DISSERTATION

The distribution of attention in RSVP tasks and its sensitivity to affect, personality traits and estradiol

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"கற்றது கைமண் அளவு

கல்லாதது உலகளவு"

- அவ்வையார்

"What we have learnt is a mere handful,

What we have not learnt is the size of the world"

- Avvaiyar

Abstract

Attention is influenced by several factors. In this thesis, the influences of positive and negative affect state, the personality factor neuroticism, and the hormone estradiol on selective attention are explored in three separate studies. In Study 1, positive and negative affect was induced before participants attended one of the two centrally overlapping streams of letters of different sizes flickering at different frequencies. This paradigm was used to study the neural basis of the diffuse and focused mental states reported in behavioural studies as modulating attention. We expected that if positive affect induced a diffusion of attention, the steady state visual evoked potential (ssVEP) power difference between the attended and ignored stream would be less. Conversely if negative affect focused attention, the difference between the attended and ignored stream of letter frequency would be more. We found an increase in power at the attended frequency compared to the when it was ignored, which validated the paradigm used. An increased power in the negative affect condition was also found, but the expected spatial expansion and contraction of the spotlight of attention was not observed during affect manipulation. This prompted us to examine the diffuse mental state as a concept relating to cognitive flexibility in Study 2. Here, the neural basis for the focused cognitive style of those with higher neuroticism was investigated. The same paradigm as in Study 1 was used and we hypothesised that those with higher neuroticism will likely overinvest attention into irrelevant information, especially when it is more salient than the relevant information. This will be reflected in an increased difficulty in switching attention from the larger, slower salient stream of letters to the smaller, faster one. In terms of ssVEP, power differences between the attended small stream and the ignored large stream were expected to be lower for those with higher scores of negative emotionality trait. This pattern was found in the results. We also found a positive correlation between this power difference and extraversion scores which suggested that as this trait increased, so did cognitive flexibility and control. This was in line with previous literature that contrasts the extraversion and neuroticism in their influence on attention. In Study 3, we departed from the psychological into the impact of the biological factor of the hormone estradiol which fluctuates through the menstrual cycle of women. Fluctuating estradiol concentrations are known to influence functional hemispheric asymmetry and attentional performance. The underlying changes in alpha band activity were investigated as a possible mediator for this influence over performance. A stream of rapid visual stimuli was presented in either visual field. Participants were asked to detect two targets in close succession within the streams. We hypothesised that

with increased estradiol concentration, the occurrence of the attentional blink (AB) in the right hemisphere would increase and the alpha asymmetry between the hemispheres would decrease. Though alpha seemed to be related to both behavioural performance as well as estradiol concentrations separately, no direct relationship between estradiol and behaviour was seen. In all, the findings in this thesis contribute to the current understanding of how attention distribution is influenced by affect state, personality trait and estradiol.

Zusammenfassung

Aufmerksamkeit wird durch verschiedene Faktoren beeinflusst. In dieser Arbeit wurde untersucht, wie geteilte Aufmerksamkeit von positiven und negativen Gefühlszuständen, vom Persönlichkeitsfaktor Neurotizismus und vom Hormon Estradiol beeinflusst wird. Die Arbeit setzt sich aus drei einzelnen Studien zusammen.

In Studie 1 wurden Probanden in einen positiven oder negativen Gefühlszustand versetzt und anschließend mit zwei sich überlappenden, seriell präsentierten Buchstabenfolgen unterschiedlicher Größe konfrontiert. Die serielle Präsentation der Buchstaben erfolgte dabei mit unterschiedlicher Geschwindigkeit für beide Buchstabenfolgen. Zweck dieses Paradigmas war es, auf Basis der bereits zu diesem Thema bestehenden Verhaltensstudien, die neuronalen Grundlagen von diffusen und fokussierten mentalen Zuständen näher zu untersuchen. Unsere Erwartung war, dass falls der positive Affektzustand eine Aufmerksamkeitsstreuung herbeiführen würde, dass sich dann die Unterschiede in der Signalstärke des steady state visual evoked potentials (ssVEP) zwischen der beachteten und ignorierten Buchstabenfolge verringern müssten. Ebenso erwarteten wir, dass falls der negative Affektzustand eine Aufmerksamkeitsfokussierung herbeiführen würde, die Differenz in der ssVEP-Signalstärke zwischen der beachteten und ignorierten Buchstabenfolge höher sein müsste. Obwohl wir einen Signalstärkeanstieg in der jeweilig beachteten Frequenz bei allen Gefühlszuständen fanden, welches die Effektivität dieses Paradigmas bestätigt, konnte eine räumliche Erweiterung und Verengung des Aufmerksamkeitsfokus während der Evozierung des negativen Gefühlzustandes nicht beobachtet werden. Dies brachte uns dazu, den diffusen mentalen Zustand als ein Konzept anzusehen, welches mit kognitiver Flexibilität im Zusammenhang steht. In der zweiten Studie wurden daher die neuronalen Grundlagen untersucht, die einem eher „fokussierten“ kognitiven Stil bei Personen mit erhöhter Neurotizismusausprägung zu Grunde liegen. Hierzu wurde dasselbe Paradigma wie in der ersten Studie verwendet. Unsere Hypothese war, dass diejenigen Personen mit höherer Neurozitismusausprägung dazu tendieren würden, übermäßig viele ihrer Aufmerksamkeitsressourcen auf irrelevante Information zu legen, insbesondere dann, wenn diese Information eine höhere Salienz aufweist, als die eigentlich relevante Information. Darüber hinaus vermuteten wir, dass es den Probanden mit höherer Neurotizismusausprägung schwerer fallen würde, ihre Aufmerksamkeit zwischen der größeren, langsameren und salienteren Buchstabenfolge und der kleineren, schnelleren Buchstabenfolge zu

verschieben.Was die ssVEPs anbelangt, erwarteten wir, dass zwischen der beachteten kleineren Buchstabenfolge und der ignorierten größeren Buchstabenfolge kleinere Signalstärkedifferenzen bestehen würden, falls diejenigen Probanden eher hohe negative emotionale Valenzen angegeben haben. Dieses Muster wurde in den Ergebnissen auch gefunden. Darüber hinaus fanden wir eine positive Korrelation zwischen der ssVEP-Signalstärke und der Persönlichkeitsskala für Extraversion, Dies weist darauf hin, dass, Extraversion mit kognitiver Flexibilität und Kontrolle zusammen hängt. Diese Beobachtung deckt sich mit der verfügbaren Literatur hinsichtlich des Einflusses von Extraversion und Neurotizismus auf Aufmerksamkeit. In Studie 3 haben wir uns dann weniger mit psychologischen Faktoren, sondern mehr mit biologischen Faktoren der Aufmerksamkeitsmodulation auseinander gesetzt. Insbesondere haben wir uns mit dem Hormon Estradiol beschäftigt, welches mit dem Menstruationszyklus der Frau fluktuiert. Fluktuationen in der Estradiolkonzentration sind dafür bekannt, funktionelle Asymmetrien der Hirnhemisphären und die Performance in Aufmerksamkeitsaufgaben zu beeinflussen. Estradiol bedingte Veränderungen im Alpha-Frequenzband wurden als ein möglicher Mediator für einen Einfluss auf Aufmerksamkeitsperformance untersucht. Eine schnell präsentierte Buchstabenfolge wurde in jedem visuellen Feld präsentiert und die Probanden wurden aufgefordert, auf zwei Zielreize zu achten, die kurz aufeinander folgend in beiden Buchstabenfolgen präsentiert wurden. Unsere Annahme war, dass mit erhöhter Estradiolkonzentration das Auftreten eines attentional blinks in der rechten Hemisphäre steigen würde und dass die Alphasymmetrie zwischen den Hemisphären niedriger werden würde. Obwohl sowohl die Signalstärke des Alpha-Frequenzbandes mit Aufgabenperformance sowie mit der Estradiolkonzentration einher ging, wurde kein direkter Zusammenhang zwischen Estradiol und Verhalten gefunden. Alles in allem leisten diese Ergebnisse einen wichtigen Beitrag zum Verständnis von Aufmerksamkeit und wie diese durch Affekt, Persönlichkeit und Estradiol beeinflusst wird.

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Author's Note

This PhD has been an enriching journey. I have learnt how to frame research questions, design paradigms that will explore them, analyse data in both exploratory and directed ways, and write up the work coherently. In the process I have picked up programming and statistics skills from scratch in using software tools like MATLAB, EEGLAB, Presentation and SPSS with the help of courses such as Introduction to Scientific Programming, Computer Controlled Experimentation, and EEG analysis with MATLAB. Other courses I took enhanced my knowledge in Neuropsychology. They included Introduction to Cognitive Neuroscience, Statistics, Psychological Assessment and Diagnostics, Neurocognitive Development, Perceptions and Illusions, and Communication of Scientific Results. I have also understood more about the processes involved in science; the amount of time, effort and detailed work that goes into each discovery, how important people are in giving critical insight and guidance. And in this gruelling struggle called a PhD, I have learnt something about humility, discipline, patience, and hard-headed perseverance and determination. I am grateful for all that I have learnt.

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List of Acronyms

AB	Attentional Blink
ADHD	Attention Deficit Hyperactive Disorder
BCI	Brain Computer Interface
DSM	Diagnostic and Statistical Manual of Mental Disorders
DTI	Diffusion Tensor Imaging
EEG	Electroencephalography
FCA	Functional Cerebral Asymmetry
fMRI	Functional Magnetic Resonance Imaging
FSH	Follicle Stimulating Hormone
Hz	Hertz
IAPS	International Affective Picture System
LH	Leuteinising Hormone
MEG	Magnetoencephalography
ms	milliseconds
NEO-FFI	NEO Five Factor Inventory
NIRS	Near Infra Red Spectroscopy
OCEAN	Openness, Conscientiousness, Extraversion, Agreeableness, Neuroticism
PANAS	Positive Affect Negative Affect Scale
RSVP	Rapid Serial Visual Presentation
SAM	Self-Assessment Manikins
SART	Sustained Attention to Response Task
ssVEP	Steady State Visual Evoked Potential
T1	Target 1
T2	Target 2
T2|T1	Detection of T2 after T1 detection

Glossary

Attentional Awakening - During a single target detection task, detection accuracy is found to be worse at the beginning of the RSVP than later (Ariga & Yokosawa 2008).

Attentional Blink - The AB is a phenomenon of temporal attention, whereby the conscious perception of a second target is impaired when it appears within about 200 - 500 ms after a first target (Raymond, Shapiro & Arnell, 1992).

Attention Deficit Hyperactivity Disorder - This is a psychiatric disorder where there is hyperactivity, problems in attention, and impulsiveness beyond what is acceptable for the patient's age.

Attention Effect – The increase in power of the frequency of the ssVEP elicited by steady flickering stimuli when it is attended as opposed to ignored

Extraversion – A personality trait which characterises the level to which one is sociable, energetic, talkative, cheerful and seeks the company of others

Hand-use Effect - In a line bisection task, the bias towards pseudoneglect is larger than for the right hand than the left.

Hemispatial Neglect - Also known as 'unilateral neglect' occurs when the one hemisphere of the brain is damaged, causing one side of the person's visual field, objects and own body to be ignored. It is most often associated with a lesion in the right parietal lobe and neglect of the left side.

Neuroticism - A personality trait which is characterised by the tendency to experience unpleasant emotions such as anxiety, anger, guilt, depression or jealousy for long periods and easily.

Pseudoneglect - A mild asymmetry in spatial attention seen where the left side of space is favoured. This is seen in line bisection tasks as well as in judgements regarding brightness, size and numerosity.

Vipassana - a type of mindfulness meditation technique which is used to become sharply aware of reality.

1.

Overview

In 1890, in the book Principles of Psychology, William James said:

"*Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called distraction, and Zerstreutheit in German.*"

Since then, much work has been done exploring the process of attention but there is still so much to learn. In this thesis we explore the influence of three factors on attention.

Chapter 2, introduction, starts with a brief note on the nature of attention and lists some overlapping types of attention. Then some common methodologies used to study selective attention, such as RSVP, AB and ssVEP, are introduced and expounded upon so the reader is able to relate to these concepts and terms later. In the next section 2.2, factors that influence selective attention are touched upon. Further detail is given about the three factors that will be explored in the empirical section of this thesis. For each of these factors - affect state, personality factors and estradiol - a brief background is given followed by useful background literature that will familiarise the reader with the current understanding of how these factors influence attention. Next, in 2.3, a few examples of the specific ways in which the previously mentioned methodologies are used to study aspects of attention are mentioned. The objectives of this thesis and the studies within are explained.

Chapter 3 presents the published study that investigates the neural basis of how short term affect state, as induced by emotional pictures, modulates attention paid to larger and narrower streams of stimuli. Chapter 4 presents the published study about the effect of the personality factor neuroticism on attention. Neuroticism was found to make it more difficult to switch attention to relevant information. Chapter 5 presents a manuscript in preparation of the third study which examines the neural underpinnings of how estradiol influences attention performance.

Chapter 6, the general discussion, summarises the three studies and goes on to offer some criticism and possibilities for future work which could follow from the insights gleaned from the work presented here. Implications to related areas are touched upon. It ends with an outlook on where studies of attention may be headed from a broader perspective.

2.

Introduction

2.1 An Introductory Note on Attention

We are constantly given sensory input through all modes. At any given instant, there is an abundance of information available to process; from colours, shapes, movements and distance of objects in our environment in a dominant sensory modality like vision, to various sounds in different frequencies, loudness and timbre in the auditory modality, to information such as temperature, tactile pressure, texture, tastes and smells. We process only a fraction of this. Attention is the ability to filter information that is relevant for our functioning in order to further process it. The objects of our attention changes based on the activity we aim to perform. For example, while listening to someone speak at a party we are able to tune ourselves into that person's voice and content, and ignore the other sounds. This is a well-known phenomenon termed 'the cocktail party effect' (Pollack & Pickett 1957). Another famous example of selective attention comes from the 'invisible gorilla experiment' where, while participants count the number of passes between white-shirted basketball players, they easily miss a human dressed as a gorilla who walks into the scene and waves directly at the camera (Simons & Chabris 1999).

Several overlapping aspects of attention have drawn the interest of researchers over time.

(1) *Attention span*, which is of special interest to educators and child psychologists. This type can be subdivided into two types; (a) focused attention, a form of short-term attention, and (b) sustained attention, the ability to concentrate on a task for extended periods of time without being distracted or becoming tired (Cornish & Dukett, 2009). It is also often studied in relation to working memory, executive functioning as well as disorders such as Attention Deficit Hyperactivity Disorder (ADHD) (Bellgrove, Hawi, Kirley, Gill & Robertson, 2005; Engle 2002).

(2) *Divided attention*, the capacity to handle more than one task simultaneously, and how the effectiveness and speed of each task is impacted by multi-tasking (Matlin 2013).

(3) *Selective attention*, which enables one to attend to relevant stimuli even in the presence of distractors. There are different models for how this works for visual attention including the two-stage processing model which includes uniform spatial attention where information is

processed in parallel in the first stage, followed by a focusing of attention when processing follows a more serial method in the second stage (Jonides 1983). Another model which has gained more attention in the recent years is the 'zoom lens model' originally proposed by William James where attention is shaped like a spotlight or doughtnut (Eriksen & James 1986; James 1890; Müller & Hübner 2002; Posner 1980). In this model, there is the central area of focus where most visual information is extracted, followed by a margin where lower level visual processing occurs, followed by the margin beyond, in which very little information is processed. This model was further improved upon by adding the ability of the zoom lens to change in size. Selective attention is an integral part of studying spatial and temporal attention.

(4) *Spatial attention*, a process that selects stimuli based on their spatial location. It is mainly studied in the context of cueing the attention to certain areas of the visual field, but also in the context of the way in which the area of attention expands, contracts and changes shape based on the task (Müller, Malinowski, Gruber & Hillyard, 2003; Müller & Hübner 2002; Müller, Picton, Valdes-Sosa, Riera, Teder-Salejarvi & Hillyard, 1998). Hemispatial neglect, also referred to as 'unilateral neglect' is a disorder which sheds more light on factors that influence spatial attention. It occurs when the one hemisphere of the brain is damaged, causing one side of the person's visual field, objects and own body to be ignored. It is most often associated with a lesion in the right parietal lobe and neglect of the left side.

