bias signals and demonstrates the usefulness of this parameter for emotion regulation research. Additional analyses of theta modulations in Study I presented in this thesis replicate some of these findings as well as confirm differences between affective modulations of alpha and theta.

Extended hypotheses
In addition to the particular contribution of each study, their findings were also integrated in order to develop a set of extended hypotheses for future research. These were derived mostly from Studies I to III which rely on two distinct but similar experiments. In both paradigms, participants viewed affective images with concurrent tasks which changed the target status of affective stimuli for ventral and dorsal attention systems. When participants were asked (Studies I and III) or left (Study II) to process the emotional meaning of the pictures, affective stimulus features became targets for both the ventral and the dorsal systems. However, when they engaged in non-affective mental activity, the ventral system presumably continued to target the affective aspects of the images while the dorsal system was otherwise engaged (to a different degree in different experiments). Comparing the data measured in these two conditions can thus reveal the neural correlates of the respective systems. This insight was used to search for (a) links between alpha, theta and event-related potential (ERP) dynamics on one hand and downstream effects of ventral and dorsal attention systems on the other; as well as (b) information flow patterns along the pathways prescribed by Figure 1 that would best explain the findings from Studies I to III.

The resulting hypotheses assume that differences in posterior EEG dynamics between responses to affective and neutral stimuli are mostly caused by affective attention signals arriving at sensory brain regions (Hajcak, MacNamara, & Olvet, 2010; Olofsson, Nordin, Sequeira, & Polich, 2008; Schupp et al., 2006). Within this framework, different EEG parameters may reflect different mixtures of signals originating from the ventral and dorsal systems. In combination, the idea that alpha oscillations are generated by inhibitory input (Klimesch et al., 2007) and the existence of only excitatory direct connections from the amygdala to visual cortices (Freese & Amaral, 2006) suggest that posterior alpha power may exclusively reflect the bias signals arriving from the dorsal rather than the ventral attention system. Meanwhile, both ERP and theta power dynamics should capture excitatory input. Although subcortical origins of theta oscillations cannot be ruled out (Lewis, 2005), the present findings suggest this fre-

quency band too may reflect predominantly dorsal biasing (c.f. Sauseng, Griesmayr, Freunberger, & Klimesch, 2010). This leaves ERPs to be the broadest measure of both ventral and dorsal excitatory modifications of sensory representations (e.g. Sabatinelli, Keil, Frank, & Lang, 2013). In summary, the first set of extended hypotheses suggests that while dorsal biasing is probably reflected in all measures analysed here, the additional contributions from the ventral system should be most visible in ERPs, less visible in theta and absent from alpha dynamics.

A second set of extended hypotheses constitutes a process model explaining how different stages of affective attention observed in the present as well as previous studies can emerge from the structure depicted on Figure 1 (see numbers there). For simplicity, the hypotheses omit processes involving the saliency map which only occasionally selects affective stimuli. Using the remaining nodes, the first stage is hypothesised to begin after the arrival of visual information at the ventral affective and dorsal relevance maps. These respond by emitting feedback signals aimed at biasing sensory representations, while the affective significance map is also relayed to the WM. Crucially, for some reason (e.g. cortical computations take more time) only direct signals from the ventral system arrive at the sensory cortices during the first processing stage. Meanwhile the output from the priority map, reflecting affective as well as cognitive relevance, complements direct affective input at sensory areas only from the second processing stage onwards. The present results also suggest that the dorsal and the ventral signals may be combined additively at the beginning of the second stage and interactively thereafter. Possibly, the WM compares the affective and goal-relevance maps and in case of a mismatch either (a) updates the relevance signals travelling to the priority map or (b) maintains the relevance map and inhibits the affective map instead. Both types of processes can conceivably produce relatively late interactive effects on sensory cortices.

2. AUTOMATICITY ACROSS THE STAGES OF AFFECTIVE ATTENTION

One manifestation of our limited understanding of the ventral-dorsal interplay in affective attention is the on-going debate about its automaticity (Dolan & Vuilleumier, 2003; Pessoa, 2005). In terms of Figure 1, this contention concerns the independence of affective significance mapping from dorsal control. This question also relates to the suitability of conceptualising affective attention in terms of two processing stages implicated in some models of cognitive attention. To address these interrelated aims, Study I investigated the automaticity of affective attention across different stages reflected in ERP components.

2.1. The automaticity debate and two-stage accounts of affective attention

For affective attention to be considered automatic, emotional stimulus prioritization should not require awareness, intention or effort nor be easy to control (Bargh, 1994). On the level of brain mechanisms, most of these aspects relate to the extent to which the ventral affective system can operate without engaging the dorsal top-down system. Operationalized in this manner, the automaticity of affective attention seems to be substantial but limited. For instance, amygdala can respond to emotional stimuli presented outside of awareness (Öhman, 2002) or focus of endogenous attention (Dolan & Vuilleumier, 2003), but only as long as at least some top-down resources remain available (Pessoa, 2005).

One way to reconcile the conflicting findings is to assume that affective attention is more automatic at an early compared to a later processing stage. For instance, Luo and colleagues (2010) studied amygdala responses to task-irrelevant emotional faces under variable cognitive loads using MEG source reconstruction. They found a load-independent emotional enhancement of amygdala activity during 40 – 140 ms that was removed by high but not low cognitive load between 280 – 340 ms. A study using intracranial recordings from an epilepsy patient also found task-independent amygdala responses to emotional expressions between 140 and 290 ms followed by an interactive effect from 710 ms onwards whereby amygdala responded only to the emotionality of spatially attended faces (Pourtois, Spinelli, Seeck, & Vuilleumier, 2010). Although these findings remain inconclusive (Pessoa, 2010), they suggest that affective attention may contain dissociable stages characterised by varying degrees of dorsal control over ventral bias signals.

Different stages of processing have also been implicated in cognitive attention research (Broadbent & Broadbent, 1987; Chun & Potter, 1995; Itti & Koch, 2001; Olivers & Meeter, 2008; Treisman & Gelade, 1980; Wolfe, 1994). These accounts construe a first stage populated by coarse stimulus representations at the verge of awareness that become available for large-capacity attention mechanisms. A few stimuli then pass on to a second stage, where their repre-

sentations are consolidated and elaborated in a limited-capacity system often equated with working memory[2]. These stages have already been implicated in affective context, for instance to explain automatic attention capture by some emotional stimuli in visual search tasks (Öhman, Flykt, & Esteves, 2001). However, as the brain mechanisms of early cognitive and affective attention may differ (see Figure 1), the suitability of two stage accounts for affective attention remains to be specified.

Given its excellent temporal resolution, EEG is well suited for studying the phases of stimulus processing. In particular, two ERP components elicited by complex stimuli[3] – the Early Posterior Negativity (EPN, 150–300 ms from stimulus onset) and the Late Positive Potential (LPP, from 300 ms onwards) – appear to represent different underlying processing stages (e.g. Codispoti et al., 2007; Schupp, Stockburger, Codispoti, et al., 2007; for a review see Schupp et al., 2006). For instance, these components exhibit different sensitivities to top-down attention (Schupp, Stockburger, Bublatzky, et al., 2007) and stimulus repetitions (Codispoti et al., 2007) suggesting that the EPN is respectively more automatic and more resistant to emotional adaptation than the LPP.

2.2. Study I "Unintentionality of affective attention across visual processing stages"

In Study I, the dual-stage interpretation of EPN and LPP dynamics was re-cruited to investigate the possible stage-dependence of the automaticity of affective attention. More specifically, the study focussed on the unintentionality aspect of automaticity by testing if emotional stimuli elicit stronger responses than neutral ones without an explicit motivation to process their affective meaning. In order to avoid confounding unintentionality with effortlessness, the processing intention was diverted without inducing high cognitive loads. Specifically, participants viewed affective images with instructions to evaluate

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[2]   Stages of attention are related to, but should not be confused with two sweeps of visual stimulus processing. The act of perception is thought to involve bidirectional flows of information along hierarchical brain regions (Bullier, 2001; Lamme & Roelfsema, 2000). An initial feed-forward sweep translates retinal input into coarse representations projected rapidly through the visual hierarchy and onwards to the PFC and other areas. The latter respond with top-down modulatory signals propagated in a reverse hierarchical order (Gilbert & Sigman, 2007). A second, re-entrant ascending sweep then integrates bottom-up and top-down information into a consistent representation. For simple stimuli, the first sweep may occur between 80 and 120 ms and the second from 200 ms onwards (Lamme & Roelfsema, 2000). While the second of the two attention stages undoubtedly requires re-entrant processing, the earlier one is also likely to involve at least some feedback from attentional source regions (Roelfsema, Lamme, & Spekreijse, 2000). The two attention stages may thus map onto iterative loops of re-entrant processing.

[3]   Simpler targets such as emotional words or faces may also systematically modulate earlier components such as the C1 (60–80 ms) and P1/N1 (100–150 ms; Pourtois, Schettino, & Vuilleumier, 2013) whose relationships to the processing stages are not specified here.

either their internal emotional experiences or physical stimulus features. The latter evaluation presumably removed the explicit intention to process affective stimulus meaning even while it remained as demanding as the former task. As a result, emotional content was affectively significant in both conditions but also goal-relevant in only one.

Slightly different subsamples of 85 healthy participants of the same experiment provided data for Studies I, III and V. In this experiment, depictions of affective scenes from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005) were used as stimuli. Evocative photographs combine relatively high emotional intensity (compared to, for example facial expressions or emotional words; Thom et al., 2013) with reasonable control over confounding stimulus features (compared to emotional films or autobiographic memories). In Studies I and III, the remaining covariance between affective and perceptual stimulus features (Delplanque, N'Diaye, Scherer, & Grandjean, 2007) was also statistically controlled for. Five stimulus sets were compiled in order to elicit different manifestations of core affect – low arousal pleasant, high arousal pleasant (erotic), low arousal unpleasant and high arousal unpleasant (aversive) as well as a neutral baseline category (see Study III for image numbers; Table 1 in Study III and Figure 1 in Study V for subjective ratings). Different image sets balanced for affective ratings, picture content and layout were presented with different evaluative tasks. Participants reported the valence and arousal of the experiences generated by each picture in the affective task, and their luminance and the number of visible objects in the non-affective condition. The tasks were presented sequentially with three repetitions of 60 images in pseudo-randomised order in each. The order and set pairing of tasks were counter-balanced across participants. Each image was presented for 1.5 seconds after a 1.5 second fixation cross and followed by two consecutive 9-point rating scales.

EEG was recorded using 32 scalp and 4 ocular electrodes. Ocular artefacts were corrected using Independent Component Analysis and the remaining ones minimized by removing noisy channels and segments. ERP components were defined using a difference wave between the maximal emotional and the neutral response (i.e. an affective envelope). While in many previous studies the LPP has been analysed as a unitary phenomenon or parsed arbitrarily, the affective envelope revealed a data-driven distinction between early P3-like (P3) and late Slow Wave (SW) portions of the LPP.

Note that the terminology of Study I diverges somewhat from the present text. While the adjectives "bottom-up" and "ascending" are reserved for exogenous cognitive attention here, they are synonymous with automatic affective attention in the original publication.

A consistent set of results emerged in Study I whereby affective as well as task effects on each of the analysed components were slightly but significantly different. The EPN (175–300 ms) was enhanced by erotic, aversive and unpleasant stimuli; P3 (300–500 ms) by erotic and aversive images and the SW (500–1500 ms) by all emotional categories in a roughly arousal-dependent

manner. Meanwhile, the intention to process emotional meaning did not modulate the EPN, additively enhanced amplitudes during the P3 and interactively during the SW.

These findings support the time-dependent automaticity hypotheses (Luo et al., 2010; Pourtois et al., 2010). More specifically, early stages of affective attention indexed by the EPN were completely independent of intentions to encode stimuli in affective terms while later stages were not. Note that this diverges from at least one observation that a demanding effortlessness manipulation can also attenuate affective EPN modulations (Schupp, Stockburger, Bublatzky, et al., 2007). In combination, the two studies indicate that explicit motivation is not required for early affective stimulus prioritisation, even while the availability of some processing resources may be.

The present results further revealed that emotional meaning extraction continued throughout the later stages of unintentional processing, suggesting that dorsal mechanisms complemented rather than dominated the ventral system. Similar simultaneous affective and cognitive attention effects on the LPP have been reported for both unintentionality (e.g. Schupp, Stockburger, Codispoti, et al., 2007; Weinberg, Hilgard, Bartholow, & Hajcak, 2012) and effortlessness manipulations (e.g. Ferrari, Codispoti, Cardinale, & Bradley, 2008).

For the extended hypotheses of this thesis, the absence of task effects on EPN amplitudes suggests that signals originating from the ventral attention system may dominate sensory biasing between 175 and 300 ms. In the present paradigm, emotional features were targeted by ventral as well as dorsal systems in the affective condition but by the ventral system alone in the non-affective condition. The lack of differences between the two tasks in EPN amplitudes therefore suggests that the ventral system determined the early affective effects in both conditions. It can thus be hypothesised that only direct ventral input reached sensory representations during the first stage of affective attention reflected in the EPN. This suggestion aligns with findings that amygdala can respond within (Pourtois et al., 2010) or even before (Luo et al., 2010) the EPN time window and its downstream effects can contribute to affective ERP modulations (Sabatinelli et al., 2013).

Another implication for the extended hypotheses can be inferred from the finding that the intention to process emotional meaning increased the P3 equally in response to affective as well as neutral pictures but modulated SW amplitudes roughly in proportion with stimulus arousal. The emergence of a task effect first of all indicates that the dorsal priority map joined the ventral affective map in modulating ERP responses from 300 ms onwards. Secondly, the subtle differences between the task sensitivities of the P3 and the SW may reflect some sort of integration of different bias signals. More specifically, the additive modulations of the P3 can be explained by dorsal priority signals blending with the ventral ones in an additive manner (either at the sensory cortices or the priority map). Meanwhile, the interactive SW response may reflect the modulatory impact of working memory. For instance, the WM may have downgraded the affective significance of emotional stimuli in the non-

affective condition or enhanced their goal-relevance in the affective condition in proportion with stimulus arousal.

2.3. Conclusions

In Study I, the question of the automaticity of affective attention was related to stages of attention captured by ERPs on one hand (Schupp et al., 2006) and specific aspects of automaticity on the other (Bargh, 1994). Such temporal and definitional specificity helped to delineate the boundaries of automatic prioritisation of emotional representations. Specifically, taken together with comparable previous studies, the findings suggest that early affective attention is completely unintentional, even if it may not be infinitely effortless. Meanwhile, the second processing stage exhibited a combination of affective significance and top-down relevance effects. More broadly, these findings support the idea that despite relying on partially different substrates, both affective and cognitive attention can be characterised by two processing stages. The study also contributed to the extended hypothesis by suggesting that subcortical as well as cortical bias signals both contribute to posterior ERPs. The findings also suggested that direct ventral affective biasing remained exclusive before 300 ms and became complemented by dorsal priority signals only after that, in an in increasingly integrative manner.

3. THETA AND EXCITATORY GAIN CONTROL

The preceding chapter illustrated the benefits of linking different EEG time windows to distinct underlying processing stages. The current and following chapters suggest that extraction of theta and alpha dynamics may provide similar gains by differentiating excitatory and inhibitory bias signals, respectively. The temporal and spectral distinctions are also combined to further increase the specificity of EEG correlates of affective attention.

3.1. Excitatory and inhibitory gain control reflected in EEG frequencies

Scalp EEG is probably generated by synchronized voltage fluctuations within spatially aligned cortical local field potentials (LFP; Lopes da Silva, 2013). The captured LFP oscillations may in turn synchronise single cell activity and thereby help to maintain local as well as global distributed brain networks underlying various psychological functions (Basar, Basar-Eroglu, Karakas, & Schürmann, 2001; Buzsaki & Draguhn, 2004; Engel, Fries, & Singer, 2001; Fries, 2005; Salinas & Sejnowski, 2001; Ward, 2003). More specifically, firing with the same rhythm enhances communication between neural populations. Synchrony can thereby form transient "software" networks on fixed connectivity "hardware", maximizing computational power and flexibility of the brain (Fries, 2005). As it happens, these functional networks may use distinct frequency bands to become synchronised. Although the relationships tend to vary between brain areas, tasks and participants (Başar & Güntekin, 2012), a rule of thumb relates slower oscillations such as theta (4–7 Hz) and alpha (8–13 Hz) to long-distance communication while faster ones such as gamma (40–90 Hz) may be involved in networks formed within rather than between cortical areas (von Stein & Sarnthein, 2000; Varela, Lachaux, Rodriguez, & Martinerie, 2001).