(5) *Temporal attention*, which can be subdivided into two aspects; (a) the attention towards time, which can inform us of the passage of time and allow us to approximate when to execute an action in order for it to have an effect at the desired time. Research shows that if fewer resources are directed to attending time, the perceived duration seems shorter (Zakay 1989). And (b) the attention within time, which is the capacity to process stimuli which are not visible for long and select the relevant information from several such stimuli that occur in quick succession (Coull 2004). The latter is primarily studied with behavioural experiments that use the rapid serial visual presentation (RSVP) paradigm, especially involving the attentional blink (AB) phenomenon (Olivers & Meeter 2008; Shapiro, Raymond & Arnell, 1997). The terms RSVP and AB are explained in the next section.

2.1.1 RSVP, AB and ssVEP

Rapid serial visual presentation (RSVP) is a common experimental model used for studying selective attention. An RSVP is a series of letters, numbers or images presented in the same visual location at a rapid frequency, with between 3.5 and 75 items per second (Beverina, Palmas, Silvoni, Piccione & Giove, 2003), to which participants of the experiment are asked to attend. Within this stream of stimuli, targets are embedded which the participants are instructed to identify or respond to. The stimuli that are not the targets are called distractors. A specific type of RSVP paradigm is the Attentional Blink (AB) task where typically ten items are presented per second. It usually contains two targets (T1 and T2), and when the second target (T2) is presented within 200 to 500 ms after the first target (T1), there is a noticeable gap in perception of the second target (T2) (Raymond et al. 1992). This phenomenon is referred to as the Attentional Blink (AB) and is widely used to study the dynamics within temporal attention (e.g., Husain, Shapiro, Martin & Kennard 1997; Olivers and Nieuwenhuis 2005). Though this is the simplest version of the AB task, other variations are possible. For instance, instead of two targets in an RSVP, a single distractor followed by a target/probe may also cause the occurrence of the blink (Bredemeier, Berenbaum, Most & Simons 2011; Folk, Leber & Egeth 2002). Terms such as lag 2 and lag 7 are commonly used in AB studies and refer to the time after the presentation of the T1-equivalent stimulus when the T2-equivalent stimulus occurs. Lag 2 is two stimuli items after T1 which is roughly 200 ms after T1 for a stimulus presentation frequency of 10 Hz. The AB will be clearly evident here, whereas lag 7 is seven stimuli after T1, roughly 700 ms after T1, which is well after an average blink. This is indicated in several examples (Chun 1997; Kranczioch, Debener & Engel 2003; Kranczioch, Debener, Schwarzbach, Goebel & Engel, 2005). Thus the comparison between the two lags and calculations of the performance at each lag are often important in determining and illustrating the magnitude and typical pattern of the AB. The occurrence of the AB shows that temporal attention is limited, but AB research also reveals the flexibility within this type of attention. Several aspects of this flexibility are still unclear.

Another common use of an RSVP is to elicit a steady-state visual evoked potential (ssVEP). An ssVEP is an unconscious and involuntary electrical response in the brain elicited by retinal level visual stimulation at a steady frequency between 3.5 and 75 Hz (Beverina et al. 2003). The ssVEP occurs at the same frequency as the stimulated frequency, and at multiples thereof (Morgan, Hansen & Hillyard 1996; Müller, Teder & Hillyard 1997). It is used commonly in experimentation as well as applications such as Brain Computer Interface (BCI) as it is a very stable and robust signal and relatively immune to artifacts (Müller-Putz, Scherer, Brauneis & Pfurtscheller 2005; Parini, Maggi, Turconi & Andreoni 2009). In research it is especially useful in studying spatial selective attention.

2.2 Factors that Influence Selective Attention

A large number of studies indicate that the efficiency of the distribution of attention is dependent on several factors. Caffeine and theanine, for example, have been associated with reduction in the alpha (neural oscillations between 8-13 Hz) power and improvements in performance in a sustained attention to response task (SART) as well as in selective attention tasks such as intersensory attentional cueing (Foxe, Morie, Laud, Powson, De Bruin & Kelly 2012; Gomez-Ramirez, Higgins, Rycroft, Owen, Mahoney et al. 2007; Kelly, Gomez-Ramirez, Montesi & Foxe 2008). Nicotine, on the other hand, has been linked with an increase in amplitudes in an induced ssVEP (Thompson, Tzambazis, Stough, Nagata & Silberstein 2000) and impairment of selective attention as measured by performance accuracy (Vangkilde, Bundesen & Coull 2011). In general, though, selective and divided attention are not as susceptible to the effects of nicotine as sustained attention (for reviews, see Heishman, Kleykamp & Singleton 2010; Heishman, Taylor & Henningfield 1994). Meditation has been related to cognitive flexibility by numerous studies and hence is advantageous to attention tasks (Brefczynski-Lewis, Lutz, Schaefer, Levinson & Davidson 2007; Moore & Malinowski 2009; Zeidan, Johnson, Diamond, David & Goolkasian 2010). This is seen for instance in AB tasks where regular meditators as well as those who were newly trained in daily mindfulness or Vipassana meditation have shown better T2 detection performance than controls (Slagter, Lutz, Greischar, Francis, Niewenhuis et al 2007; van Leeuwen, Müller & Melloni 2009). The AB and thus the distribution of attention in time is also linked to psychological disorders such as dysphoria that are associated with an increase in the length of the AB (Koster, Raedt, Verschuere, Tibboel & De Jong 2009; Rokke, Arnell, Koch & Andrews 2002). Spatial neglect has also been linked to an increase in the length of the blink to up to three times the normal length (Husain et al. 1997) demonstrating that hemispatial neglect is characterised by impairment in not only spatial but also temporal attention. Those with dyslexia also are also seen to have roughly a 30% increase in the length of the blink (Hari, Valta & Uutela 1999) and those with ADHD display great difficulty in T2 detection (Armstrong & Munoz 2003).

Three major factors that have an important effect on selective attention are affect state, personality trait and hormones (Holländer, Hausmann, Hamm & Corballis 2005; MacLean & Arnell 2010; Olivers & Nieuwenhuis 2006), and they are of primary interest in this thesis. Following is a more detailed introduction to each of the factors.

2.2.1 Affect State

Emotional states are often measured in terms of valence and arousal. While valence ranges from highly positive to highly negative, arousal ranges from calming or soothing to exciting or agitating. (Lang, Greenwald, Bradley & Hamm 1993; Russell 1980). The concept of valence has been used in most psychological studies on emotions since it was first coined in 1935 by Kurt Lewin (Lewin, Heider & Heider 1936; Solomon & Stone 2002). Positive valence implies intrinsic attractiveness and a positive affect state, as opposed to negative valence, which implies aversiveness to an object or situation and a negative affect state (Frijda 1986). Emotion has been shown to affect cognition by several studies, having specific effects on aspects like perception and attention, learning and memory, and behavioural inhibition and working memory (Damasio 2000; LeDoux & Bemporad 1997; Phelps 2006).

Of particular interest here is how one's emotional state remarkably influences how one's attentional resources are distributed, both spatially and temporally. Spatially, negative affect state has been shown to narrow the attentional field and positive affect has been shown to broaden the scope of attention (Fenske & Eastwood 2003; Fredrickson & Branigan 2005; Gable & Harmon-Jones 2010). These studies used tasks that shed light on the changing breadth of attention, such as flanker tasks, global-local visual processing task, and others that compare processing at a central location to peripheral processing. They also use thought-action tendencies, a measure of cognitive inclination which may lead to action, to reflect on relative breadth of the momentary thought-action repertoire (Fredrickson 1998).

Studies on the impact of affect on temporal visual attention distribution have shown that negative affect causes impairment in second-target detection in an AB task (Most, Chun, Widders & Zald 2005; Smith, Most, Newsome & Zald 2006). As a corollary, positive affect states are associated with better AB task performance. Olivers and Nieuwenhuis (2005) found that when participants performed an AB task while either simultaneously free-associating on a task-irrelevant theme or listening to music, the AB was diminished. In their subsequent study in 2006, they proposed that overinvestment of the limited resources of attention was the reason for the occurrence of the AB. They suggested that this can be countered by introducing an activity that defocuses, or diffuses attention. In one of the behavioural experiments of their 2006 study, they demonstrated an improvement in AB task performance when the RSVP AB trials were preceded by positive International Affective Picture System (IAPS) pictures. They suggested in their positive affect hypothesis, that positive affect diffuses the attentional resources up to an optimal level where, though T1 would be processed, there would still be enough resources to process the closely-following T2. Other studies have also found the same impact of affect state on attention distribution. Vermeulen (2010) for instance, found that participants reporting a higher score in the positive affect measure of a questionnaire more often reported the second target than those who scored higher on the negative affect measure. Shapiro, Schmitz, Martens, Hommel and Schnitzler (2006) used whole-head magnetoencephalography (MEG) to reveal that the AB could be successfully predicted based on how much of the attentional resources were allocated to the processing of T1. This finding seems to support the suggestion that the AB is more due to processing strategy than a structural processing bottle-neck.

Though the impact of affect states on temporal attention has been demonstrated by behavioural studies, especially using the AB paradigm, few studies have explored the neural mechanisms behind the diffuse mental state. In this state, is it only temporal attentional distribution that is diffused or focused by the overinvestment of attention or is it also the spatial distribution? And what is the meaning of the overinvestment of attention at a neural level? The underlying mechanisms are not clear at present.

2.2.2 Personality Traits

Closely related to the influence of affect states is the impact that certain personality traits have on the distribution of attention. There are several ways of dividing personality factors of which the five factor model, also known as 'the Big Five' is widely accepted and commonly used in research (Goldberg 1990). It includes (1) openness to experience, characterised by the appreciation for unusual ideas, adventure, art, and overall curiosity; (2) conscientiousness, characterised by efficiency, organisation, self-discipline and reliability; (3) extraversion, the level to which one is sociable, energetic, talkative, cheerful and seeks the company of others; (4) agreeableness, characterised by friendliness, helpfulness and patience; and (5) neuroticism, characterised by the tendency to experience unpleasant emotions such as anxiety, anger, guilt, depression or jealousy for long periods and easily. These five factors (OCEAN) are regarded as largely independent of each other. Another characterisation called the Temperament and Character Inventory (Cloninger, Przybeck & Svrakic 1994) labels four temperaments - novelty seeking, harm avoidance, reward dependence, persistence - and three characters – self-directedness, cooperativeness and self-transcendence. Another type of division of traits is Raymond Cattell's 16 Personality Factors (Cattell & Eber 1950) and includes factors such as warmth, reasoning, emotional stability, dominance, vigilance, abstractedness etc.

Studies that investigate how personality factors influence spatial attention seem to focus on the use of vertical space. Neuroticism is shown to favour the faster and more accurate processing of spatial attention targets in lower physical space (Meier & Robinson 2006). And individuals with higher levels of the factor dominance seem to process targets along the vertical space better than in the horizontal space (Moeller, Robinson & Zabelina 2008).

In terms of temporal selective attention, people with higher harm-avoidance trait were found to be unable to use an attentional strategy to reduce the occurrence of the AB, while those with lower levels of this trait were able to use the strategy to their advantage (Most et al. 2005). MacLean and Arnell (2010) showed that smaller ABs were linked with greater openness and extraversion, whereas larger ABs and lower accuracy were linked with higher neuroticism and conscientiousness. MacLean, Arnell and Busseri (2010) also found that positive disposition shortened the AB, whereas negative disposition lengthened it. They explained this in terms of variations in cognitive flexibility that each trait bestows upon the individual. While the diffuse mental style is associated with cognitive flexibility, the focused cognitive style associated with negative emotionality is associated with overinvestment of attentional resources. The overinvestment theory suggests that there is a tendency to overinvest attentional resources into the RSVP stream such that there is an attempt not only to process the targets but also the distractors. The diffuse mental state idea suggests that by using positive affect or simultaneous secondary tasks, it may be possible to create a diffusion of the attentional resources so that the threshold of attention is moved up optimally, only the intended targets are processed, and the distractors are ignored. Similar to affect state studies, this explanation fits well with the behavioural findings in studies that explore the influence of personality traits on selective attention. However, studies that could shed light on the neural mechanisms underlying the effects are lacking.

2.2.3 Estradiol of the Menstrual Cycle

Various hormones are involved in the female menstrual cycle. This is illustrated in Figure 1. *Follicle stimulating hormone (FSH)* starts to increase in concentrations at the beginning of the cycle, which stimulates a follicular cell in one of the ovaries to grow and develop, absorbing nutrition from its surroundings. When it has grown, on day 14, a spike in *oestrogen*, *FSH* and *leuteinising hormone (LH)* causes the ova to be released out of the ovary in a process called ovulation. This stage is referred to as the ‘follicular’ phase. This leaves the shell of the ova near the outer edge of the ovary from where it releases *progesterone* and the *oestrogen* family of hormones in order to stimulate the thickening of the endometrial lining preparing for possible implantation of a fertilised egg. This stage, in which the corpus luteum releases *progesterone* and *estradiol* and the ova is travelling down the fallopian tube, is called the ‘luteal’ phase. When the egg is not fertilised and continues down toward the uterus, the levels of progesterone and estradiol also drop. This weakens and sloughs off the endometrial lining leading to menstrual bleeding in what is called ‘menses’ (Silverthorn, Ober, Garrison, Silverthorn & Johnson 2009).

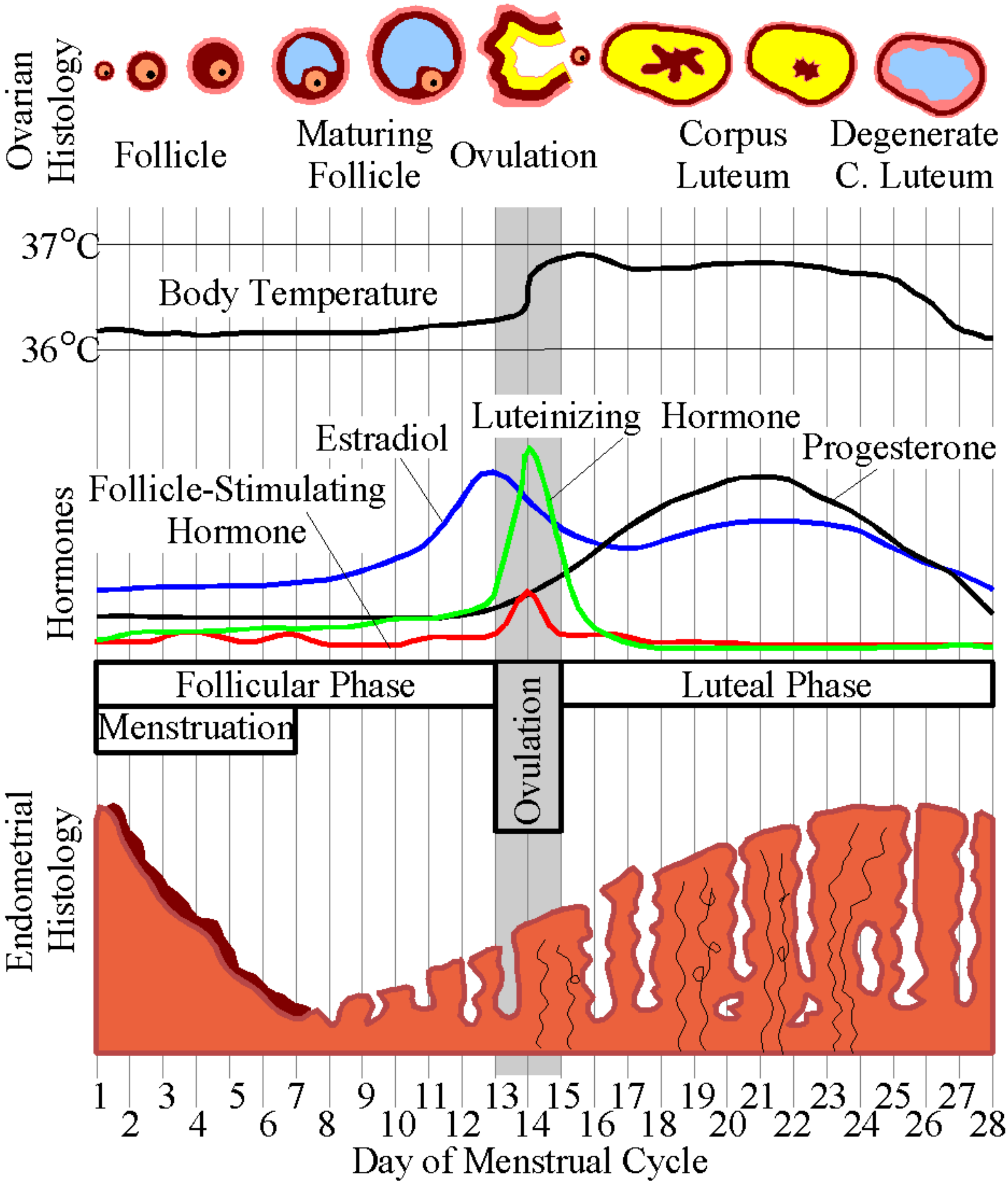

Figure 1. An illustration of the fluctuations in hormone levels during an average menstrual cycle. Image credit: WikiCommons

Estradiol and progesterone have been shown to modulate the functional cerebral asymmetries (FCA) of the brain during the menstrual cycle (Hausmann & Güntürkün 2000; Rode, Wagner & Güntürkün 1995). Depending on the task, higher asymmetry is seen either during the follicular phase or during menses (Bibawi, Cherry & Hellige 1995; Rode et al. 1995). During attentional tasks, menses shows a higher brain asymmetry than the follicular phase. In terms of spatial attention, a study by Hausmann (2005) showed that the hand-use effect in a visual line bisection task decreased during high estradiol levels in the mid-luteal phase compared to during menses. The usual observation is that when the left hand is used in a line bisection task, the bias towards pseudoneglect is larger than for the right hand. However this effect is reduced during the mid-luteal phase where asymmetry between the hemispheres is seemingly reduced. In the Holländer et al. (2005) study, an RSVP was used in either the left or the right visual field with an AB task. The authors also measured both progesterone and estradiol levels. Their results showed that the AB seemed to be restricted to the left hemisphere during menses, but occurred in both hemispheres in the mid-luteal phase. Furthermore they found that this effect seemed to be mediated by estradiol rather than progesterone.