Brain oscillations are particularly relevant for attention processes (Womelsdorf & Fries, 2007). On the local level, attentional biasing may manifest in enhanced synchrony among neurons encoding attended stimuli (Deco & Thiele, 2009; Womelsdorf & Fries, 2007). For instance, neural representations of the targets of attention become more synchronised in the gamma range than neighbouring cells representing unattended distractors (Fries, Reynolds, Rorie, & Desimone, 2001). Global synchrony on the other hand is probably involved in relaying bias signals from sources of attention such as the frontoparietal network to targets such as the visual cortex (Deco & Thiele, 2009; Ward, 2003; Womelsdorf & Fries, 2007). Given the proposed inverse relationship between distance and frequency, these long-range networks probably use beta (Gross et al., 2004), alpha (Foxe & Snyder, 2011; Ward, 2003), and theta (Sauseng et al., 2010) oscillations, although gamma coupling has also been observed (e.g. Gregoriou, Gotts, Zhou, & Desimone, 2009).

Within this framework, Studies II and III explore the involvement of theta and alpha dynamics in affective attention. Both papers assume that synchronised communication between distant brain areas enhances local synchrony within the participating regions. This in turn amplifies oscillatory power picked up by adjacent scalp electrodes, rendering the latter a measure of underlying event-related synchronisation (ERS) and desynchronization (ERD; Pfurtscheller & Lopes da Silva, 1999). Given these premises, posterior theta and alpha power may reflect the extent to which sensory representations are incorporated into large-scale brain networks oscillating at the analysed frequency. Although the precise composition of these networks cannot be determined from the EEG signal alone, they may well involve the substrate of attention given the proposed role of theta oscillations in information integration for cognitive as well as affective purposes (Lewis, 2005; Roux & Uhlhaas, 2014; Sauseng et al., 2010; Womelsdorf, Vinck, Leung, & Everling, 2010); and implication of alpha in selective cortical inhibition and top-down control (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch et al., 2007).

3.2. Theta and affective attention

Theta dynamics have been implicated in a wide range of cognitive phenomena such as decision-making (Womelsdorf et al., 2010), spatial navigation (Buzsáki, 2005), multimodal perception (Basar, Schürmann, & Sakowitz, 2001), sensorimotor integration (Cruikshank, Singhal, Hueppelsheuser, & Caplan, 2011), action monitoring (Cavanagh, Zambrano-Vazquez, & Allen, 2012; Mitchell, McNaughton, Flanagan, & Kirk, 2008), episodic memory (Nyhus & Curran, 2010) and in particular, working memory (Roux & Uhlhaas, 2014; Sauseng et al., 2010).

A common function performed by theta dynamics in these different processes may be the integration of distributed neural representations, including binding sensory representations with central WM mechanisms (Roux & Uhlhaas, 2014; Sauseng et al., 2010). Given the overlap between WM and attention, theta oscillations may thus also mediate sensory biasing originating from cortical as well as subcortical affective attention regions (Lewis, 2005; Womelsdorf et al., 2010). Indeed, theta power has been observed to correlate with affective content (Aftanas, Reva, Varlamov, Pavlov, & Makhnev, 2004; Knyazev, Slobodskoj-Plusnin, & Bocharov, 2009), emotional arousal (e.g. Aftanas, Varlamov, Pavlov, Makhnev, & Reva, 2002; Balconi & Lucchiari, 2006), as well as negative valence of visual stimuli (Balconi, Brambilla, & Falbo, 2009a; Sun, Sun, Wang, & Gong, 2012; for reviews see Bekkedal, Rossi III, & Panksepp, 2011; Knyazev, 2007). Various lines of evidence thus suggest that theta oscillations may facilitate communication between the source and target regions of affective attention. On this backdrop, Study II proposes posterior theta power to be a measure of re-entrant amplification of affective stimulus representations by emotional attention.

3.3. Study II "Using distraction to regulate emotion: insights from theta dynamics"

Beyond contributions to emotion regulation literature elaborated in the publication, Study II also has implication for affective attention research. Distraction, the emotion regulation strategy of interest in the study, dampens emotional reactions by precluding full comprehension of affective situations (Gross, 1998, 2013; Koole, 2009). For instance, the distress of a dental procedure can be mitigated by actively visualizing more pleasant circumstances. At closer inspection, doing so interferes specifically with affective attention processes. Even while mentally time travelling, the dental patient remains aware of the actual situation. Instead of completely preventing the representation of evocative stimuli, distraction thus predominantly reduces the processing advantage these stimuli would otherwise receive, i.e. affective attention. Framed in these terms, distraction becomes a tool for discovering the neural correlates of affective attention – if occipital theta indeed results from attentional biasing, it should thus be modulated when participants engage in distraction.

Data from an earlier experiment (Thiruchselvam, Blechert, Sheppes, Rydstrom, & Gross, 2011) were reanalysed for Study II. EEG was recorded while 18 participants (9 men) viewed neutral and unpleasant IAPS images with and without instructions to regulate ensuing emotions using distraction and reappraisal. For distraction, they were instructed to engage in emotionally neutral mental imagery (visualise geometrical designs or neighbourhood sceneries) and for reappraisal to construe the unpleasant images in neutral terms. Similar regulation manipulations have proved to be effective in numerous previous studies (McRae et al., 2010; Webb, Miles, & Sheeran, 2012) and were also shown to elicit expected self-report and ERP dynamics in the present dataset (Thiruchselvam et al., 2011). Unregulated viewing of neutral and negative stimuli together with one type of regulation trials were presented in random order in one of four blocks. Two seconds prior to the onset of each stimulus, a cue introduced the type of the upcoming trial. Stimuli were presented for 5 seconds followed by affective rating scales. EEG data from 48 electrodes were pre-processed in a similar manner to other studies in this thesis. Event-related spectral perturbations (ERSP) computed using Morlet wavelets with variable cycles were averaged within individually-defined theta bands (3–8 Hz) at occipital electrodes.

The results revealed two event-related synchronisation peaks (150–350 and 350 – 550 ms) followed by a sustained power level (see Figure 2 in Study II). Experimental modulations of these dynamics could indeed be explained by considering theta power as a selective correlate of affective attention. First of all, in the unregulated conditions, negative images generated more theta than neutral ones throughout the analysis window (c.f. Balconi et al., 2009a; Sun et al., 2012). This can be explained by unpleasant representations being more vigorously incorporated into affective attention networks than neutral ones. From the second ERS peak onwards however, distraction but not reappraisal

reduced the theta response to unpleasant images down to, and later even below the level generated by neutral images (c.f. Zhang et al., 2013). The dissociation between distraction and reappraisal is particularly informative here, given that both regulation strategies explicitly asked participants to feel neutral in response to the stimuli and also induced some cognitive load. Nevertheless, theta ERS was exclusively modulated by distraction suggesting this EEG feature correlates with something that is unique to this particular regulation strategy, such as affective attention.

These results underlie the extended hypothesis that theta power predominantly reflects bias signals arriving from the cortical priority map (Sauseng et al., 2010). The distraction instruction asking participants to visualize geometric objects or familiar neighbourhoods presumably reduced the goal-relevance of affective images as well as the availability of resources for processing them. In oscillatory terms, this probably manifested in enhanced synchrony between cortical WM areas and regions required for mental imagery coupled with reduced synchrony between the central regions and external stimulus representations. The ensuing loss of synchrony in sensory areas is a plausible explanation for the abrupt reduction of occipital theta power from 350 ms onwards. In terms of Figure 1, theta could therefore be considered a measure of the extent to which sensory representations receive excitatory re-entrant input from the priority map.

While Study II associated occipital theta with dorsal bias signals, it remained less clear on the role of direct inputs from the ventral system. On one hand, theta power was sensitive to emotional content already during the first processing stage that was associated with direct amygdala input in Study I (see also Aftanas et al., 2002; Knyazev et al., 2009). Theta ERS may thus reflect the excitatory input arriving from both dorsal and ventral sources. On the other hand however, the early affective effect might also have dorsal origins as the preparatory cue gave affective significance information time to travel from the amygdala to the priority map. Further research is thus needed for informed hypothesis about the extent to which occipital theta power reflects direct amygdala input to visual cortices.