Hausmann and colleagues explain this by hormone-mediated decoupling of the two hemispheres (Hausmann & Güntürkün 2000; Hausmann, Hamm, Waldie & Kirk 2013). During menses, in the asymmetrical state, the dominant hemisphere has an inhibitory effect on the non-dominant hemisphere. The increase in estradiol and/or progesterone reflects in the decoupling and equal participation of both hemispheres. As a result, higher estradiol and progesterone concentrations are seen to enhance the occurrence of the AB in the right hemisphere. Hausmann's theory has evolved over time to acknowledge the role of estradiol, and with the study by Holländer et al. (2005) it seems likely that estradiol may indeed be the primary hormone driving this process. The idea that an increase in estradiol results in more equal activation of the two hemispheres has been tested only in a few studies (Holländer et al. 2005; Hausmann et al. 2013) and not specifically for temporal attention. More direct physiological research is necessary to support this idea.

2.3 The Use of RSVP and ssVEP in Attention Studies

2.3.1 The Use of RSVP in Distractor Processing

Several studies involving RSVP offer insight into the processing of distractors. Distractors that share some property with the target are effective in causing a blink. For example, Folk et al. (2002) explored whether the certain foreknowledge of the location of the target would eliminate attentional capture induced by irrelevant stimuli at a spatially-different location. They showed that a T1-equivalent of the same colour peripheral distractor as the T2-equivalent target did lead to a decrement in the identification of the central target causing what they called a spatial blink. In a related study, Bredemeier et al. (2011) showed that those with higher levels of the personality trait neuroticism, found it more difficult to disengage from an irrelevant distractor such as a green letter before the target red letter than those with lower scores. The authors interpreted these findings with respect to attentional capture and salience of the distractor, as the same difficulty in disengaging was not found when the distractor was less salient. These studies showed how a distractor sharing the features of the target, either colour or form, can interfere with target detection performance.

2.3.2 RSVP Reveals Attentional Awakening

Ariga and Yokosawa (2008) found that in a single target detection task, detection accuracy was worse at the beginning of the RSVP than later. They named this phenomenon attentional awakening. Kranczioch and Bryant (2011) found that between the focus of temporal attention and resource allocation, the latter contributed more to influencing the attentional awakening. Kranczioch and Dhinakaran (2013) found that temporal context, meaning the position of the target in the stream, rather than expectancy, based on the increased probability of target occurrence at later time positions, was a key reason why attentional resources were allocated to the processing of the target.

2.3.3 Uses of ssVEP in Studying Spatial Selective Attention

While the RSVP is commonly used to study temporal attention, when there is more than one stream simultaneously presented it can also be used to study the distribution of spatial attention. This is because when a flicker of a certain frequency is attended, the power of the ssVEP at that frequency is known to increase. This phenomenon is sometimes referred to as the ‘attention effect’. For example, in a study by Müller et al. (1998), when flickering LED displays of different frequencies (20.8 Hz and 27.8 Hz) were presented in the left and right visual fields respectively, the power values of the frequency of the ssVEPs indicated which visual field the participant was attending more strongly. Thus ssVEPs can be useful in determining where attention is being paid. In another study by Müller and Hübner (2002) RSVP streams were presented centrally but in different sizes, one inside the other, and at different frequencies. Within this double-RSVP ‘doughnut’ paradigm, a comparison of the power at each induced frequency when attended as opposed to when ignored, indicated that the shape of the spotlight of attention could be similar to a doughnut or ring torus. It showed that the spotlight is not an absolute area but that it is able to flexibly ignore irrelevant parts within the same physical space. Müller et al. (2003) further looked to give a more detailed picture of the spotlight or spatial distribution of attention by using four RSVP streams of different frequencies. The authors asked participants to focus on a combination of two of the four streams and respond quickly once they spotted the target combination. They found that the spotlight of attention can be divided for sustained periods of time, an efficient way of distributing attention to different parts of a visual scene. These studies attribute remarkable flexibility to the ability of the visual system to engage in effective early search as well as attention distribution with regard to what is most relevant to the performance of the task.

2.4 Objectives

The three factors of primary interest in this thesis are short lived affect state, long term personality traits, and estradiol concentrations that fluctuate over each month in women. The experiments presented in this thesis used ssVEP and RSVP paradigms and aimed to increase the understanding of the mechanisms behind the modulation of selective attention by these three factors.

In the **first study** included in this thesis, the influence of affect states on attention was explored. Based on the positive affect hypothesis (Olivers & Nieuwenhuis 2006), the neural mechanisms of the diffusion and focusing of attention were explored using a double RSVP doughnut paradigm similar to that used in Müller and Hübner (2002). We reasoned that this annular, doughnut shaped ssVEP paradigm would be most apt to study the modulation of spatial attention, that is, the diffusion or focusing of the spotlight of attention. This modulation was expected to be reflected in the power values of the two ssVEP streams. We predicted that following the positive affect induction, attention would be diffuse. This would lead to a more even power distribution between the two flickering streams, with less power in the attended stream. Hence there would be less power difference between the two streams. Following negative emotion induction, attention was expected to be more focused and accordingly, more power was expected in the attended stream. This would result in the difference between the attended and the to-be-ignored streams being greater. Finding the predicted pattern would support the diffuse mental state hypothesis and contribute to the current understanding of how affect states modulate attention.

The spatial interpretation of the diffuse mental state followed in the first study led us to hypothesise that there would be a literal expansion and contraction of the spotlight. We could not confirm this prediction. An alternative interpretation of the idea of overinvestment of attention was followed in the **second study**. (It must be noted here that the data in the first and second study were collected in the same experiment.) MacLean et al. (2010) interpret the diffuse mental state as that which enhances cognitive flexibility and leads to a more optimal distribution of attention. Overinvestment of attention here takes on a more temporal meaning, as opposed to a spatially orientated interpretation, involving a focused cognitive style that results in difficulty in disengagement after attention capture in individuals with higher dispositional negative affect. Along with this interpretation, and using the same RSVP doughnut paradigm as in the first study, we endeavoured to study the neural correlates of the distribution of attention and its correlation with neuroticism and negative trait emotionality. The strength of attentional engagement was measured by the power values of the ssVEPs induced at different frequencies by the two RSVP streams. We expected that the amount of attentional resources invested in the salient and irrelevant stream as reflected by the difference in power between the attended and unattended stream would be higher with increasing neuroticism scores. Due to its close link, a similar relationship was expected for negative emotionality. As before, finding the predicted pattern would support the diffuse mental state idea. Further, it would contribute to a greater understanding of the underlying neural mechanisms behind the changes in attentional resource distribution with negative trait emotionality.

The **third study** aimed at studying the influence of estradiol on functional cerebral asymmetry (FCA) with respect to temporal attention. A paradigm using RSVPs in both visual fields was used in combination with an AB task. Together with behavioural performance, electroencephalographic (EEG) data were collected both during the task and at rest. Based on previous research (Holländer et al. 2005) it was predicted that AB performance in the right hemisphere, or in the left visual field, would be worse with higher estradiol levels. According to the theory proposed by Hausmann and Güntürkün (2000) this should be caused by estradiol-mediated decoupling of the two hemispheres. We reasoned that given the body of evidence linking brain activity in the alpha band and attention in general (Klimesch 2012) and the AB in particular (Janson & Kranczioch 2011; Janson, Thorne & Kranczioch 2014; Kranczioch et al. 2007; MacLean & Arnell 2011), the postulated change in the hemispheric coupling should be evident in the symmetry of alpha band activity. Moreover, if the estradiol-related modulation of FCA in attention is mediated by a neural process reflected in alpha band activity, mutual correlations would be expected between FCA/performance, estradiol and alpha.

3.

Study 1: *Affect and the Modulation of Attention*

Published as:

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3.1 Abstract

Positive affect has been associated with improvement in performance in various attentional domains. Negative affect has been associated with narrowing of attention and lowering of performance in attentional tasks. Previous behavioural studies have put forth the diffuse mental state idea as the mechanism of these effects, where attentional resources are more evenly distributed during positive affect and more focused during negative affect. To explore neural correlates of this mechanism, a two-stream rapid serial visual presentation (RSVP) paradigm with centrally presented, overlapping streams was used. Participants attended one of the streams at a time and steady-state visual evoked potentials (ssVEP) in response to the attended and unattended streams were recorded in a positive, negative or neutral affect state. We predicted that in the positive affect condition, ssVEP responses to the attended and the unattended stream would be more alike than in a neutral condition. In the negative affect condition, as an expression of a less diffuse mental state, ssVEP responses were predicted to be more dissimilar. Self-assessments confirmed the effectiveness of the emotional manipulation. In the negative affect condition power was found to be higher than in the neutral condition. However, the modulations in the ssVEP did not reflect the predicted neural correlate of the diffuse mental state mechanism. Thus, the results provide evidence for negative affect modulating attention but suggest that the diffuse mental state is not a spatially oriented phenomenon.

3.2 Introduction

Human attention has been shown to be flexible within a range of capacity. This has been explored in studies of temporal attention, in which mood changes are induced, or secondary working memory tasks introduced while participants perform a temporal attention task (Dreisbach & Goschke, 2004; Olivers & Nieuwenhuis, 2005; 2006). Evidence shows that both the positive emotion manipulation and the task-irrelevant mental activity improved temporal attention (Olivers & Nieuwenhuis, 2005; 2006). Similar findings for the effect of emotionally potent positive stimuli have also been reported for other aspects of attention and cognitive domains such as visual neglect, overall breadth of attention, cognitive flexibility, conscious perception, early perception, sustained attention, sensory motor skills and spatial abilities (Beilock, Carr, MacMahon, & Starkes, 2002; Dreisbach & Goschke, 2004; Kuhbandner et al., 2009; Phelps, Ling, & Carrasco, 2006; Rowe, Hirsh, & Anderson, 2007; Schellenberg, Nakata, Hunter, & Tamoto, 2007; Soto et al., 2009; Thompson, Schellenberg, & Husain, 2001). Olivers and Nieuwenhuis were the first to suggest that the mechanism by which this enhancement may work is that of a 'diffuse mental state'. They explain this with respect to what they coined the 'overinvestment hypothesis' in which they suggest that if too much attentional resource is invested in a task, distractors are likely to be processed and this may in turn impede target detection. If attentional resources are instead diffused, either because of a secondary task that diverts attention from the primary task, or by the induction of positive affect, the threshold of attention would change to a level that would aid target detection because distractors would be ignored. In other words, the diffuse mental state, as caused by positive affect or a secondary task, would prevent over- processing of attended information and hence reduce the interference from distractors. Olivers and Nieuwenhuis refer to the effect of positive affect on attention as the 'positive affect hypothesis' (Olivers & Nieuwenhuis, 2006). Though they do not offer a detailed definition of the term 'diffuse', they indicate that this state is characterised by a more even distribution of attentional resources.

Studies also show that the converse effect occurs such that negative affect is associated with a narrowing and focusing of cognitive processing (Bäuml & Kuhbandner, 2007; Fredrickson & Branigan, 2005; Gable & Harmon-Jones, 2010; Storbeck & Clore, 2005). Jefferies, Smilek, Eich and Enns (2008) focused on the experimental modulation of valence and arousal and its effect on the attentional blink (AB). The AB is a phenomenon of temporal attention, whereby the conscious perception of a second target is impaired when it appears within about 200 - 500 ms after a first target (Raymond, Shapiro, & Arnell, 1992). Jefferies et al. (2008) found that the AB was largest for participants in a state of high arousal combined with negative affect (anxious) and lowest for those in a state of low arousal combined with negative affect (sad). Participants with positive affect combined with either high or low arousal showed intermediate performance. Moreover, other studies show that those with severe dysphoria (an emotional state characterised by anxiety, depression or unease) tend to show longer and larger ABs (Rokke, Arnell, Koch, & Andrews, 2002), and that negative disposition increases the AB magnitude (MacLean, Arnell, & Busseri, 2010). MacLean and colleagues (2010) used the positive affect hypothesis as proposed by Olivers and Nieuwenhuis (2006) to interpret their findings and suggested that the performance differences they observed related to a more focused cognitive style in individuals with greater dispositional negative affect. The authors argued that this focused cognitive style causes these individuals to overinvest their attention to the rapid stream of non-targets, which then negatively affects the processing of the second target. To our knowledge, previous studies have not explored the neural correlates of the modulation of the focus of attention resulting from either positive or negative affect state.

Several physiological and behavioural studies have suggested that spatial location plays an important role in visual processing. This is often referred to by phrases such as 'spotlight of attention', 'zoom lens' or 'doughnut' (e.g., Eriksen & St. James, 1986; Müller & Hübner, 2002; Posner & Petersen, 1990). Among other findings, this idea is supported by the finding that in the electroencephalogram (EEG), visual evoked potentials (VEPs) elicited by stimuli presented inside the spotlight or inside the attended area have higher amplitudes than VEPs evoked by stimuli presented outside (Hillyard, Vogel, & Luck, 1998; Luck & Ford, 1998; Luck & Hillyard, 1994). Similar findings have been reported for the steady-state visual evoked potentials (ssVEP) (Müller & Hillyard, 2000; Müller & Hübner, 2002; Müller, Malinowski, Gruber, & Hillyard, 2003). The ssVEP can be evoked by flickering light, but also by a rapid serial visual presentation (RSVP) of simple or complex visual stimuli, and is seen as a robust and sensitive physiological measure of visual information processing (for a recent review, see Vialatte, Maurice, Dauwels, & Cichocki, 2010). Most relevant for the present study, it has been convincingly shown that ssVEP power reflects whether central visual information is attended or ignored (Müller & Hübner, 2002).

The diffuse mental state idea has to date been based on indirect, behavioural evidence (MacLean et al., 2010; Olivers & Nieuwenhuis, 2006). With the present study we therefore aimed to add more direct evidence by studying neural correlates of the diffuse mental state as a spatially-oriented phenomenon. We reasoned that the sensitivity of the ssVEP to attentional manipulations makes it ideally suited for this purpose. We hypothesised that if an experimental manipulation of affect results in a more diffuse mental state or a more focused state, this should be reflected in a modulation of the annular or doughnut shaped spotlight of attention, i.e., the ssVEP attention effect. The attention effect is the increase in ssVEP power if the evoking stimulus stream is attended. In detail, the inducing of positive affect should result in a more diffuse mental state, a spatially more even distribution of attention, and, in consequence, the use of less attentional resource to process a to-be-attended RSVP stream. This would be reflected in a smaller power difference between the ssVEPs evoked by the to-be-attended and the to-be-ignored RSVP streams in a positive affect condition as compared to a neutral affect condition. Following the converse of the positive affect hypothesis, we furthermore hypothesised that a negative affect manipulation would induce a less diffuse mental state and help the focusing of attentional resources on the to-be-attended RSVP stream. This would be reflected in a larger power difference between the ssVEPs evoked by the to-be-attended and the to-be-ignored RSVP streams in a negative affect condition as compared to a neutral affect condition. Finding such differences would substantiate the idea of a 'diffuse mental state' and would add to our understanding of how affect states can influence attention.

3.3 Methods

3.3.1 Participants

The aim was to have 15 participants in the negative affect and the positive affect groups. Allowing for elimination based on effectiveness of emotional manipulation or quality of the EEG data, we recorded a total of 39 right-handed subjects (24 females) between the ages of 19 and 33 (M = 23.9 years) who were monetarily compensated for their time. All had normal or corrected-to-normal vision and were free of past or current neurological or psychiatric disorders. All participants were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Due to technical problems during recording of the EEG two participants had to be excluded from the sample. Five more subjects were excluded because they reported feeling the opposite effect of the intended emotional manipulation; for example, if they were in the positive group and the affect conditions made them feel more negative instead of more positive. The final sample consisted of 18 participants in the positive affect group (12 female, mean age 23.5, range 21 to 28 years), and 14 in the negative affect group (10 female, mean age 24.2, range 21 to 27 years). Beck Depression Inventory-II (Beck, Steer, Ball and William 1996) scores gave no indication of the presence of clinical depression (M=5.6, Std. Dev = 4.9). The study was run in accordance to the declaration of Helsinki and was approved by the ethics committee of the University of Oldenburg.

3.3.2 Stimuli and Procedure

Stimuli and setup

A trial consisted of a picture taken from the international affective picture system (IAPS; Lang, Bradley and Cuthbert, 1999) and a two-stream RSVP of flickering, uppercase letters. The trial started with the presentation of a fixation cross for 500 ms, which was followed by an IAPS picture presented for 1500 ms. This was then followed by another 500 ms of the fixation cross and the RSVP streams of flickering letters that continued for 2500 ms. Thus a whole trial lasted for five seconds (see Figure 2). All stimuli were presented on a 23.6 inch computer screen approximately 160 cm in front of the fixed chair in which the participants were seated. The computer screen was mounted outside the recording booth. Presentation Version 14.8 Build 12 30.10 (Neurobehavioral Systems, San Francisco, USA) was used to deliver the stimuli.

IAPS pictures fell into one of three categories: positive, negative, or neutral. For each category 20 pictures were chosen from the IAPS. Each picture has a standardised rating on a nine-point scale version of self-assessment-manikins (SAM) (Bradley & Lang, 1994) for three dimensions of inner state: valence (from positive to negative), arousal (excited to calm), and dominance (big to small). SAM ratings for the selected IAPS pictures had valence means of 7.5, 2.9 and 5.0 and arousal means of 4.6, 5.2 and 3.4 for the positive, negative, and neutral pictures, respectively. Dominance ratings were of no interest for the present study and are therefore not discussed in this paper. (Please note: there are several versions of SAM, apart from the nine-point version used for standardising IAPS pictures. They include the modified-nine-point scale, five and seven point scale versions as well as all options with a flipped scale.) IAPS pictures were shown in colour, and delimited a viewing angle of 10°x7.5°. Within each experimental block, pictures were all of the same emotional category. Order of presentation was randomised both within each block and across participants.

Similar to the trials in the study by Müller & Hübner (2002) the trials consisted of two RSVP streams, one of large uppercase letters and the other of small uppercase letters within the larger letter presented at fixation. Letters as well as the fixation cross were presented white on black. The large letters that made up the first RSVP stream delimited a viewing angle of 2.11° x 1.94°. The second RSVP stream consisted of the smaller letters that subtended a viewing angle of 0.53° x 0.53°. All letters of the Latin alphabet were used for the RSVP streams except I, J, O, P and W. Presentation frequencies of the two streams were synchronised to the 120 Hz refresh rate of the monitor. Each large letter was presented for 17 frames or 141.7 ms resulting in a frequency of 7.06 Hz. Each small letter was presented for 11 frames or 91.7 ms resulting in a frequency of 10.91 Hz. For the sake of convenience, we will henceforth refer to the two frequencies as simply 7 or 11 Hz.

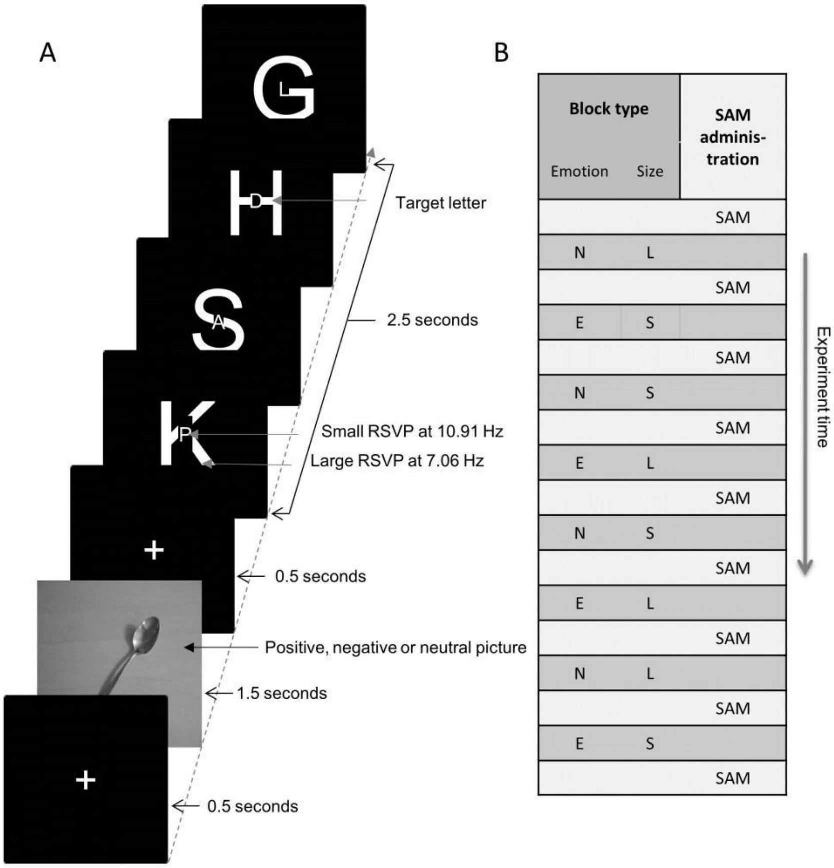

Figure 2(A) Schematic illustration of the experimental paradigm that depicts the arrangement of the RSVP stimuli in terms of the time layout of a single trial. The duration of each section of the trial is indicated alongside. The picture of the spoon is courtesy of the authors and serves for illustration only. **(B)** Schematic layout of a possible block order. N and E indicate blocks where either neutral pictures (N), or emotion pictures (E being positive or negative pictures based on which group the participant was assigned to) were shown before each trial. L and S stand for whether the instructions asked the participant to attend the large or small letter stream. SAM scores were taken once before the experiment began and then again after each block.

Procedure

Before the start of the experiment subjects answered a set of questionnaires. These included our standard lab questionnaire inquiring about the current health state of the participant, the Edinburgh Handedness Inventory (Oldfield, 1971) and the Beck Depression Inventory (Beck et al., 1996).

After completing the questionnaires, the EEG recording was set up. Participants then completed a brief non-verbal self-report measure of their current emotional states, a three-dimension, flipped modified-nine-point scale version of the SAM which included valence, arousal and dominance to serve as a baseline for later measurements of the effectiveness of the emotional manipulation. Finally, general task instructions were given to the participants and an example neutral trial was shown on the screen. Participants were encouraged to ask if they had any questions. If they had no further questions the experiment started with the first block-specific instruction which asked participants to fixate on the centre of the screen, and to attend to the large or small letter stream.

In each block there were 72 trials, resulting in a block duration of about six minutes. As illustrated in Figure 2B, the experiment consisted of eight blocks, with alternating neutral and emotion condition blocks. Half of the subjects began with the neutral and the other half of subjects began with the emotional condition. The emotion condition would be either positive or negative based on which group the participant was randomly assigned to. Whether participants started with the 'attend large' or the 'attend small' instruction was counterbalanced across participants. The order of instructions within an experiment followed an ABBABAAB design. That is, if a participant started with the instruction 'attend large' the order of instructions was LSSLSLLS, while starting with the instruction 'attend small' was linked to the order SLLSLSSL, where L denotes attending the large letter stream and S denotes attending the small letter stream. Combining the alternation of emotion and neutral conditions with the two size orders resulted in four different orders in which the blocks could be presented to the participants. As an example, block order could be L/Neutral - S/Emotion - S/Neutral - L/Emotion - S/Neutral - L/Emotion - L/Neutral - S/Emotion. After each block, participants filled in the SAM again and were given a short break.

To ensure that participants paid attention to the instructed RSVP stream a behavioural task was introduced. Participants were told to press a button as quickly as possible if they detected the letter H in the to-be-attended RSVP stream. The button was mounted on a custom-made response pad that lay on a table in front of the participant and was to be pressed with the right index finger. The letter H could occur from 700 to 2125 ms after the onset of the RSVP streams. Within a given trial, the target letter H occurred up to two times either in the small or the large RSVP stream, but never in both. In cases of two target letters, Hs were separated by

990 ms so as to completely avoid any interference from the attentional blink phenomenon (Raymond et al., 1992).

3.3.3 Physiological Recordings

EEG was recorded from a 94-channel equidistant Ag-AgCl electrode cap (EASYCAP, Herrsching, Germany). One additional electrode was mounted below the right eye to monitor eye movements. An electrode placed on the nose tip served as online-reference. Data were recorded using BrainVision recorder (Version 1.10), together with Brainamp DC Amplifiers (Brain Products GmbH, Gilching, Germany). Electrode impedances were kept below 8 kΩ before data acquisition. Resolution was 0.1 μV with a range of ±3.28 mV. Data were recorded with a sampling rate of 1000 Hz with filter settings of 0.016 Hz for the high pass filter and 250 Hz for the low pass filter.

3.3.4 Data Processing

Behavioural data

Hits and false alarms were calculated for the target detection task. SAM ratings were extracted for the dimensions arousal and valence.

EEG

EEG data were analysed using EEGLAB v9.0.4.4b (Delorme & Makeig, 2004), an open source MATLAB R2010b (The MathWorks Inc., Natick, MA, USA) based software, and custom Matlab-based scripts. The EEG was filtered offline with a low pass filter of 100 Hz, resampled to 250 Hz, and passed through a high pass filter of 1 Hz. In a two-pass procedure, dummy events were first created and the continuous data set epoched into segments of 5000 ms duration. According to lab procedures (see De Vos, Thorne, Yovel, & Debener, 2012), principal components analysis (PCA) was run prior to ICA to reduce the dimensionality of the data, and ICA was then based on 45 principal components. Extended infomax Independent Component Analysis (ICA) was run (Bell & Sejnowski, 1995; Lee, Girolami, & Sejnowski, 1999) and ICA weights obtained from this were stored for later use. In the second pass, the original data of the experiment were reloaded and then filtered with a low pass filter of 100 Hz, resampled to 250 Hz, and passed through a high pass filter of 0.1 Hz. ICA weights from the first pass were then imported. ICs were examined individually in the epoched data set and ICs reflecting stereotypical artefacts such as eye blinks, heartbeats, and lateral eye movements were removed. After ICA-based data pruning, an automatic rejection algorithm was run to identify and remove any strange epochs using joint probability of recorded electrodes at each time point and visual inspection.

The cleaned EEG epochs were then split based on condition. To examine the effect of attention at each frequency, a fast Fourier transform (FFT) was run on the averaged trials of these condition sets to extract power values for each channel at the two frequencies at which the letters were presented. In order to avoid the visual evoked response to flicker onset, the first 500 ms of each trial was excluded from this analysis. Grand mean averages of the power values were used to make topographical maps of the neutral condition. Based on visual inspection of peak ssVEP topography, a region of interest was defined in the posterior region, which included eight parieto-occipital channels, four in each hemisphere. These roughly corresponded to the region occupied by PO7, PO3, O1 and the analogous channels PO4, PO8 and O2 in the 10-10 system. Power values from these channels were extracted for statistical analysis.

3.3.5 Statistical Analysis

Firstly, to determine whether there was an impact of the emotion manipulation, SAM data was tested for a significant difference between the neutral and emotion conditions in each group.

D prime (d') was calculated using the Z-transformed values of the proportion of hits and false alarms. D' is a statistical measure of the difference between hits and false alarms and indicates sensitivity in a detection task. The larger the d' value, the more sensitive participants are to the difference between signal present and signal absent distributions. The behavioural task served only to ensure attention on the instructed stream, and it varied considerably from standard AB tasks in which behavioural effects have been previously observed. Therefore, no hypothesis was made regarding this data. However, a two-way ANOVA was run on these values with affect condition (neutral, emotion) and attended letter stream (large, small) as factors, for each group separately, to test whether performance was affected by either the affect manipulation or the attention condition.

To test the main hypotheses, a three-way repeated measures ANOVA was run on the log EEG power values (Gasser, Bacher, & Mocks, 1982) of each group with the frequency measured [7 Hz (slow and large RSVP stream), 11 Hz (fast and small RSVP stream)], the attended letter stream (7 Hz, 11 Hz) and the affect condition (emotion, neutral) as factors. If present, interactions were followed by t-tests. Mauchly's sphericity assumption was met for all reported values.

3.4 Results

3.4.1 SAM

Table 1 shows the mean SAM valence and arousal values and respective standard error of the mean in each group according to emotion condition. An independent-samples t-test was run to explore pre-existing group differences in valence and arousal values. No significant group differences were found. Paired t-tests were performed to compare the emotion and neutral conditions in each group. A significant effect of the emotional manipulation found in both groups confirmed its effectiveness: the positive group had a significantly lower mean valence during the emotion conditions than during the neutral conditions ($t(17)=-2.13$, $p<0.05$) and the negative group had a significantly higher mean valence during the emotion conditions compared to the neutral conditions ($t(13)=2.25$, $p<0.05$). Please note: the scoring of the flipped modified-nine-point scale version of SAM used here decreased with positive valence and increased with negative valence. There was no significant difference between the arousal ratings of the neutral or emotion conditions of either group.

Table 1

SAM Scores for Both Groups in Both Affect Conditions.

Group	Positive group valence*	SEM	Negative group valence*	SEM	Positive group arousal	SEM	Negative group arousal	SEM
Neutral condition	5.0	0.25	4.5	0.27	5.5	0.25	5.4	0.27
Emotion condition	4.7	0.29	5.0	0.27	5.4	0.29	5.4	0.27

$Note_1$. *Group difference was significant $p<0.05$

$Note_2$. Lower scores in the valence scale indicated more positive affect

3.4.2 Behaviour

Considering that 69% accuracy would be indicated by a d' of 1.0, the mean d' values on this task clearly indicated that participants paid attention to the stream they were instructed to attend. This was reflected by adequate performance of the target detection task in all conditions in both groups (Positive group: Emotion condition 2.3 and Neutral condition 2.24; Negative group: Emotion condition 2.16 and Neutral condition 2.18). A two-way ANOVA with affect condition (neutral, emotion) and attended letter stream (large, small) as factors was run to analyse the data further. In the positive group, a main effect of attended letter stream was found ($F(1,17)=12.69$, $p<0.01$) where response accuracy was significantly better in the large letter stream compared to the small letter stream (2.54 vs. 2.01). No other effects or interactions were seen in either group.