To some extent, this question can be addressed using data from Study I. Replication of other aspects of Study II is also advisable due to its small sample size and the absence of a condition where distraction would have been applied to neutral stimuli. This common time-saving feature of emotion regulation paradigms leaves it unclear if theta power tracks prioritised processing of all external stimuli or is specific to the fate of affective ones.

3.4. Theta modulations in Study I

Given the similarities between Studies I and II, the affective sensitivities of theta power observed in Study II should also be visible in Study I. Both experiments contained a pair of conditions where affective stimuli were either task-relevant (affective evaluations in Study I and passive viewing in Study II) or task-irrelevant (non-affective evaluations and distraction, respectively). These manipulations differed, however, by the extent to which processing resources were occupied in the task-irrelevant condition (low in Study I, high in Study II). Data from Study I can therefore be also used to test if occipital theta ERS tracks the availability of processing resources or alternatively, the intentions to process visual representations. Finally, the full-factorial design of Study I enables to ask if this tracking is selective to affective stimuli or not.

To these ends, theta perturbations were computed from the data of Study I using settings similar to Studies II and III (Morlet wavelets between 2–10 Hz; 1–5 cycles; full trial normalization; –1500 to –500 ms baseline). The perturbations were averaged within individually defined theta band between 3–8 Hz at O1, Oz, O2, PO3 and PO4 electrodes and time windows spanning 100–300 and 300–600 ms (see Figure 2). Average power levels were analysed using repeated measures ANOVA with factors for picture category and task as well as their interaction. Greenhouse-Geisser corrected p-values and results of Tukey post-hoc tests of these analyses are reported here.
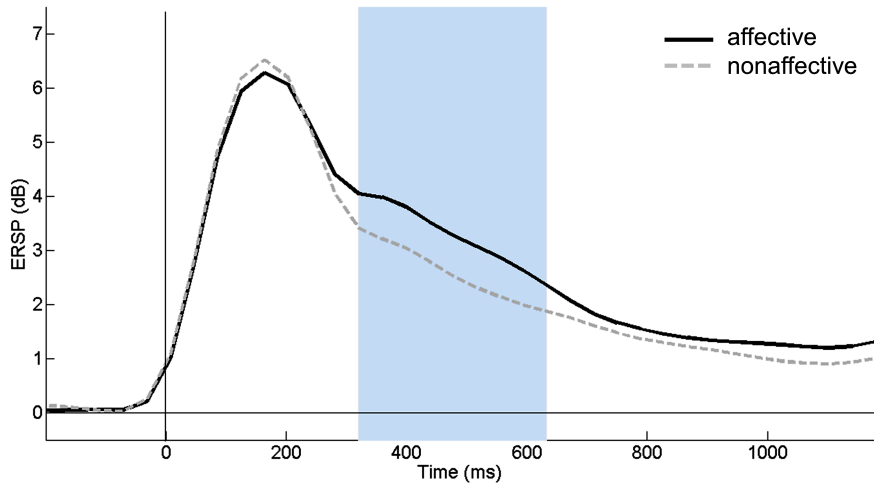

Figure 2. Task-relevance effect on occipital theta perturbations in Study I data. The shaded area denotes significant differences between conditions (paired t-test, false discovery rate corrected p < .05)

As can be seen on Figure 2, the dual-peaked ERS observed in Study II was broadly replicated in Study I. The modulations of the first peak however, were

quite different between the two experiments. Instead of a clear valence sensitivity observed in Study II, stimulus category had a non-affective effect on early theta ERS in Study I data ($F(4,312) = 5.28$, $\eta_p^2 = .06$, $p < .001$; pleasant images induced more power at $p < .001$ than erotic ones without either extreme being significantly different from undistinguished responses to neutral, pleasant and unpleasant images in between them). Task main effect ($F(1,78) = 0.13$, $\eta_p^2 = .001$, $p = .71$) as well as the task-by-picture interaction $F(4,312) = 0.17$, $\eta_p^2 = .002$, $p = .95$) were not significant. Taken together, these results reiterate the need for caution in linking early theta ERS to emotional biasing. Being early and occipital, the signal may also or instead reflect processing of physical stimulus features that can co-vary with affective dimensions in the IAPS (Delplanque et al., 2007).

Meanwhile, the second ERS dynamics were broadly similar in Studies I and II. Unlike the first peak, the second one was clearly sensitive to affective content (see Figure 2; $F(3,314) = 11.27$, $\eta_p^2 = .13$, $p < .001$; all affective images differed from neutral at $p < .001$ but not form each-other beyond trend level). Also in line with Study II, the second peak of Study I exhibited sensitivity to the task-relevance manipulation whereby power was decreased when emotional stimulus features ceased to be task-relevant (c.f. Figure 1 in Study II and Figure 2 here; $F(1,78) = 31.56$, $\eta_p^2 = .29$, $p < .001$). Given that unlike distraction, the nonaffective task in Study I did not substantially consume processing resources, this finding links theta power to the goal-relevance of emotional stimuli in addition to their engagement of capacity-limited resources. In summary, its sensitivity to goal-relevance indicates that the second occipital theta peak may reflect biasing originating primarily from the priority map.
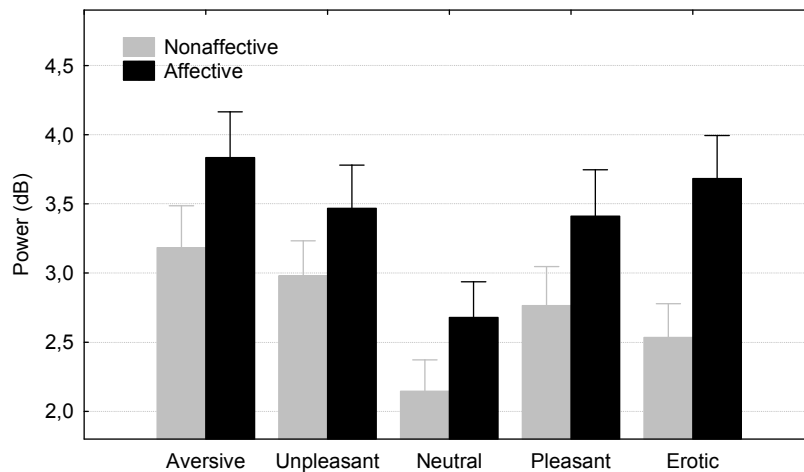

Figure 3. Affective and task-relevance effects on the second theta ERS peak in data from Study I.

3.5. Conclusions

Two valence-sensitive power peaks were observed in occipital theta in Study II, the second of which was selectively attenuated by using distraction to regulate emotions. Insofar as distraction disrupts prioritised rather than entire processing of emotional stimuli, this result renders occipital theta power a neural correlate of affective attention. Re-analysis of data from Study I replicated the task-sensitive dual-peaked nature of occipital theta dynamics as well as helped to further specify the conceptual origins of the second peak. As it was attenuated by non-affective tasks in both studies, it may be sensitive not only to the availability of processing resources (restricted in Study II, but not in Study I) but also to the intention to process affective meaning (restricted in both studies). This pattern can be explained by considering occipital theta power a reflection of the extent to which sensory representations are synchronised with the dorsal top-down attention system.

In light of the extended hypotheses, the re-analysis of Study I provides an informative comparison between temporally overlapping theta and ERP dynamics recorded from the same dataset. Within the early time window, the findings were very different – while ERPs reflected meaningful emotional differences between stimulus categories, theta dynamics did not. This discrepancy inspired the extended hypotheses to associate occipital theta power with excitatory signals originating primarily in the dorsal priority map which were assumed to arrive not before the second processing stage. ERPs meanwhile were associated with sensory modulations induced both by cortical as well as subcortical inputs - as the latter were assumed to be available already during the first stage, they can account for the early emotional effect observed in ERPs. The second theta peak meanwhile showed similar dynamics to the P3 component with both exhibiting a task main effect with no interactions. Both were also sensitive to affective content, although theta power did not differentiate emotional stimuli by arousal while the P3 did.

4. ALPHA AND INHIBITORY GAIN CONTROL

In the previous chapter, extraction of theta frequency dynamics from posterior EEG was shown to reveal predominantly cortical biasing involved in affective attention. This chapter extends the usefulness of spectral analyses for affective attention research by linking posterior alpha dynamics to inhibition of affect-irrelevant brain processes.

4.1. Alpha and inhibition
of affect-irrelevant representations

Having long been considered a simple manifestation of cortical idling, alpha oscillations (7–13 Hz) are increasingly associated with more meaningful cognitive processes (Başar & Güntekin, 2012). Prominent among these is the active inhibition of irrelevant brain activity (Foxe & Snyder, 2011; Hanslmayr, Staudigl, & Fellner, 2012; Jensen & Mazaheri, 2010; Klimesch et al., 2007; Palva & Palva, 2007). For instance, alpha power increases when participants actively suppress competing working memory input (Klimesch, 1999) or motor responses (e.g. Hummel, Andres, Altenmüller, Dichgans, & Gerloff, 2002). On the neural level, this reconceptualization of alpha dynamics realizes that an inhibitory input can simultaneously reduce the intensity of neural activity and increase its temporal synchrony (Klimesch et al., 2007). As EEG power is mainly a function of synchrony, increased inhibition can therefore, somewhat counter-intuitively, increase rather than decrease scalp EEG amplitudes.

Given that competition between neural representations can be biased by amplifying the relevant as well as by inhibiting the irrelevant (e.g. Luck et al., 1997; Moran & Desimone, 1985; Reynolds et al., 1999), alpha oscillations have also been suggested to be a basic building block of selective attention (Foxe & Snyder, 2011; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Jensen, Bonnefond, & VanRullen, 2012; Klimesch, 2012). For instance, a cue shifting anticipatory attention to one side of the visual field increases alpha power over ipsilateral representations of the unattended space (Worden, Foxe, Wang, & Simpson, 2000). The same holds in reverse – when hemispheric distribution of alpha is experimentally changed using transcranial magnetic stimulation, objects within the visual field contralateral to the stimulation become less visible than ipsilateral ones (Romei, Gross, & Thut, 2010). Alpha ERS also accompanies unattended sensory modalities (Foxe et al., 1998; Fu et al., 2001) as well as perceptual features (Snyder & Foxe, 2010). Finally, posterior alpha dynamics can be modulated by magnetic disruption of areas within the fronto-parietal attention network suggesting that alpha oscillations may indeed reflect long-distance synchronisation involved in conveying inhibitory bias signals from the dorsal attention system to visual cortices (Capotosto, Babiloni, Romani, & Corbetta, 2009).

4.2. Study III "EEG alpha and cortical inhibition in affective attention"

Although emotion-induced alpha modulations have sometimes been reported (Başar & Güntekin, 2012; Knyazev, 2007), they have rarely been explained in inhibitory terms (e.g. Knyazev, Savostyanov, & Levin, 2006; Parvaz, MacNamara, Goldstein, & Hajcak, 2012). On this backdrop, Study III tested if inhibitory origins could explain alpha power variations in data from Study I. After similar pre-processing, ERSPs were calculated using Morlet wavelets with variable cycles. Following a preliminary mass-univariate analysis, power within individually defined upper alpha band (11–13 Hz) was averaged in three regions of interest for each trial and analysed in a mixed model ANOVA to detect experimental effects while controlling for perceptual confounds.

Significant modulations were observed in upper alpha power from 350 ms onwards at posterior as well as central scalp areas. The central alpha dynamics probably reflected sensorimotor activity and are therefore not considered here. In posterior alpha, three main findings emerged. First, affective arousal increased rather than decreased alpha power. Second, a negativity bias occurred whereby high, although not low arousal unpleasant images generated the highest alpha power levels. Third, a task-by-affect interaction occurred after 575 ms.

These findings were explained by relating alpha power to inhibition of affect-irrelevant brain processes. This enabled first of all to solve an apparent contradiction between previous ERP and imaging studies demonstrating affect-induced increases in posterior brain activity (Hajcak et al., 2010; Lindquist et al., 2012; Sabatinelli et al., 2011) and the present findings implying the opposite (as higher alpha power reflects more inhibition/less activity). This inconsistency can be dissolved by considering alpha not as an inverse measure of brain activity but as a selective reflection of LFP synchrony generated by regions under top-down inhibitory control (Klimesch et al., 2007). The activity enhancements recorded with other methods presumably originate from the actual neural representations of emotional stimuli that become amplified by affective attention. Meanwhile, neural populations encoding affect-irrelevant locations, features, and modalities may be simultaneously inhibited in order to bias neural competition further in favour of the selected representations. Increased local synchrony within these distributed brain regions under inhibitory control may then determine scalp alpha power, especially given the spatial mixing of EEG sources.

Intriguingly, the extent to which affective attention engages inhibitory gain control seems to vary across situations. This is suggested by comparing Study III to a very similar experiment where IAPS images elicited analogous LPP dynamics but diametrically different alpha responses with emotional arousal correlating negatively rather than positively with alpha power (De Cesarei & Codispoti, 2011). At closer inspection, this discrepancy may relate to the different concurrent task requirements used in these studies. Apparently, when

participants are asked to somehow evaluate affective images, emotional arousal increases alpha power (Study III; see also Aftanas et al., 2004, 2002) while an opposite relationship may prevail in passive viewing paradigms (Balconi, Brambilla, & Falbo, 2009b; De Cesarei & Codispoti, 2011). Possibly, alpha power reflects the variable need for inhibition of affect-irrelevant processes in different situations. Passive viewing generates little competition for emotional representations which can therefore be sufficiently amplified by excitatory biasing, resulting in relative increase in disinhibition and a negative correlation between arousal and alpha power. For affective stimuli to stand out in the concurrent task context however, their disinhibition needs to be complemented by inhibition of affect-irrelevant activity resulting in the opposite effect. Even while this explanation awaits further research, it suggests that alpha dynamics may differentiate emotional states that remain indistinguishable for other neural correlates of affective attention.

A selective correlate of affect-induced inhibition may also be useful for the study of emotional modulations of the breadth of attention and thinking (i.e. affective tuning). For instance, unpleasant emotions enhance the perception of local as opposed to global stimulus features, presumably reflecting evolutionary advantages of focussing on threatening details (Fredrickson, 2004; Friedman & Forster, 2010; Gable & Harmon-Jones, 2010). In the brain, narrowed attentional scope is likely to involve inhibition of peripheral representations which in turn may amplify scalp alpha power. Study III provided preliminary evidence for this hypothesis by showing that aversive images generated significantly more alpha power across all analysed scalp locations and time windows than pleasant or neutral pictures. Although low arousal unpleasant images did not have a comparable impact, they might have lacked the motivational intensity required for tuning effects to appear (Gable & Harmon-Jones, 2010).

The main contribution of Study III to the extended hypotheses of this thesis is the inference that if alpha power indeed reflects inhibition, then it cannot be generated by the direct excitatory feedback signals arriving at sensory cortices from the amygdala (Freese & Amaral, 2006). Given that the ventral system was inferred to modulate sensory representations already from 150 ms onwards (see Study I), this hypothesis is supported by the absence of affective modulations of alpha power prior to 350 ms. Alpha may thus be a highly selective measure of the inhibitory biasing arriving from the priority map.

At first sight, this conclusion seems to be at odds with the absence of any task effects on alpha power at the beginning of the second processing stage (350–575 ms) despite the fact that dorsal inputs were implicated in this time window in Studies I and II. One way to account for this apparent anomaly is to assume that inhibitory biasing is computed differently than excitatory biasing. For instance, when sufficient calls for inhibition of affect-irrelevant activity have already arrived from one system (e.g. the ventral affective map), the priority map may ignore further calls from other systems (e.g. the relevance map). Such nonlinear computations of inhibitory biasing may also explain a task-by-affect interaction that occurred in alpha between 575 and 900 ms

whereby the affective task increased inhibition only for low arousal and neutral stimuli but not for high arousal pictures. Conceivably, the task-relevance of affect did not result in additional inhibitory amplification of high arousal stimuli which already stood out under orders from the affective map. By contrast, the low arousal stimuli did not elicit strong calls for inhibition from the affective map and had therefore room to be further biased at the behest of the goal-relevance map.