3.4.3 EEG

As illustrated in Figure 3, both RSVP streams evoked frequency specific responses that were modulated by attention in that they were enhanced when the RSVP stream of corresponding frequency was attended. A three-way ANOVA, with power of the measured frequencies as the dependent variable and affect condition (positive or negative - depending on the group - and neutral), attended stream of letters (large, small) and measured frequency (7 Hz, 11 Hz) as factors, was performed for each group separately. Of particular interest was a three-way interaction between affect condition, attended stream of letters and measured frequency, which would indicate that emotion modulates the attention effect in the doughnut model of attention proposed by Müller and Hübner (2002).

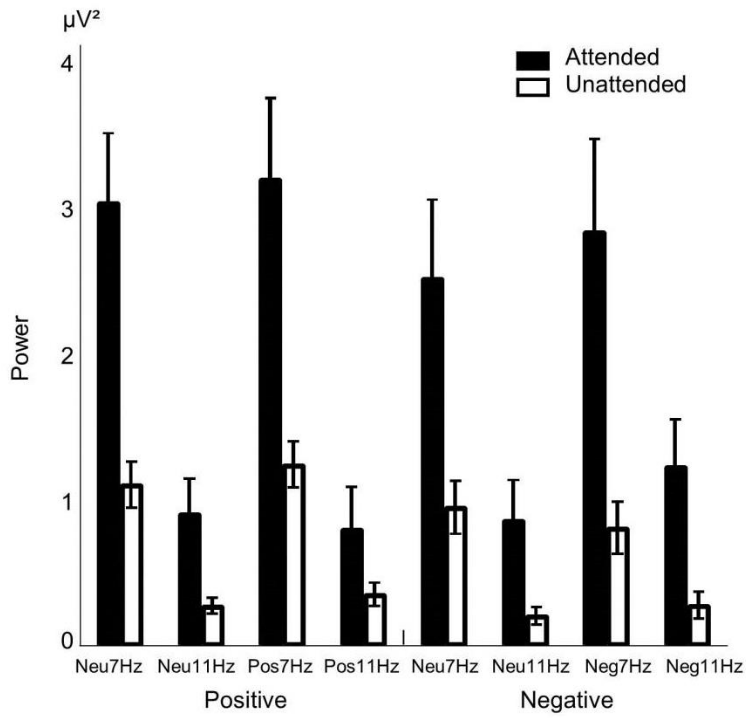

Figure 3. Mean power values of the ssVEP and their respective standard errors of the mean (SEM) illustrating the attention effect. Black bars show power values at the labeled frequency (7 or 11 Hz) when attended; white bars show power when unattended. Illustrated are the neutral and emotion conditions of the positive and negative groups.

Analysis in Positive Group

(1) Presence of attention effect

As expected, in the positive group the ANOVA showed a main effect of the measured frequency where the log power of the 7 Hz response was higher than that of the 11 Hz response (0.13 μV^2 vs. -0.57 μV^2; ($F(1,17)=63.37$, $p<0.0001$)), as well as an interaction between the attended letter stream and the measured frequency ($F(1,17)=42.9$, $p<0.0001$). T-tests revealed that the log power of the 7 Hz response when attending the 7 Hz stream of large letters was significantly higher than the 7 Hz response when attending the 11 Hz stream of small letters (0.35 μV^2 vs. -0.98 μV^2; $t(17)=6.90$, $p<0.0001$). Similarly, the log power of the 11 Hz response when attending the 11 Hz stream of small letters was significantly higher than the 11 Hz response when attending the 7 Hz stream of large letters (-0.34 μV^2 vs. -0.80 μV^2; $t(17)=4.60$, $p<0.0001$). This shows the expected increase of power when a stream is attended as opposed to ignored.

(2) Presence of effect of affect

Contrary to our hypothesis, a three-way interaction was not observed ($F(1,17)=0.045$, $p=0.83$). An interaction between affect condition and measured frequency and the main effect of affect condition were also absent.

Analysis in Negative Group

(1) Presence of attention effect

A similar analysis of the negative group showed the same effects as earlier mentioned in the positive group, that is, a main effect of measured frequency (7 Hz 0.003 μV^2 vs. 11 Hz -0.61 μV^2; $F(1,13)=61.94$, $p<0.0001$) as well as the interaction observed between attended stream and frequency measured ($F(1,13)=60.90$, $p<0.0001$). T-tests revealed that the log power of the 7 Hz response when attending the 7 Hz stream of large letters was significantly higher than the 7 Hz response when attending the 11 Hz stream of small letters (0.26 μV^2 vs. -0.25 μV^2; $t(13)=6.6$, $p<0.0001$). Similarly, the log power of the 11 Hz response when attending the 11 Hz stream of small letters was significantly higher than the 11 Hz response when attending the 7 Hz stream of large letters (-0.31 μV^2 vs. -0.91 μV^2; $t(13)=7.59$, $p<0.0001$). Just as in the positive group, this shows the expected increase of power when a stream is attended as opposed to ignored.

(2) Presence of effect of affect

Contrary to our hypothesis, the three-way interaction between affect condition (negative, neutral), attended stream of letters (large, small) and measured frequency (7 Hz, 11 Hz) was again not observed ($F(1,13)=0.068$, $p=0.8$). However, a main effect of affect condition was seen where the mean power of the negative condition was significantly higher than that of the neutral condition ($-0.28\ \mu V^2$ vs. $-0.33\ \mu V^2$; $F(1,13)=4.66$, $p=0.05$). This is illustrated in Figure 4. A significant interaction between the measured frequency and affect condition was also observed ($F(1,13)=6.01$, $p<0.05$). When this was followed up by t-tests, it was found that the 11 Hz response was significantly higher in the negative condition than in the neutral condition ($-0.55\ \mu V^2$ vs. $-0.67\ \mu V^2$; $t(13)=-2.912$, $p<0.05$). No equivalent difference was seen in the 7 Hz response ($t(13)=0.61$ $p=0.555$).

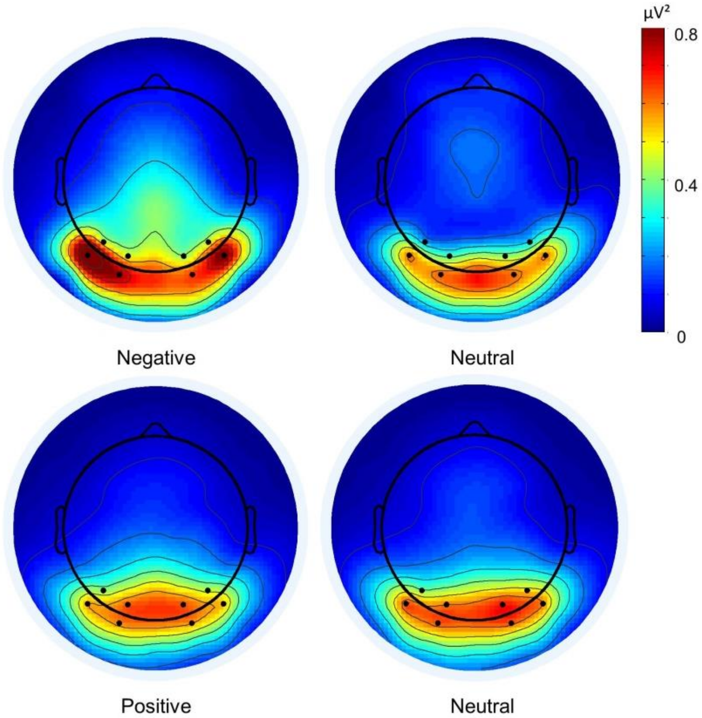

Figure 4. Topographical maps of mean power values of the negative group during negative and neutral conditions. The dots indicate the electrode locations (i.e. the region of interest) chosen for statistical analysis. Power is higher in the negative condition than in its neutral condition. The positive condition and its respective neutral condition are shown for comparison.

3.5 Discussion

The goal of this study was to investigate the neural correlates of the diffuse mental state idea proposed by Olivers and Nieuwenhuis (2006) as a spatially-oriented phenomenon. To this end, a two-stream RSVP paradigm was used (Müller & Hübner, 2002) in combination with an emotion manipulation. The attentional resources directed at processing the RSVP streams were measured by means of ssVEPs. The emotion manipulation was carried out between groups, with one group being exposed to positive and neutral pictures, the other group to negative and neutral pictures. We expected that if positive affect results in a more diffuse mental state, this would result in a more even distribution of attentional resources. This should be reflected in a reduction of the normally observed ssVEP attention effect, that is, the power increase seen when a stimulus stream is attended as compared to when it is ignored. Conversely, we expected that when negative affect focuses the attentional resources, this should be reflected in a corresponding enhancement in the ssVEP attention effect.

The basic paradigm was successful in that the attention effect was observed in both groups. Our EEG findings clearly replicate the finding of Müller and colleagues (2002) in that attention to one of two simultaneously presented RSVP streams resulted in an increase in power in the frequency corresponding to the attended stream's presentation rate. Performance data also confirm that participants attended the correct stream. It is important to note here, that the behavioural task was used for the verification of attention. It was not expected to be sensitive to the emotional manipulation. However, the changes in the SAM valence ratings clearly indicate that the emotional manipulation succeeded.

In the negative group, a main effect of affect was seen in which the power of the ssVEP in the negative condition was higher than that of the neutral condition. An interaction between measured frequency and affect condition was also seen whereby the increase in power observed in the negative condition was particularly strong in the 11 Hz response but absent in the 7 Hz response. This can be interpreted as an indication that negative affect had a task-independent, narrowing effect on the focus of attention. This is in line with the idea that negative affect narrows the mental state (Fenske & Eastwood, 2003; MacLean et al., 2010; Smilek, Enns, Eastwood, & Merikle, 2006).

While we see a reflection of the emotional manipulation in the negative group, a similar effect is not observed in the positive group. Perhaps this is because the emotional manipulation is not strong enough to reflect clearly in the physiology. IAPS pictures were chosen as a method of manipulating the mood, as they have been used widely and have effectively manipulated moods and performances in earlier studies (Dreisbach & Goschke, 2004; Olivers & Nieuwenhuis, 2006), however, other methods for manipulating mood might be more effective in inducing a positive affect state. For instance, it has been found that music positively affects performance on several tasks and tests, and also temporarily eliminates spatial neglect

(Graham, Robinson, & Mulhall, 2009; Olivers & Nieuwenhuis, 2005; Rowe, Hirsh & Anderson, 2007; Soto, Funes, Guzman-Garcia, Warbrick, Rotshtein et al. 2009; Thompson et al., 2001). Thus, future research could investigate whether the ssVEP attention effect can be modulated if positive affect is induced by other methods than IAPS pictures.

In addition to the above idea, Schupp, Stockburger, Bublatzky, Junghofer, Weike et al (2007) showed that emotional attentional capture is reduced by the competing processing demands of a concurrent attentionally-demanding task. In the present study a related mechanism might have influenced the results. That is, the combination of attending either the small or the large letter stream while ignoring the other and looking for a target letter may have increased the attention demand to a level that similarly diminished the effect of the positive pictures.

With respect to the expected modulations based on the diffuse mental state idea, we did not observe the relative reduction in the ssVEP attention effect compared to the neutral condition in the positive condition, or the relative increase in attention effect in the negative condition. Although it remains possible that this result was due to a weak emotion manipulation, the significant main effect of SAM valence scores in both groups argues against this. Our experimental design was based upon the interpretation of the diffuse mental state as being a spatially-oriented phenomenon. We therefore expected that with the diffuse mental state as induced by positive affect, the spotlight of attention would expand spatially, and with negative affect causing a narrowing and focusing of attention, the spotlight would narrow. Our null result therefore suggests that the spatial ‘doughnut’ model is tough and inflexible. However, another interpretation of this state is possible. MacLean et al. (2010) refer to the diffuse mental state in connection with increased cognitive flexibility and control that comes from more open and positive dispositions, implying that it can be seen more as an enhancer of more efficient resource allocation. Thus we do not discount the principle of a diffuse mental state per se. Instead we suggest that an interpretation of such a state beyond a merely spatial phenomenon may be appropriate, although this remains to be directly tested.

In conclusion, this study provides further evidence for the modulation of attention by negative emotion. However, there was no evidence of a neural correlate of the diffuse mental state in a spatial conception. Future studies could try alternative tasks with less emphasis on the spatial component, as these may be better able to reflect a more, or less, diffuse mental state. Further studies may also benefit from a stronger affect manipulation, in particular for the induction of the positive affect state.

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4.

Study 2 – *Personality Traits*

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4.1 Abstract

Neuroticism and negative affect have been associated with an increase of attentional investment and the greater processing of irrelevant stimuli. Previous research proposes the overinvestment of attention and a focused mental state as the mechanism of this effect. We investigated the neural correlates of this idea using a dual-stream rapid serial visual presentation (RSVP) paradigm with centrally presented, overlapping streams of letters that changed at different frequencies. Participants attended one stream at a time. We predicted that the more focused cognitive style associated with higher neuroticism would be reflected in the overinvestment of attention in the irrelevant stream of to-be-ignored letters, in particular, when the ignored stream was the more salient one. This was expected to lead to a smaller difference in power between the attended and unattended frequencies. Results showed that power differences between attended and unattended streams were negatively correlated with neuroticism scores in direct support of our hypothesis. Exploratory correlations also showed that extraversion was positively related to the attention difference. As extraversion has been contrasted to neuroticism and linked to increased cognitive flexibility and control in previous studies, it is possible that this trait may help in disengagement from salient stimuli. Together, these results provide the first neural correlates of the focused cognitive style idea. That the effect of extraversion is seen in the centro-parietal region and the effect of neuroticism is seen in the occipital region indicate that these personality traits may affect the hierarchy of visual information processing. These findings provide new insight into the influence of personality traits on attention mechanisms and open up questions regarding the relationship between neuroticism, extraversion and information processing.

4.2 Introduction

Many different factors influence the guidance of visual attention. In addition to the visual characteristics of the stimulus, these include the internal state of the individual such as the current emotional state or motivation, and the more time-independent personality traits (Kaspar & König 2012). Neuroticism is a trait commonly found in those with depression (Boyle et al., 2010; Kendler, Kuhn, & Prescott, 2004; Rusting & Larsen 1997; Saklofske, Kelly, & Janzen, 1995). Negative affect is linked to neuroticism conceptually (Carver, Sutton, & Scheier, 2000) and when considered alongside avoidance, represents one of the basic behavioural dispositions (Elliott R. 2002). The high correlation between negative affect and neuroticism has been described in several studies (e.g., Nemanick Jr & Munz 1997; Rusting & Larsen 1997).

Both negative affect and neuroticism have been linked to variations in cognitive processing (Bäuml & Kuhbandner, 2007; Storbeck & Clore, 2005). Findings generally imply that negative affect is associated with an increase in intensity and a concentration of the attentional focus. Yet while some researchers have suggested that this is expressed in a stronger spatial focus of attention when negative affect is high (Fenske & Eastwood 2003; Gable & Harmon-Jones 2010), others have suggested that the association is between negative affect and overinvestment and difficulty disengaging attention (Bredemeier, Berenbaum, Most, and Simons 2011; Maclean & Arnell 2010; MacLean et al. 2010). The research that centres on the attentional blink (AB) is particularly informative about the latter idea. The AB is a phenomenon of temporal attention, where the conscious perception of a second target is impaired when it appears between about 200 - 500 ms after a first target (Raymond et al. 1992). The targets are normally embedded in a rapid stream of non-targets, a presentation mode also referred to as rapid serial visual presentation (RSVP). The AB has been shown to be largest for participants with high arousal and negative affect (anxious) (Gable & Harmon-Jones, 2010) and lowest for those with low arousal and negative affect (sad), with participants with high or low arousal combined with positive affect showing intermediate performance (Jefferies et al. 2008). Studies interested in the effects of long-lasting, trait aspects of negative emotionality on the AB have reported that higher neuroticism is associated with longer ABs, which authors have connected to less efficient cognitive control (Maclean & Arnell 2010). Moreover, these studies have shown that people with severe dysphoria tend to show longer and larger ABs (Rokke et al. 2002), and that negative, compared to positive, disposition increases the AB magnitude (MacLean et al. 2010). MacLean and colleagues (2010) suggested that the performance differences they observed relate to a more focused, less flexible, cognitive style in individuals with greater dispositional negative affect. As a consequence of this style, these individuals are assumed to overinvest their attention in the rapid stream of non-targets, which then negatively affects the processing of the second target. With their interpretation MacLean and colleagues (2010) follow the proposal by Olivers and Nieuwenhuis (2006), who originally referred to the diffuse mental state idea to explain their observation of a reduced AB magnitude when participants were shown positive pictures before performing the dual-target task that normally results in an AB. Olivers and Nieuwenhuis (2006) suggested that positive affect can diffuse the attentional state, hence preventing the overinvestment of attentional resources in the non-target stream.