4.3. Conclusions

Study III extended the inhibitory account of alpha oscillations to affective attention processes, although in a rather explorative manner. The findings first of all suggest that affective arousal can increase posterior alpha power in response to emotional stimuli, possibly when brain processes competing with emotional representations need to be supressed. Alpha and inhibition may also be involved in constricting the breadth of attention under sufficiently intense unpleasant affect. Compared with posterior theta and ERP dynamics, alpha responses to emotional stimuli were markedly different showing an affective main effect at the beginning of the second stage and a unique interaction following it. These findings primarily indicate that inhibitory biasing of sensory representations does not mirror excitatory inputs captured by theta and ERP dynamics. Instead, the extended hypotheses propose alpha power to reflect the output of the priority map that is determined by a nonlinear combination of subcortical affective significance and prefrontal goal-relevance.

5. EEG CORRELATES
OF AFFECTIVE ATTENTION AS TOOLS
FOR AFFECTIVE NEUROSCIENCE

The preceding chapters have suggested that focussing on certain time windows as well as frequency bands can increase the specificity of EEG correlates of affective attention. The final chapter will now investigate the usefulness of such correlates for the study of broader emotional phenomena, such as emotion regulation, affective time modulations and approach-avoidance motivation.

5.1. Implications for emotion regulation
from Studies I to III

Study II as well as Studies I and III help to specify some of the mechanisms involved in emotion regulation. Different strategies for regulating emotions are usually defined in fairly broad terms. According to an influential process model (Gross, 1998; Gross & Thompson, 2007), on one hand people use methods aimed at removing the antecedents of emotional reactions by avoiding or changing the situations that would elicit them. At the other end are attempts to suppress or hide the ensuing emotional responses. In between these extremes are cognitive strategies such as distraction and reappraisal, capable of altering the internal unfolding of an emotional episode (Ochsner & Gross, 2005).

Distraction is believed to work by restricting the allocation of processing resources to emotional stimuli. It has been unclear however, when exactly this occurs along the stages outlined in chapter 2. An earlier publication of the data re-analysed in Study II (Thiruchselvam et al., 2011) provided half of the answer – given that distraction modulated the LPP, it probably restricted the second stage processing of emotional stimuli. However, their fate on the first stage remained undetermined in this study as the EPN was not analysed. As occipital theta dynamics covered both stages, Study II was able to reveal that distraction indeed became effective only from the second stage onwards. This finding supports explaining distraction effectiveness in terms of capacity-limited processing resources as the failure to halt early affective attention did not prevent distraction from being effective in reducing both self-reported and LPP-reflected emotional intensity (Thiruchselvam et al., 2011).

Note that the question of distraction effectiveness is a reversed version of the question of affective attention effortlessness. This conceptual link can be extended to other members of the attention-control family of emotion regulation techniques where distraction hails from (Ochsner & Gross, 2005). Whereas distraction works by tapping into limited effortlessness of emotional attention, other strategies such as focussing on less emotional aspects of emotional stimuli need its' unintentionality to be finite as well (compare Bargh, 1994; and Ochsner & Gross, 2005). In this regard, Study I revealed that simply making

emotions task-irrelevant had no effect on early affective attention and only a limited impact on subsequent emotional modulations of ERPs as well as theta dynamics. These findings imply that substantial employment of second-stage capacity-limited resources (i.e. working memory) may be required for successful emotion regulation by attention-control. In fact, sufficiently demanding tasks may also prevent the first-stage affective attention that was found to be inaccessible to the distraction manipulation of Study II (Schupp, Stockburger, Bublatzky, et al., 2007).

5.2. Study IV "Emotional modulation of attention affects time perception"

Study IV recruited ERP correlates of processing stages (see Study I) to the investigation of affective modulations of subjective time (Droit-Volet & Meck, 2007). Time perception can be modelled as a conceptual clock consisting of pulses emitted by a pacemaker reaching an accumulator through a switch (Grondin, 2010). Emotions can distort this mechanism in at least two ways. On one hand, affect-induced changes in bodily arousal may increase the number of pulses emitted by the pacemaker in one objective unit of time (e.g. Tamm et al., 2014). This modulates the subjective flow of time, much like slow motion effects can be created by playing a high-frame-rate recording back at normal speed. On the other hand, given that the switch component needs attention to transfer pulses from the pacemaker to the accumulator, emotional stimuli can also modulate time by increasing or decreasing the resources available for that purpose (Schirmer, 2011).

Study IV explored if ERP correlates of visual stimulus processing stages can help to distinguish the sources of time modulations. The data were collected from 62 students (42 females) who produced short time intervals (0.9, 1.5, 2.7 and 3.3 seconds) while viewing erotic, aversive, and neutral IAPS images or an empty screen. Behaviourally, the emotional effects varied with the required interval. Specifically, affective distortions were observed for 0.9, 1.5 and 2.7 s durations. For the 0.9 s target, the intervals produced during unpleasant images where shorter and more variable than in neutral or pleasant trials. In the remaining intervals however, only pleasant stimuli significantly lengthened produced durations for 1.5 and shortened them for 2.7 s. The main inference supported by this complex pattern of results is that it cannot be explained by any single underlying mechanism.

EEG was recorded and processed similarly to other studies of this thesis. Stimulus- as well as response-locked sections of EEG were analysed. In the latter, the Contingent Negative Variation (CNV) remained unrelated to production performance as well as emotional modulations, in line with recent questioning (van Rijn, Kononowicz, Meck, Ng, & Penney, 2011) of the idea that CNV reflects the accumulation of pulses involved in time perception (Macar & Vidal, 2004). Meanwhile, the stimulus-locked ERPs revealed expected

emotional effects whereby pleasant and unpleasant stimuli enhanced amplitudes equally in P1 and LPP components. The EPN however, exhibited stronger responses to erotic compared to aversive images (see Figure 3 in Study IV).

These results suggest two ways how ERP correlates of affective attention can be useful for time perception research. First of all, the extent to which a stimulus captures sustained affective attention can reflect the arousal it induces. Thus, the absence of a valence effect throughout most of the ERP response in Study IV was interpreted as evidence that the behavioural differences between erotic and aversive time modulations cannot be ascribed to differences in the affective arousal induced by the stimuli. Instead, the behavioural effects may relate to the valence difference observed at EPN suggesting that positive images initially engaged the ventral attention network more vigorously than the unpleasant ones. This implies that the affective modulation of early attention may have a particular impact on the switch component of the internal clock. Even while Study IV did not provide conclusive evidence, it made a case for using a similar strategy in future research.

5.3. Study V "Approach-avoidance activation without anterior asymmetry"

In Study V, the level of affective attention attracted by stimuli was employed as a measure of their perceived motivational significance. Doing so helped to address a conundrum regarding the conceptual origins of anterior alpha asymmetry. According to a dominant biphasic model, less alpha power over left than right frontal hemisphere reflects more approach-motivational activity while the opposite pattern is associated with avoidance (Coan & Allen, 2002, 2004; Harmon-Jones, Gable, & Peterson, 2010). This model explains experimental asymmetry shifts in response to manipulations of motivational and affective states as well as correlations between trait-like baseline asymmetry and outcomes such as affective dispositions and mood disorders. However, not all available evidence concurs with this view (Miller, Crocker, Spielberg, Infantolino, & Heller, 2013).

Among the challengers of the biphasic model are failures to find expected asymmetries from EEG responses to affective images (see Study V and Harmon-Jones et al., 2010). The conceptual importance of such null findings can be summarised in a series of simple premises: affective images reliably elicit core affect (e.g. Bradley & Lang, 2007); core affect either overlaps with or is closely related to approach-avoidance motivation (e.g. Hamann, 2012); and approach-avoidance motivation induces anterior asymmetry (e.g Harmon-Jones et al., 2010). As each of these premises is individually uncontroversial, it is puzzling why core affect elicited by images sometimes does not induce expected shifts in asymmetry. To explain this conundrum, researchers have suggested (a) that pictures lack sufficient motivational urgency and (b) that individually different responsiveness may mask expected effects (Gable &

Harmon-Jones, 2008; Harmon-Jones et al., 2010). Study V systematically tested both hypotheses, relying in part on the link between affective attention and LPP.

More specifically, we assumed that if a stimulus attracts sufficient affective attention to modulate LPP amplitudes, it must be motivationally significant for the participant to a non-negligible degree. Therefore, the stimuli with insufficient motivational urgency for asymmetry effects to occur should also fail to significantly modulate LPP amplitudes. To test this, we used the data collected in the affective condition of the experiment analysed in Studies I and III. Asymmetries were calculated from ERSPs quantified in a similar manner to Study III. To assess individual differences, the data were analysed using a mixed model ANOVA capable of isolating three sources of variability: the stimulus effect together with stimulus-independent as well as stimulus-dependent individual differences (Stemmler & Wacker, 2010).