A recent study also demonstrates this link between more pronounced ABs and negative emotionality, particularly neuroticism. Bredemeier et al. (2011) asked participants to perform a single-target RSVP task using salient distractors, one, two, three or seven items before the target. Salient distractors elicited an AB at the intermediate lags, and self-reported neuroticism levels were found to be positively associated with this distracter-elicited AB. The authors interpreted this as indicating that those with higher neuroticism find it generally harder to disengage from salient stimuli after initial attention capture. These findings could also be explained within the diffuse mental state idea. Within this framework one would expect, for people scoring high in neuroticism, a general overinvestment of attention in the central RSVP stream that would affect processing of salient distracters, and in consequence, performance. Nevertheless, even though overinvestment of processing resources to the RSVP distracter stream is an important element of the proposed link between negative emotionality and the diffuse mental state idea (Olivers & Nieuwenhuis, 2006; MacLean et al., 2010), studies assessing the processing of the RSVP stream in relation to emotionality are lacking so far.

The present study aimed to contribute to fill this gap, at least in part, by studying the neural correlates of voluntarily focusing attention to a rapid stream of visual stimuli and relating these to negative emotionality. To this end, a dual-stream RSVP task was used, in which the streams were presented, overlapping, at fixation, but with different frequencies and stimulus sizes (Müller & Hübner, 2002). The steady-state visual evoked potential (ssVEP) evoked by the two RSVP streams was recorded as an indicator of resources invested in processing the streams. We based our predictions on the diffuse mental state idea, and hypothesised that individuals high in neuroticism or negative affect would display a more focused cognitive style, associated with cognitive inflexibility (MacLean et al. 2010) and a difficulty in ignoring irrelevant stimuli. The latter should be particularly prominent when attending the smaller stream because, as proposed by Bredemeier et al. (2011), higher neuroticism may also be linked to difficulty in disengaging from salient stimuli, which is, in this case, the larger letter stream. In other words, individuals with high scores in measures of negative emotionality were predicted to overinvest resources in the processing of salient and irrelevant stimuli. Empirically, this should be reflected in a negative relationship between negative emotionality scores and the difference between the ssVEP evoked by the attended and the unattended stimulus streams, in particular when the large stream is the unattended stream. Findings confirming this prediction would provide direct evidence for a link between trait negative emotionality and an overinvestment of attention, and thus support the diffuse mental state idea.

4.3 Methods

4.3.1 Participants

Data were collected from a total of 39 right handed participants (24 females) between the ages of 19 and 33 (M = 23.9 years) who were monetarily compensated for their time. All had normal or corrected-to-normal vision and were free of past or current neurological or psychiatric disorders. All participants were right handed as assessed by the Edinburgh Handedness (Oldfield 1971). Due to technical problems during recording of the EEG two participants had to be excluded from the sample. Four more participants were excluded because they performed below chance level (50% hits) in the behavioural task. The final sample consisted of 33 participants (23 female, mean age 23.7, range 19 to 33 years). Beck Depression Inventory scores gave no indication of the presence of clinically relevant depression (M=5.6, range 0 to 21). The study was run in accordance with the declaration of Helsinki and was approved by the ethics committee of the University of Oldenburg.

4.3.2 Stimuli and Procedure

Stimuli and setup

In a design similar to that used in the study by (Müller & Hübner 2002) two overlapping RSVP streams were used, both presented at fixation. One of the streams consisted of large uppercase letters, the other of small uppercase letters, such that the latter was presented within the former. The letters that made up the large RSVP stream subtended a viewing angle of 2.11° x 1.94°. The letters of the small RSVP stream subtended a viewing angle of 0.53° x 0.53°. All letters of the Roman alphabet were used for the RSVP streams except I, J, O, P and

W due to their similarity to other letters. Presentation frequencies of the two streams were synchronised to the 120 Hz refresh rate of the monitor. Each large letter was presented for 17 frames or 141.7 ms before it changed to the next random letter, resulting in a frequency of about 7.1 Hz. Each small letter was presented for 11 frames or 91.7 ms before it changed to the next random letter, resulting in a frequency of about 10.9 Hz. For the sake of convenience, we will henceforth refer to the two frequencies as simply 7 or 11 Hz. The presentation of the RSVP streams continued for 2500 ms.

The RSVP sequence was preceded by a fixation cross, presented for 500 ms, and a picture taken from the international affective picture system (IAPS: Lang et al. 1999), presented in colour for 1500 ms. IAPS pictures fell into one of the three categories positive, negative, and neutral. Categories were not changed within an experimental block and only blocks with neutral pictures were of interest for the present study.

In total, a trial lasted five seconds. All stimuli were presented on a 23.6 inch computer screen approximately 160 cm in front of the fixed chair in which the participants were seated. Letters and fixation crosses were presented white on black. The computer screen was mounted outside the recording booth. Presentation Version 14.8 Build 12 30.10 (Neurobehavioral Systems, San Francisco, USA) was used to deliver the stimuli.

Procedure

Before the start of the experiment participants answered our standard lab questionnaire inquiring about the current health state of the participant, the Edinburgh Handedness Inventory (Oldfield 1971), the Beck Depression Inventory (Beck et al. 1996), the Positive Affect Negative Affect Scale (PANAS) with a past 12-months instruction (Watson, Clark and Tellegen 1988) and the NEO-FFI (Costa & McCrae 1992). The German NEO-FFI is a 60 item scale measuring the five domains of the NEO-PI-R (Costa & McCrae 1990). For the NEO-FFI, T-scores (M=50, SD=10) were derived that were calculated for sex and age (Borkenau & Ostendorf 2008).

After completion of the questionnaires EEG recording was prepared. General task instructions were then given to the participants. In brief, participants were told that in different experimental blocks they would be asked to attend to either the small or the large letter stream and to press a button as fast as possible whenever they detected the letter H in the attended letter stream. The task was introduced to ensure that participants paid attention to the instructed RSVP stream. Next, participants were shown an example neutral trial, after which they were asked whether they had any questions. If they had no further questions the experiment started with the first block-specific instruction which asked participants to fixate on the centre of the screen and attend to the large or small letter stream.

Each block consisted of 72 trials, resulting in block duration of about six minutes. Half of the eight experimental blocks belonged to the neutral condition. The other half belonged to either the negative or the positive condition. Participants were randomly assigned to the group that saw either the negative or the positive IAPS pictures. Neutral and emotional condition blocks were alternated, with the starting condition counterbalanced across participants. Results of the emotional manipulation are beyond the scope of the present study and will be reported elsewhere (Dhinakaran et al., in revision). Whether participants started with the 'attend large' or the 'attend small' instruction at the beginning of the block was counterbalanced across participants, with the order of instructions following an ABBABAAB design. That is, if a participant started with the instruction 'attend large' the order of instructions was LSSLSLLS, while starting with the instruction 'attend small' was linked to the order SLLSLSSL, where L denotes attending the large letter stream and S denotes attending the small letter stream. Combining the alternation of emotion and neutral conditions with the two size orders resulted in four different orders in which the blocks could be presented to the participants. As an example, block order could be L/Neutral - S/Emotion - S/Neutral - L/Emotion - S/Neutral - L/Emotion - L/Neutral - S/Emotion. Participants were given short breaks between the blocks.

The letter H on which the behavioural task was based could occur at any time between 700 and 2125 ms after the onset of the RSVP streams. Within a given trial, the target letter H occurred up to two times either in the small or the large RSVP stream, but never in both. In cases of two target letters, Hs were separated by 990 ms so as to completely avoid any interference from the attentional blink phenomenon (Raymond et al. 1992). Double Hs occurred 10 times per block in both large and small letter streams. Single Hs occurred 19 times in the small stream and 11 times in the large stream. This difference occurred due to the difference in presentation frequency of the two streams.

4.3.3 Physiological Recordings

EEG was recorded from a 94-channel equidistant Ag-AgCl electrode cap (EASYCAP, Herrsching, Germany). One electrode was mounted below the right eye to monitor eye movements. An additional electrode placed on the nose tip served as online-reference. Data were recorded using BrainVision recorder (Version 1.10), together with Brainamp DC Amplifiers (Brain Products GmbH, Gilching, Germany). Electrode impedances were kept below 8 kΩ before data acquisition. Resolution was 0.1 µV with a range of ±3.28 mV. Data were recorded with a sampling rate of 1000 Hz with filter settings of 0.016 Hz for the high pass filter and 250 Hz for the low pass filter.

4.3.4 Data Processing

EEG data were analysed using EEGLAB v9.0.4.4b (Delorme & Makeig 2004), an open source Matlab (version R2010b, The MathWorks Inc., Natick, MA, 2000) based software, and custom Matlab-based scripts. In a two-step procedure, the EEG was first filtered with a low pass filter of 100 Hz, resampled to 250 Hz, and passed through a high pass filter of 1 Hz. Dummy events were created and the continuous data set was epoched into segments of 5000 ms duration. According to lab procedures (see De Vos et al. 2012), principal components analysis (PCA) was run prior to ICA to reduce the dimensionality of the data. ICA was then based on 45 principal components. Extended infomax Independent Component Analysis (ICA) was run (Bell & Sejnowski 1995) and ICA weights obtained from this were saved. In the second pre-processing step, the original raw data were filtered with a low pass filter of 100 Hz, resampled to 250 Hz, and then passed through a high pass filter of 0.1 Hz. The ICs from the first step were then imported, and those reflecting stereotypical artefacts such as eye blinks, heartbeats, and lateral eye movement were removed. After ICA-based data pruning, an automatic rejection algorithm was run to identify and remove any strange epochs using the EEGLAB joint probability function and visual inspection.

The cleaned EEG epochs were then split based on condition. To examine the effect of attention at each frequency, a fast Fourier transform (FFT) was run on the averaged trials of these condition sets to extract power values for each channel at the two frequencies at which the letters were presented. These values were log-transformed for statistical analysis (Gasser et al. 1982). In order to avoid the visual evoked response to flicker onset, the first 500 ms of each trial were excluded from this analysis. In order to identify topographical regions of interest amplitude values were obtained by taking the square root of the power values at each frequency for the purpose of creating the grand mean averages used in the topographical maps. These maps were visually inspected to determine where the ssVEP signal was strongest. Three regions were defined: a left region of interest (ROI) consisting of four left occipital channels; a right ROI consisting of the four homologous right occipital channels; and a middle ROI consisting of three channels in the central region of the head.

4.3.5 Statistical Analysis

For statistical analyses power differences were calculated for the attended and the unattended RSVP stream. For the condition in which the slow and large RSVP stream was attended this entailed subtracting power at 11 Hz (unattended) from power at 7 Hz (attended) ; for the condition in which the fast and small RSVP stream was attended subtracting power at 7 Hz (unattended) from power at 11 Hz (attended). The resulting difference measures will be referred to as d_A7 (difference for 'attend slow (7 Hz) stream' condition) and d_A11 (difference for 'attend fast (11 Hz) stream' condition). For both measures a higher value would indicate that attention was focused on the to-be-attended stream. However, values for d_A11 were expected to extend into the negative range as the slow and large 7 Hz stream was expected to generally create higher power than the fast and small 11 Hz stream, because of their relative size, even if participants were instructed to attend the latter (Müller & Hübner 2002). To confirm the presence of this effect in the data set two ANOVAS were run with factors ROI (left, middle, right) and attended frequency (in one ANOVA, 7 Hz attended, 11 Hz unattended, and the other ANOVA 7 Hz unattended, 11 Hz attended).

For each ROI, Pearson's correlations were run for the two difference measures with NEO-FFI neuroticism scores, PANAS_neg, and BDI scores. An additional exploratory analysis included the remaining four NEO-FFI dimensions and PANAS_pos scores.

Correlations between self-report scales were run to validate BDI, PANAS and NEO-FFI scores. As expected, BDI was seen to have significant positive correlations with PANAS_neg (r=0.63, $p<0.0001$), as well as neuroticism (r=0.49, $p<0.01$), and was correlated negatively with PANAS_pos (r=-0.41, $p<0.05$). A positive correlation was seen between PANAS_neg and neuroticism (r=0.51, p=0.01), and a negative correlation between PANAS_neg and agreeableness (r=-0.46, $p<0.01$). Within the NEO-FFI, only one significant correlation was found between conscientiousness and extroversion (r=0.37, $p<0.05$).

4.4 Results

Effects of stimulus characteristics on power

Power values for each region and stream are shown in Figure 6. As illustrated in Figure 5(a), when the slow and large 7 Hz stream was attended, 7 Hz power was significantly increased in all three ROIs (main effect of the factor attended frequency $F(1,32)=212.8$, $p<0.0001$; 7 Hz attended 0.025 $\log(\mu V^2)$, 11 Hz unattended -0.993 $\log(\mu V^2)$). When the fast and small 11 Hz stream was attended, 7 Hz power was larger than 11 Hz power but the difference was only near significant (main effect of the factor attended frequency $F(1,32)=2.89$, $p=0.099$; 11 Hz attended -0.477 $\log(\mu V^2)$, 7 Hz unattended -0.367 $\log(\mu V^2)$).

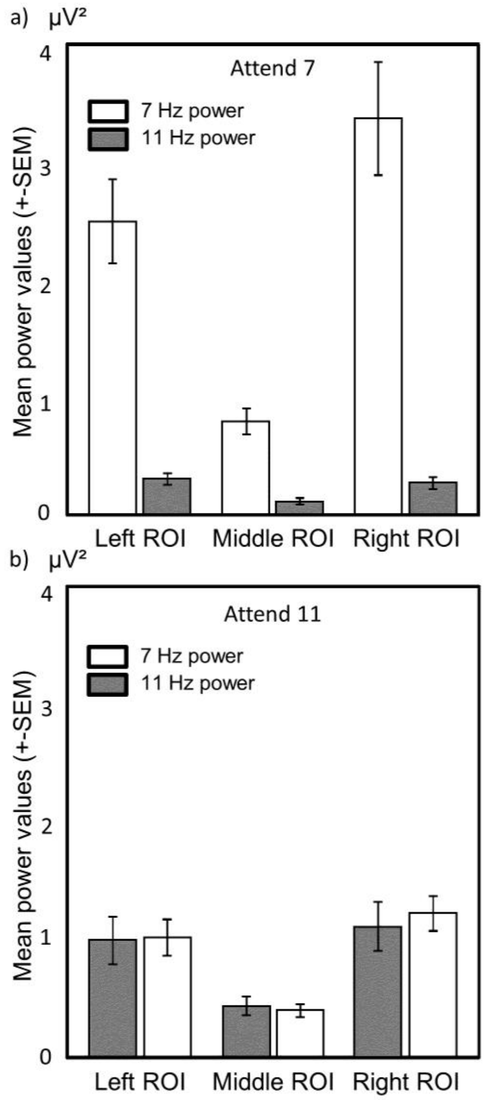

Figure 5. Mean power values and respective standard errors of mean (SEM) in the left, middle and right regions of interest, for the attended and unattended frequencies when participants attended **(a)** the large letter 7 Hz stream and **(b)** the small letter 11 Hz stream

Correlation analyses

To test the hypothesis that higher neuroticism scores would correlate with overinvestment of attention in the task-irrelevant stream, attention differences were compared with neuroticism scores from NEO-FFI and PANAS_neg. In the left ROI, significant negative correlations of d_A11 and PANAS_neg (*r*=-0.41, p<0.05) and neuroticism (*r*=-0.50, p<0.01) were observed. Similarly, in the right ROI, a significant negative correlation of d_A11 with neuroticism was observed (*r*=-0.37, p<0.05). No significant correlation was observed for d_A11 and PANAS_neg in this ROI (*r*=-.21, p=0.251).

Exploratory analyses run on the full data set for the remaining dimensions of the NEO-FFI and PANAS_pos indicated additionally a significant positive correlation between d_A11 and extroversion (*r*=0.35, p<0.05) in the middle ROI. Significant correlations are shown in Figure 6.

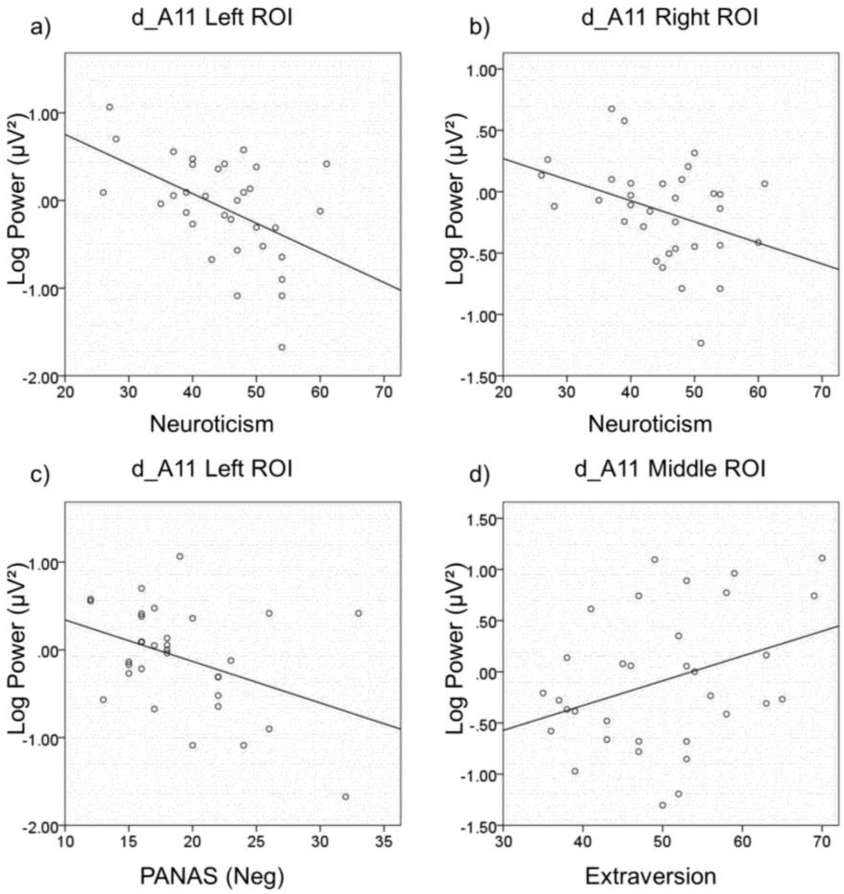

Figure 6. Scatter plots showing the negative correlations between **(a)** d_A11 (the difference in log power between the attended small letter stream and the unattended large letter stream) for the left region of interest (ROI) and neuroticism scores; **(b)** d_A11 for the right ROI and neuroticism; **(c)** d_A11 for the left ROI and the negative measure of PANAS. **(d)** shows the positive correlation between d_A11 for the middle ROI and extraversion

PANAS_neg and neuroticism were found to correlate significantly with each other and with d_A11. To determine the unique degree of association between d_A11 and PANAS_neg, and d_A11 and neuroticism, partial correlations were run with the effect of neuroticism and PANAS_neg removed in each. The correlation between d_A11 and neuroticism remained significant ($r_{d\_A11\ neuro\ \cdot\ PANAS\_neg}$=-0.37, p<0.05). The correlation between d_A11 and PANAS_neg was strongly reduced and no longer significant ($r_{d\_A11\ PANAS\_neg\ \cdot\ neuro}$ =-0.21, p=0.256).

Comparison of high and low neuroticism groups

In order to better understand whether the contributing factor to the results came from the tendency of participants with higher neuroticism scores to show an increase in attention to the ignored stream or a decrease in attention to the attended stream, a repeated measures ANOVA was run. Participants were split evenly into three groups of high neuroticism scores (HNS; 10 females, 1 male; mean age 24.3, range 21 to 27 years; mean neuroticism score 53.6, range 49 to 61), intermediate neuroticism scores (INS; 8 females, 3 males mean age 24; mean neuroticism score 45.6, range 42 to 48) and low neuroticism scores (LNS; 5 females, 6 males; mean age 23.5; mean neuroticism score 35.3, range 26 to 40) as this would enable us to directly compare data for the two extremes of the spectrum. Group (HNS, INS, LNS) served as between-subjects factor in the ANOVA and frequency (11 Hz attended and 7 Hz ignored) as within-subjects factor. An interaction between frequency and group was found (F(2,30)=4.6 , p<0.05). To investigate this, independent samples t-tests for both frequencies were run to distinguish between the two extreme groups, HNS and LNS. T-tests revealed a near significant difference between the groups in the attend 11 Hz frequency (t(20)=1.99, p=0.06) where the HNS group paid less attention to the 11 Hz stream than the LNS group (-0.62 vs. -0.31 μV^2). However, in the ignore 7 Hz frequency, no significant difference was found (t(20)=-0.77, p=0.45) though the HNS group paid more attention to the 7 Hz stream then the LNS group (-0.32 vs. -0.45). This suggests that reduction of attention to the relevant stream may play a larger role than the increase of attention to the unattended stream. As a control, a similar ANOVA was run for 7 Hz attended and 11Hz ignored as levels of the within-subjects factor. No significant interactions were found.

4.5 Discussion

This study aimed to investigate the neural correlates of the modulation of attention by negative emotionality. Participants were asked to attend one of two centrally-presented RSVP streams. The differences between the ssVEP responses evoked by the attended and the unattended streams were compared with the neuroticism score of the NEO-FFI questionnaire, the negative measure of PANAS, and BDI scores. Based on the overinvestment hypothesis that negative affect and neuroticism intensify and concentrate attention, we expected that individuals with more negative emotionality would find it difficult to disengage from and ignore the – by instruction – unattended stream, in particular when the unattended stream was the large and therefore the more salient stream. This would be reflected in the difference between the ssVEP evoked by the attended and the unattended stimulus streams being negatively correlated with measures of negative emotionality. As expected, significant negative correlations were found with both neuroticism and the negative measure of PANAS, but only in the condition where participants were instructed to attend the smaller letter stream.

Significant correlations between measures of negative emotionality and measures of the focus of attention were restricted to the difference in power evoked by the attended (small) 11 Hz stream and the unattended (large) 7 Hz stream. In the left and right ROIs, this difference correlated negatively with the factor neuroticism. In the left ROI, a similar negative relationship was also seen with the negative measure of PANAS. However, partial correlations run for the left ROI indicated that this negative correlation was no longer evident after controlling for the effect of neuroticism. The finding that the strength of the focus of attention is negatively linked to neuroticism is consistent with the diffuse mental state idea and also supports and extends the suggestion by Bredemeier et al. (2011), that neuroticism is linked to difficulties in disengaging from salient stimuli after initial attention capture. That is, given that the stream containing the large letters flickering at a slower frequency is more salient than the stream containing small letters flickering at a faster rate, participants with higher neuroticism scores likely had difficulties disengaging from the larger letter stream when required at the cost of some attention to the stream of small letters. Such difficulties would result in a smaller difference between power evoked by the to-be-attended small letter stream and the to-be-unattended large letter stream in participants with higher neuroticism as compared to participants with lower neuroticism. This could also explain why no correlations were found when considering the difference in power when the large letter stream was to be attended and the small letter stream was to be ignored: Here, the task required attending the more salient stimulus stream, and thus a disengagement of attention from the salient stimulus was not required. In consequence, neuroticism-related modulations in stimulus processing would be expected to disappear or, as a result of an even stronger engagement of attention, change direction. That we did not observe the latter may indicate that the power evoked by the large letter stream, when attended, reached ceiling, and therefore could not differentiate between participants of any level of neuroticism.

The comparison between participants with high and low neuroticism scores suggests that the observed link between neuroticism and ssVEP power modulations may be more due to high scorers paying less attention to the attended stream than due to paying more attention to the more salient, but ignored stream. This may be because of the paradigm used here, where there is a simultaneous stream of distractors. Therefore a reduction in power to relevant stream may be caused by the increase in attention to the irrelevant stream. It would be interesting for future studies to investigate whether this is a general phenomenon or specific to the two-stream paradigm used here.

Exploratory analyses furthermore revealed a positive correlation between d_A11, (i.e., the difference in power evoked by the attended, small, 11 Hz stream and the unattended, large, 7 Hz stream in the middle ROI) and the extroversion factor. As this correlation is in the opposite direction to that seen with neuroticism, it can be supported by previous literature which has suggested that neuroticism and extraversion are parts of opposite personality dispositions (Elliott R, 2002) and opposite emotionality, with extraversion being associated with positive affect (Carver et al. 2000; Nemanick Jr & Munz 1997; Rusting & Larsen 1997). Maclean and Arnell (2010) also found that AB magnitude correlated in opposite directions with extraversion compared with neuroticism. Considering the better performance of extraverts on tasks involving working memory and executive control (Lieberman, 2000) it may be that our results support the idea that individuals with high extraversion scores are better able to exert cognitive flexibility and control during the present RSVP task than those with low scores.

Interestingly, the effect of extraversion was seen in the middle ROI only, consisting of centro-parietal electrodes. In contrast, the effect of neuroticism was restricted to the two occipital ROIs. The latter ROIs can be assumed to come close to, or cover, primary visual areas. In a recent review Vialatte et al. (2010) concluded that in spite of considerable differences in theories about the propagation of ssVEPs, theories concur insofar as ssVEPs originate in the primary visual cortex and involve more than one additional source dipole to reach non-visual areas. This may imply that the effect of extraversion on stimulus processing may act later in the processing hierarchy than the effect of neuroticism.

In conclusion, the findings of the present study show that stimulus processing relates to negative trait affect, in particular neuroticism. Results support the hypothesis that individuals with high levels of trait neuroticism display a more focused cognitive style. This is seen in the fact that participants find it difficult to ignore irrelevant stimuli, especially when they are more salient, and find it difficult to disengage and to switch attention to less salient but task-relevant stimuli. The present findings provide supporting evidence for a link between neuroticism or negative emotionality and the focused cognitive state as encapsulated in the overinvestment hypothesis. The observation that the correlation between ssVEP measures of attention and extraversion is opposite to the correlation between the same measure of attention and neuroticism is in line with literature that contrasts the two traits. Prior findings that link extraversion to more cognitive flexibility and control also suggest that the trait may aid in the disengagement from salient stimuli. Regional differences in the EEG observed for the effects of extraversion and neuroticism indicate that different personality traits may affect the visual processing hierarchy at distinct stages.

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5.

Study 3 – *Estradiol*

To be submitted as:

Dhinakaran J, Thorne JD, Lindig A, Braun N, Janson J, Hausmann M, and Kranczioch C. Alpha Asymmetry Fluctuates over Menstrual Cycle.

5.1 Abstract

Previous research suggests the role of sex hormones such as estradiol in the modulation of functional cerebral asymmetries (FCA) over the menstrual cycle. It has been found that the attentional blink occurs in the left and right visual fields in a high-steroid cycle phase, but only the right visual field in the low-steroid menses phase. In the present study, the underlying changes in alpha band activity were investigated as a possible mediator for the influence of estradiol over attentional performance. Although results showed that alpha band asymmetries changed with estradiol concentrations, and alpha activity was related to the behavioural performance, no direct relationship between estradiol and behaviour was observed. However, these relationships provide evidence for the role of alpha as a possible neural mediator of the impact of estradiol on attention performance.

5.2 Introduction

Considerable evidence suggests that functional cerebral asymmetries (FCA) dynamically change across the menstrual cycle (Bibawi, Cherry & Hellige 1995; Hausmann & Güntürkün 2000; Heister, Landis, Regard & Schroeder-Heister 1989; Rode et al. 1995; Weis, Hausmann, Stoffers & Sturm 2011). Sex hormones such as estradiol and progesterone have been associated with the modulation of FCA. Studies related to attention have shown that there seems to be more asymmetry during the low steroid menstrual phase compared to either follicular or midluteal phases when estradiol and progesterone are in higher concentration (Hausmann et al. 2013; Holländer et al. 2005; Thimm, Weis, Hausmann & Sturm 2014).

Hausmann and Güntürkün (2000) propose that the modulation of FCA by gonadal steroid hormones may occur due to the interactions between the cerebral hemispheres in different cycle phases. In detail, they postulate that progesterone decreases glutamatergic receptor activation and increases GABA activation. This would lead to a decrease in transcallosal activation and hemispheric decoupling, which would reduce the FCA. This assumes that an important role of callosal communication is the inhibition of the non-dominant hemisphere by the dominant hemisphere. This idea was further supported by an fMRI study investigating cycle related fluctuations in the behavioural and neural activity using a word matching task (Weis, Hausmann, Stoffers, Vohn, Kellermann et al. 2008). Their connectivity analysis revealed an inhibitory influence of the dominant on the non-dominant hemisphere, specifically the left inferior frontal gyrus on homotopic areas of the contralateral hemisphere, during menses. During the follicular phase, however, inhibition was reduced. This fluctuation was not observed in male controls. The hypothesis of sex hormone-modulated cortical interaction has been extended and modified since its initial proposal and now also acknowledges the important influence of estradiol (Hausmann & Bayer 2010) and proposes that sex hormones influence interhemispheric as well as intrahemispheric interactions (Hausmann et al. 2013).

Holländer et al. (2005) examined the fluctuation of FCA in a temporal attention task. In this task a rapid series of visual stimuli is presented in which two targets are embedded. The conscious perception of the second target (T2) is impaired when it occurs 200 – 500 ms after the occurrence of the first target (T1). This impairment is referred to as the Attentional Blink (AB) (Raymond et al. 1992). Holländer et al. used a version of the AB task in which one rapid serial visual presentation (RSVP) stream of letters was presented in each visual field. Analysis focused on trials in which both targets were presented in either the left or the right stream. It was found that during the midluteal phase an AB occurred in both streams. During menses however, an AB occurred only in the right stream. Regression analyses indicated that this fluctuation in FCA was mediated by fluctuations in estradiol but not progesterone levels. In line with the decoupling idea postulated by Hausmann and Güntürkün (2000), Holländer et al. suggested that high estradiol levels suppress right hemisphere functions, resulting in a selective right-hemispheric AB during the midluteal phase. The aim of the present study was to follow up this finding and to investigate whether estradiol-related FCA modulations in the AB are linked to modulations in the symmetry of brain activity. Observing such link would support the hypothesis of sex hormone-modulated cortical interaction.

The FCA in brain activity can be studied from many different perspectives, at different frequency bands reflecting various activities. Here we focused on the asymmetry of alpha activity as oscillatory activity in the alpha frequency range is one of the most prominent features of the human electroencephalogram (EEG). Generally, it is noted that asymmetries in alpha activity in anterior regions are associated with affective processing while those in posterior brain regions are related to attentional and cognitive processing, especially during verbal and spatial tasks (Davidson, 1987; Luria, 1973; Davidson, 1990; Ray & Cole 1985). For example, a study by Thut, Nietzel, Brandt and Pascual-Leone (2006) showed that during a spatially cued target detection task, cueing caused visuospatial shifts in attention to the direction from which the auditory cue came. In the EEG, this was reflected by alpha (8 to 14 Hz) power decrease (desynchronisation) in the hemisphere contralateral to the cue direction, in posterior sites of the brain. More of such a decrease was seen in the right hemisphere which led to a left visual field target processing advantage. In addition, Davidson and colleagues (Davidson, Taylor & Saron 1979) showed that participants performed letter and word recognition tasks better when, during rest, there was more alpha in the left parietal region than in the right. The only study so far that has investigated changes in asymmetry with respect to the menstrual cycle in humans used MEG and showed that at rest there was relatively higher right frontal alpha activity in the ovulation phase, and higher left frontal alpha activity during menses (Hwang, Chen, Yeh, Tu, Tu et al. 2008)

Whether asymmetries in alpha activity relate to performance in the AB task is currently unknown. A number of studies report however that alpha activity is related to the size of the AB (for recent reviews, see Janson & Kranczioch 2011; Klimesch 2012). Results of these studies on the role of alpha oscillatory activity in the AB have been difficult to interpret due to the presence of an RSVP at 10 Hz. Consequent ssVEP at this frequency obscures endogenous alpha activity which would be present at rest. Recently Janson et al. (2014) found evidence for opposite roles for RSVP-induced alpha and rest endogenous alpha at the individual alpha frequency. Higher power in the individual alpha frequency, as seen at rest, was related to having an AB, whereas higher power at the prestimulus RSVP-frequency was related to escaping the AB. This is in line with a study by MacLean, Arnell and Cote (2012) who showed that higher alpha power at rest (i.e. endogenous activity) is associated with larger AB magnitudes. It is important to explore the influence of estradiol on rest, but also on task alpha activity.