The results rather compellingly revealed significant and expected LPP modulations (also reported in Study I) together with a complete lack of stimulus effects on anterior asymmetry. The mixed model analyses also assured that expected asymmetries were not concealed by individual differences. Given that both previously proposed explanations for the affective images conundrum were not supported, the study calls for renewed search for alternative explanations. To this end, the findings implicated the role of stimulus-independent individual differences, either truly trait-like or induced by the experimental setting. For instance, faced with unpredictable encounters with highly arousing stimuli some participants might have experienced anxious apprehension or engaged in spontaneous emotion regulation, both of which have been related to frontal brain asymmetries. Note also that an important building block for a revised model of anterior asymmetry may be the inhibitory account discussed in Study III (Miller et al., 2013; Parvaz et al., 2012).

5.4. Conclusions

The wide conceptual scope of the problems addressed in this chapter illustrates the broader usefulness of EEG correlates of emotional attention for affective neuroscience. Studies IV and V demonstrated how LPP as the currently best understood EEG measure of emotional attention can be used to characterise experimentally generated affective states, with higher temporal resolution and resistance to reporting bias that traditional self-report manipulation checks. More provisionally, Study IV recommended using the link between ERP components and processing stages to isolate emotional attention effects on time perception. The promise of this approach was further illustrated by Study II, where the two-stage interpretation of theta dynamics helped to specify some of the mechanisms involved in emotion regulation by distraction.

The usefulness of EEG correlates of affective attention need of course not be confined to these contexts. Affective attention is relatively unique among emotional process in that its subcortical dynamics are relayed to cortical areas

and can thereby be picked up by EEG. In this regard, the extended hypotheses of this thesis may further enhance the specificity with which EEG dynamics can be related to underlying processes. For instance, if ERPs indeed reflect both subcortical and cortical biases while theta power is more confined to the latter, their combined use may help to dissociate ventral and dorsal responses to stimuli – a dichotomy relevant for several phenomena at the intersection of affective and cognitive neurosciences (Dolcos, Iordan, & Dolcos, 2011).

6. GENERAL SUMMARY AND CONCLUSIONS

This thesis employed more as well as less developed EEG-correlates of affective attention to enhance our understanding of the brain mechanisms underlying this as well as related phenomenon. More specifically, temporal and spectral distinctions within posterior EEG were associated with different processing stages and types of gain control, respectively. These developments were used to address several particular research problems as well as propose extended hypotheses based on a model of underlying brain mechanisms.

The temporal dissociations were first of all used to investigate the automaticity of affective attention. The two main datasets of this thesis constituted manipulations of the intentionality (Study I and III) and effortlessness (Study II) aspects of automaticity (Bargh, 1994) – while both experiments involved manipulations of the motivation to attend to emotional meaning, the task in Study II also limited the available processing resources. Different findings supported considering affective attention more automatic on the first than on the second processing stage. In the present data this held for unintentionality as well as effortlessness, although the latter may also be dependent on the level of cognitive load (Pessoa, 2010; Schupp, Stockburger, Bublatzky, et al., 2007).

More broadly, the present findings support construing affective attention as a two-stage process (Öhman et al., 2001; Schupp et al., 2006). Given that the brain mechanisms of cognitive and affective attention differ, this inference contributes to the growing body of evidence suggesting that the two-stage models intended for the former type of attention can indeed be extrapolated to the latter. More specifically, top-down attention may interact with bottom-up salience and affective significance maps in somewhat similar ways. For instance, in both cases direct signals from the faster maps may reach sensory cortices earlier than integrated biasing from the priority map. Meanwhile, during the second processing stage the salience and affective maps may become under increasingly effective top-down WM control.

The spectral dissociations explored here suggest that theta and alpha correlates of affective attention can reveal distinct underlying dynamics. The stimulus and task effects on these frequencies differed in terms of direction as well as time-course. These observations imply differential involvement of excitatory and inhibitory gain control in affective attention processes. Neural enhancement of affective representations, presumably reflected in scalp theta power, may be the default means for biasing neural competition in favour of emotional stimuli. Meanwhile, depending on circumstances such as competing task demands, effective biasing may also require inhibition of affect-irrelevant brain processes, the extent of which may be visible in posterior alpha dynamics.

These temporal and/or spectral dissociations were also demonstrated to contribute to research areas beyond affective attention. In Studies I and II, emotion regulation relying on attention-control was inferred to operate by limiting working memory resources available for affective attention, even without interfering with the initial prioritisation of emotional stimuli. Meanwhile,

the EPN and the LPP were used to assess the attentional causes of emotional time distortions (Study IV) and the LPP employed to re-establish the affective images conundrum in anterior EEG asymmetry literature (Study V).

Individual findings were also integrated into two sets of extended hypotheses aimed at inspiring future research. These originated from a simplified model of brain mechanisms (Figure 1; Baluch & Itti, 2011; Beck & Kastner, 2009; Katsuki & Constantinidis, 2013; Knudsen, 2007; Pourtois et al., 2013) specifying that emotional attention relies on sensory biasing (Lindquist et al., 2012; Sabatinelli et al., 2011) originating directly from the amygdala (Freese & Amaral, 2006; Tamietto & de Gelder, 2010) as well as from a frontoparietal priority map integrating bottom-up and top-down cognitive importance (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Gottlieb & Balan, 2010) with ventral affective significance (Baluch & Itti, 2011; Mohanty & Sussman, 2013). The downstream consequences of various types of bias signals were assumed to be observable in posterior EEG dynamics (Lopes da Silva, 2013).

Some of extended hypotheses aimed to explain the emergence of two stages of affective attention from this basic structural model. An early stage was suggested to result from excitatory amygdala input preceding cortically generated bias signals at sensory brain regions (Luo et al., 2010; Pourtois et al., 2010). In line with this prediction, early ERP dynamics were determined by affective stimulus features (Studies I and IV) irrespective of task-relevance (Study I). Meanwhile, the arrival of integrated priority signals was considered to mark the beginning of the second stage, explaining various combinations of affective and task effects found from 300 ms onwards (Studies I to III). During later sections of that stage, working memory was assumed to down-regulate the affective significance map (Ochsner, Silvers, & Buhle, 2012) and/or integrate it with the goal-relevance map (Baluch & Itti, 2011; Mohanty & Sussman, 2013).

A second set of extended hypotheses ascribed partially independent origins for different EEG parameters. Based on early emotional effects, ERPs were the only measure related to dorsal as well as ventral bias signals. Theta was implicated in cortical priority signals by consistent task-relevance effects within the second processing stage. Possible subcortical origins of theta (Lewis, 2005) could not be determined however, as an affective effect during the first processing stage was absent in Study I and could have been caused by anticipatory cortical processing in Study II. Meanwhile, alpha power was considered to be predominantly cortical due to the lack of inhibitory connections between amygdala and visual cortices (Freese & Amaral, 2006) as well as the late onset of emotional effects in Study III.

In conclusion, this thesis calls for analysing posterior EEG dynamics as well as affective attention processes in terms of two processing stages as well as excitatory and inhibitory gain control. It also invites future research, preferably using concurrent analyses of different frequencies (e.g. Roux & Uhlhaas, 2014; Siegel, Donner, & Engel, 2012) as well as connectivity patterns (e.g. Popov, Steffen, Weisz, Miller, & Rockstroh, 2012) to test the proposed extended hypotheses regarding the origins of different posterior EEG modulations.

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SUMMARY IN ESTONIAN

Elektroentsefalograafiline vaade emotsionaalse tähelepanu mehhanismidele

Inimmõistus on varustatud mitmete teabe ülekülluse eest kaitsvate tähelepanu mehhanismidega. Ühed aitavad keskenduda olulisele ja teised märgata ootamatusi. Käesoleva doktoritöö fookuses on kolmandat tüüpi tähelepanu, mis tõstab esile emotsionaalset informatsiooni.

Varasemast on teada, et erinevad visuaalse tähelepanu fenomenid toetuvad osaliselt jagatud ajumehhanismidele. Ilmselt realiseerub igasugune tähelepanu neuraalsete representatsioonide valikulises võimendumises. Selle võivad algatada nii ajas ja ruumis ebatüüpilist avastav tahtmatu tähelepanu kui ka tahtlik süsteem, mis eelistab aktuaalsete eesmärkide jaoks olulist teavet. Mõlema süsteemi valikud integreeritakse ajus ilmselt ka ühtseks prioriteedikaardiks, mis võimendab nii ühes kui teises mõttes esiletõstmist väärivaid asukohti ja objekte. Emotsionaalse teabe eelistöötlus toetub osaliselt samadele mehhanismidele, kuid kaasab ka spetsiaalse emotsionaalse olulisuse kaardi, mida seostatakse ajus ennekõike amügdala talitlusega. Käesoleva doktoritöö peateemaks on geneeriliste ja spetsiifiliselt afektiivsete tähelepanumehhanismide koos- ja vastasmõjud. Nende uurimiseks kasutati elektroentsefalograafilist (EEG) signaali, mis on tundlik visuaalsete representatsioonide tähelepanulisele võimendumisele. Töö peamiseks uuenduseks on EEG rakendamine tähelepanu faaside ja võimenduse tüüpide eristamiseks emotsionaalses kontekstis.

Kahe-faasiliste käsitluste kohaselt otsib varajane tähelepanu ebaküpsete mentaalsete representatsioonide seast teatud võtmetunnuste alusel potentsiaalselt olulisi stiimuleid. Valitud kuvandid pääsevad seejärel eelisjärjekorras teise, põhjalikuma töötluse faasi. Kaht etappi eristab töötlusmaht – kui esimeses võrreldakse suurt hulka tunnuseid paralleelselt, siis teises saab korraga ette võtta vaid üksikud stiimulid. Käesoleva doktoritöö esimene tulemustering toetab ka emotsionaalse tähelepanu käsitlemist kahe-faasilise protsessina. Ennekõike leidis kinnitust faaside mahupiirangust tulenev hüpotees, et emotsionaalne tähelepanu on varases töötlusfaasis automaatsem kui hilises. Uuringutes I ja II vaatlesid osalejad emotsionaalse sisuga fotosid suunates ühes katsetingimuses oma tahtliku tähelepanu piltidest tingitud tunnetele, teises aga mujale. Nende katsetingimuste võrdlemine lubas tuvastada automaatsust – kui afektiivne tähelepanu on tõepoolest tahtmatu, peaks see võimendama emotsionaalseid kujutisi neutraalsetest enam ka siis, kui inimesed ei pööra pildi afektiivsusele teadlikku tähelepanu. Tulemused näitasid, et nii see tõepoolest on, kuid ennekõike 150 ja 350 stiimulile järgneva millisekundi jooksul. Seejärel hakkab aju vastus sõltuma nii stiimuli emotsionaalsest sisust kui üha enam ka vaatleja huvist. Selline automaatsuse muutlikkus ajas on seletatav emotsionaalse tähelepanu kahe faasi hüpoteesiga.

Doktoritöö teine tulemusklaster toetab ideed, et EEG kui lainelise signaali amplituudid teeta (4–7 Hz) ja alfa (8–13 Hz) sagedusribas peegeldava kaht

erinevat tähelepanulise võimenduse liiki – tähelepandu tugevdamist ja tähele-
panuvälise pidurdamist. Varasemast on teada, et erinevad EEG sagedusribad
väljendavad erinevates funktsionaalsetes võrgustikes osalevate närvirakkude
kommunikatsiooni rütmilisust. Tõenäoliselt suhtlevad tähelepanulise võimen-
duse allikad ja sihtmärgid samuti sünkroonsuse abil ning seejuures on alfa-sage-
duslik aktiivsus pigem seotud representatsioonide pidurdamisega ning teeta
nende tugevdamisega. Uuringud II ja III toetasid seda mõttekäiku näidates, et
piltstiimuli emotsionaalne intensiivsus peegeldub nii alfa kui teeta võimsuses.
Seejuures olid mõõdetud modulatsioonid sageduseti erinevad, viidates pidur-
duse ja tugevduse eristatavatele rollidele emotsionaalses tähelepanus. Näiteks
võrreldes Uuringut III varasemate sarnaste töödega, ilmnes, et samasugust
emotsionaalse sisu tugevdust esilekutsuvad olukorrad võivad diametraalselt
erineda pidurduse poolest. Võimalik et pidurdust rakendatakse tugevduse kõrval
ennekõike siis, kui ajus on emotsionaalsete stiimulite tajumise ja mõtestamisega
konkureerimas muid protsesse.

Kolmandaks demonstreerib see doktoritöö emotsionaalse tähelepanu EEG
korrelaatide laiemaid kasutusvõimalusi afektiivses neuroteaduses. Esmalt aita-
vad tulemused täpsustada tähelepanu kõrvalejuhtimise kui emotsioonide
reguleerimise strateegia toimemehhanisme. Uuringud I ja II osutavad, et katsed
näiteks valusa raviprotseduuri ebameeldivust vähendada millestki muust mõel-
des, on tõhusad ennekõike siis, kui tähelepanu suunatakse emotsionaalselt sünd-
muselt mitte lihtsalt eemale vaid märkimisväärselt keerukale mõttetegevusele.
Näiteks uuringus II paluti katseisikutel vaimusilmas detailselt kujutleda oma
kodutänavat. Selline kõrvaltegevus tõepoolest piiras emotsionaalsete stiimulite
pääsu tähelepanu teise faasi, millest piisas kogetava seisundi intensiivsuse
vähenemiseks. Uuringus I juhiti katseisikute tähelepanu kõrvale aga lihtsama
ülesandega, mille tulemusel emotsionaalne tähelepanu küll vähenes, kuid suhte-
lised erinevused stiimulikategooriate vahel säilisid.

Doktoritöö uuringud IV ja V pakkusid rakendusi Uuringus I demonstreeritud
seostele EEG sündmuspotentsiaali komponentide ja emotsionaalse tähelepanu
ning selle töötlusfaaside vahel. Uuring IV demonstreeris, kuidas afektiivse
tähelepanu neurokorrelaadid lubavad jooksvalt analüüsida tähelepanu ressurs-
side jaotust afektiivse informatsiooni ning aja tajumise vahel. Selline strateegia
võib osutuda väärtuslikuks emotsionaalsete ajamodulatsioonide alusmehhanis-
mide väljaselgitamisel. Uuringus V rakendati afektiivse tähelepanu korrelaate
aga aju eesmise aktiivsuse asümmeetria teoreetilise käsitluse uuendusvajadusele
osutamiseks. Kuigi ajupoolkerade esiosade erinevat aktivatsiooni on seostatud
afektiiv-motivatsiooniliste lähenemis- ja eemaldumissüsteemide tööga, ei leia
selle mudeli ennustused alati kinnitust, eriti kui süsteemide aktiviseerimiseks
kasutatakse emotsionaalseid fotosid. Seni on kummastavas probleemis süüdis-
tatud peamiselt piltide nõrka ja inimeseti varieeruvat motivatsioonilist olulisust.
Kui see oleks aga ammendav põhjus, peaks puuduvaid asümmeetria efekte saat-
ma ka puuduv emotsionaalne tähelepanu. Uuringu V tulemused seda versiooni
aga ei toeta ning osutavad seega vajadusele parandada olemasolevat asüm-
meetria raamistikku.

Viimaks püstitati antud doktoritöös ka rida laiendatud hüpoteese tulevasteks uuringuteks. Esiteks pakuti emotsionaalse tähelepanu kahe faasiga seotud fenomenide seletuseks välja, et spetsiifiliselt emotsionaalne tähelepanuline võimendus mõjub sensoorsetele representatsioonidele varem kui tahtliku tähelepanu signaalid. Teiseks on tõenäoline, et alfa ja ka teeta võimsuses peegelduv dünaamika pärineb ennekõike kognitiivsetest süsteemidest samal ajal kui sündmuspotentsiaalid võivad peegeldada nii kognitiivseid kui afektiivseid sisendeid. Need, nagu ka paljud teised selle töö tulemused, vajavad ja väärivad edasist uurimist.

PUBLICATIONS

CURRICULUM VITAE

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2008–…   researcher, Institute of Psychology, University of Tartu
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Scientific publications
Uusberg, A., Thiruchselvam, R., & Gross, J. J. (2014). Using Distraction to Regulate Emotion: Insights from EEG Theta Dynamics. *International Journal of Psychophysiology*, *91*(3), 254–260.

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