In sum, empirical evidence suggests that FCA in the AB and other cognitive tasks is modulated by sex hormones. Sex hormones seem to modulate alpha asymmetry, and modulations in resting and task-related alpha activity have been linked to AB performance. It can therefore be hypothesised that estradiol-related modulations in FCA in the AB are mediated by modulations in alpha activity, and that this should in particular be evident in modulations of alpha asymmetry. To investigate this, we collected EEG data from regular cycling women during the high-steroid follicular phase, and the low-steroid menses. Data were collected both at rest and while performing a dual-stream AB task. A relationship between estradiol and FCA in the AB has been suggested by previous research and it was expected that this relationship would also be evident in the present data set. Moreover, if alpha activity is a mediating factor in the link between FCA in the AB and estradiol levels, then a relationship should be evident between alpha activity and AB performance, and also between alpha activity and estradiol levels. The relationship should not only be evident for rest data but also during task performance.

5.3 Methods

5.3.1 Participants

Twenty-six women participated in the present study. They were recruited by announcement, naïve to the hypotheses and financially compensated for their participation. All women were right handed according to the Edinburgh Handedness Index (Oldfield 1971), had normal or corrected to normal vision, no neurological or psychiatric diseases and a mother tongue with Latin letters. Only women with a regular menstrual cycle (mean cycle days = 28.5, SD = 1.87, range 26 to 32 days) took part. None of them had used hormonal contraceptives, hormone replacement or any other medication in the last three months that could affect the nervous system or the natural menstrual cycle. Each woman was monitored for at least three consecutive cycles before entering the experiment, thus details about the individual cycle lengths were collected and this information was used to plan individual testing sessions. Appointments were planned during the predicted menses (cycle day 1-3), low levels of estradiol and follicular (cycle day 9-16, high levels of estradiol, low levels of progesterone) phases, randomising the order of recording sessions to avoid the order effect. Day time of recordings was kept constant to reduce potential circadian fluctuations in hormone levels. Saliva samples were taken before the EEG measurement and send to IBL International, Hamburg, for analysis of estradiol levels. The intra-assay variability was about 10% and inter-assay variability was about 11%. In a normal menstrual cycle, estradiol levels at the follicular phase are significantly higher than during menses. One participant was excluded because her estradiol levels were higher during menses. Another participant was excluded because she reported having a migraine during testing. Three participants only attended the first session, and as this impeded a repeated measures design of analysis, these three participants also had to be excluded. Four more participants were excluded based on behavioural performance. This left a remaining 17 women (mean age = 28, SD = 4.92, range 22 to 38 years) who were included in the final analysis. Before the experiment, participants filled out a consent form and a standard lab questionnaire inquiring about their current health state. The study was run in accordance to the declaration of Helsinki and was approved by the ethics committee of the University of Oldenburg.

5.3.2 Setup

After the participants were prepared for the EEG recording, they were seated in a fixed chair approximately 190cm away from a 19 inch computer screen (Belinea BT10002) in an electromagnetically shielded and sound attenuated room with dim lighting. The participants received written instruction and were requested to reduce head movement and eyes movements to a minimum during the experiment. Stimuli presentation was synchronised with a display refresh rate of 100 Hz. The experimental task was programmed in Presentation 12.04 (Neurobehavioral Systems Development Team, 2010). Answers for the behavioural task were recorded by a modified keyboard on the table in front of the participants where only the keys for possible answers were visible.

5.3.3 Stimulus and Experimental Design

The main experiment consisted of seven blocks with 64 trials each. Breaks of at least one minute were given after each block. Participants saw a double-stream RSVP task with one visual stream in each visual field. The task was to identify specific target stimuli presented in the left or right visual stream after each trial. Each trial consisted of a series of upper case letters of Arial font and size 120. On a light grey background the letters were successively presented in black, with the exception of the first target which presented in white. The center-to-center distance between the two lateralised streams was 5 degrees which enabled participants to identify items in either of the two locations without eye movements (Holländer et al. 2005).

Figure 7 illustrates the experimental paradigm. At the beginning of each trial, participants were instructed to fixate on a black fixation cross at the centre of the screen at all times. The fixation cross was present during letter presentation and ensured that stimuli were presented in the right visual field and left visual field stream, corresponding to the left and right hemispheres respectively. After 800 ms of fixation, the streams of black letters appeared simultaneously in the left and right visual field. The letters distended an angle of 1.05° in width and 1.21° in height. They flashed at an angle of 2.5° on either side of the central fixation cross. Each letter was present for 50 ms with an SOA of 100 ms, producing a presentation rate of 10 letters per second on each side. Distractors were selected randomly among all letters of the alphabet except D, F, G, and K. No letter was presented twice within a visual field. The number of distractor letter pairs varied randomly between six and ten. In each trial, the two targets were T1, a white letter, one of D, F, G or K, and T2, a number, one of 2, 4, 7 or 9. Participants were informed beforehand about the possible targets. T2 was presented either 200 ms (lag 2) or 700 ms (lag 7) after T1, with equal probability. These two T2 positions were chosen because previous studies showed most severe impairments of T2 detection at lag 2 and hardly any impairment at lag 7 (Holländer et al. 2005; Raymond et al. 1992). Hence performance comparison for both T2 positions would provide the most sensitive measure of the AB phenomenon. Immediately after the offset of the last distractor at the end of the trial, a response screen appeared where participants were asked for the white letter (T1) and then for the black number (T2). They responded by typing in their answers by the modified keyboard placed directly in front of them. Participants were asked to answer even if they did not know the answer and were given as much time as they needed to correct their responses. The next trial started after the participant confirmed their T2 response.

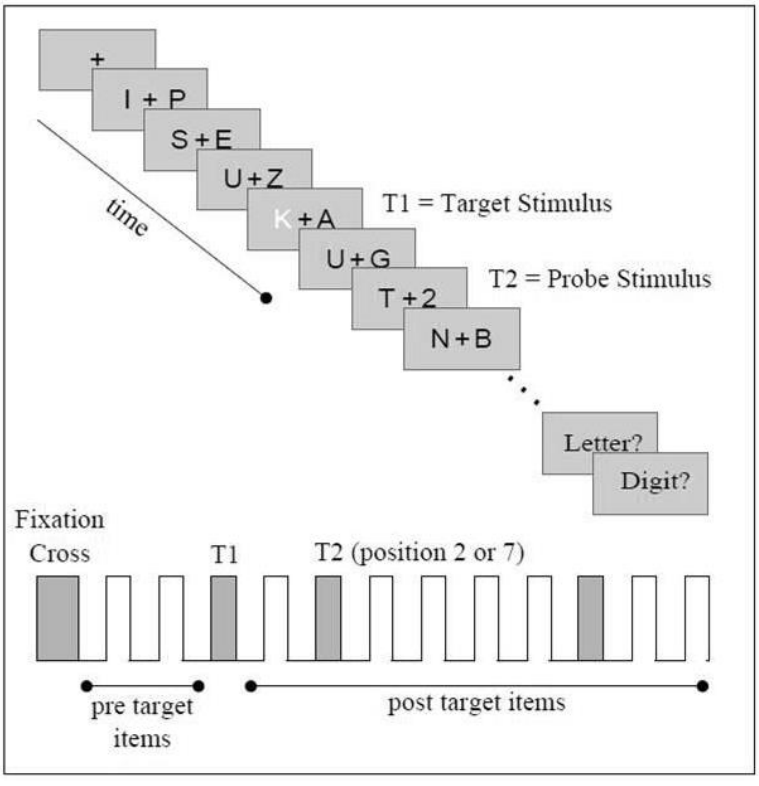

Figure 7. Schematic illustration of the experimental paradigm that depicts the RSVP streams on the left and right visual field. The time position of the targets are also illustrated.

There were four possible conditions for the presentation of T1 and T2 in the left and right visual field which occurred with equal probability. Either T1 and T2 were both presented in the same visual field (both in left or right), or they were presented in separate visual fields (one in the left and the other in the right). The former two conditions were important for the behavioural analysis. The latter two were necessary to inhibit expectations about the side of appearance of T2 and any priming of the participant to either side of the screen. As lag 2 and lag 7 occurrence of T2 were equal and the four conditions for the behavioural task were equal, there were eight trials in each block for each condition.

Before the main experiment, participants performed two practice blocks. The first consisted of four trials and stimuli were shown in slow motion (SOA 200 ms). The second practice block consisted of 16 trials and stimuli were presented at the same speed as used in the main experiment (SOA 100 ms).

5.3.4 EEG Recordings and Analysis

Brain activity was continuously recorded with 30 Ag/AgCl electrodes (EASYCAP GmbH, Herrsching, Germany), placed on an elastic intra-cerebral EEG cap. The position of the electrodes corresponded to the international 10-20 system. The central frontopolar electrode served as ground electrode and the nose tip was used as reference. To control eye movement, two additional electrooculography (EOG) electrodes were placed below each eye. All electrodes were connected to an EEG amplifier (BrainAmp, Brain Products GmbH, Munich, 2012). Electrode impedances were kept below 10kΩ for all channels if possible. Brain Vision Recorder (Brain Products GmbH, Neurobehavioral System, 2010) was used as recording software. Recorded data were digitised with a sampling rate of 500 Hz.

EEG pre-processing was done using EEGLAB v9.0.4.4b (Delorme & Makeig, 2004), an open source MATLAB R2010b (The MathWorks Inc., Natick, MA, USA) based software, and custom Matlab-based scripts. The EEG was filtered offline with a low pass filter of 100 Hz, resampled to 250 Hz, and passed through a high pass filter of 1 Hz. In a two-pass procedure, dummy events were first created and the continuous data set epoched into segments of 5000 ms duration. According to lab procedures (see De Vos et al. 2012), principal components analysis (PCA) was run prior to ICA to reduce the dimensionality of the data, and ICA was then based on 18 principal components. Extended infomax Independent Component Analysis (ICA) was run (Bell & Sejnowski 1995; Lee et al. 1999) and ICA weights obtained from this were stored for later use. In the second pass, the original data of the experiment were reloaded and then filtered with a low pass filter of 100 Hz, resampled to 250 Hz, and passed through a high pass filter of 0.1 Hz. ICA weights from the first pass were then imported. ICs were examined individually in the epoched data set and ICs reflecting stereotypical artefacts such as eye blinks, heartbeats, and lateral eye movements were removed. After ICA-based data pruning, the rest data was separated into eyes opened and eyes closed data. Data were epoched into two seconds segments with 50% overlap. An EEGLAB automatic rejection algorithm was then run to identify and remove any strange epochs using joint probability of recorded electrodes at each time point. Results were inspected visually. A fast fourier transform (FFT) was run on the cleaned resting EEG data. The alpha band was defined as 8–13 Hz (The main analyses were also run on alpha 1 (8 -10.5 Hz) and alpha 2 (10.6 -13 Hz) bands and for eyes open and eyes closed conditions of the rest data. As the pattern of results was generally the same we here report results for the whole alpha band and averaged for eyes open and closed conditions). Power values were extracted and log-transformed before statistical analysis. In the case of the task data, the same procedure was followed with the exception that the segments entering FFT were the 500 ms before T1 presentation.

5.3.5 Statistical Analysis

To determine the validity of the two cycle phases, levels of estradiol and progesterone were tested by a t-test for a significant difference between the follicular and menses phases.

We expected that right-hemispheric AB performance would be influenced by fluctuations in estradiol level. This should be reflected in a phase-related difference in right-hemispheric but not left-hemispheric performance. To test this prediction, behavioural data was analysed using a 2 x 2 x 2 repeated measures ANOVA with factors phase (follicular, menses), visual half-field (left, right) and lag (2, 7). We also expected a negative correlation between right-hemispheric performance and estradiol concentration in support of the assumption that the right-hemispheric advantage in the AB is modulated by estradiol (Holländer et al., 2005). This was analysed by Pearson correlation between lag 2 performance for left visual field trials and estradiol levels during menses and in the follicular phase.

Analysis of EEG data focused on five electrode pairs, namely those corresponding to F3/F4, C1/C2, P3/P4, T5/T6, O1/O2 marked in Figure 8, as we expected that alpha asymmetries would be most evident here (Çiçek & Nalçacı 2001; Davidson & Fox 1988). The asymmetry index was calculated as log(left)–log(right). EEG data were firstly analysed in an ANOVA to test for variations in alpha asymmetry across recording sides and cycle phase; A 2 x 5 repeated measures ANOVA was conducted with factors phase (follicular, menses) and electrode pairs (F3/F4, C1/C2, P3/P4, T5/T6, O1/O2) as repeated measures. Paired t-tests explored the interactions found. To further explore the differences between rest and task conditions, a 2 x 2 x 5 ANOVA was run with cycle phase (follicular, menses), condition (rest, pre-T1), and electrode pairs (F3/F4, C1/C2, P3/P4, T5/T6, O1/O2) as repeated measures with a focus on effects including the factor condition. Paired t-tests explored the interactions found.

The relationship between alpha activity and AB performance, alpha activity and estradiol levels during menses and follicular phase was further investigated by Pearson correlations between right hemispheric lag 2 performance and alpha asymmetry on the one hand, and alpha asymmetry and estradiol levels on the other hand. We predicted a correlation between asymmetry and performance, (i.e. a stronger asymmetry should be linked to better performance). The direction of the correlation would depend on the sign of the asymmetry. Furthermore a correlation between asymmetry and estrogen was expected, i.e. more asymmetry should be linked to less estradiol, again with the direction of the asymmetry determining the direction of the correlation. Correlations were run separately for task and rest data, for menses and follicular phase in the electrodes of interest as well as for pair differences.

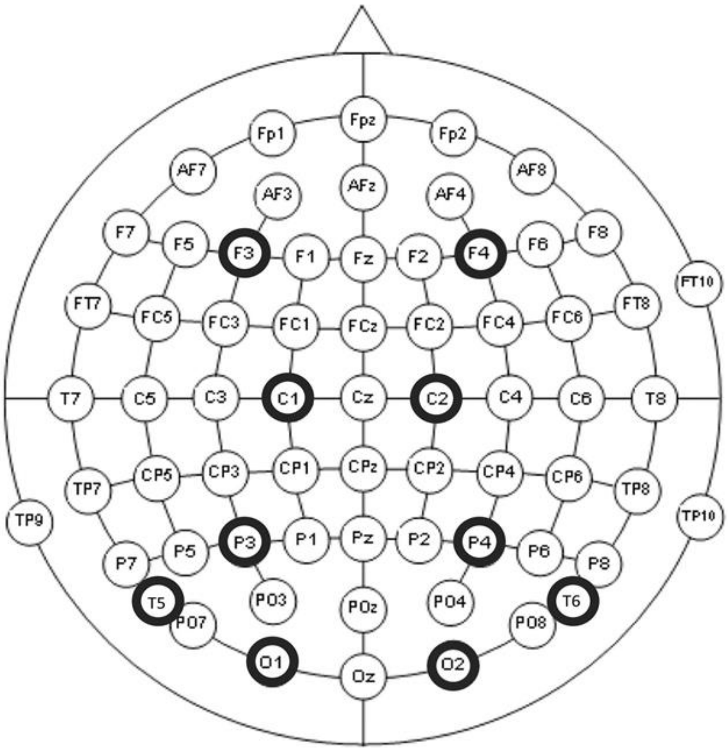

Figure 8. Layout of the electrodes of interest marked with black rings.

6.4 Results

Estradiol levels

The estradiol concentrations were compared between the cycle phases using a paired t-test. The concentration was found to be significantly higher in the follicular phase (4.1pg/ml, SD = 1.71, range 1.5-7.7pg/ml) as compared to menses (1.8pg/ml, SD = 1.05, range 0.2-5.0) (t(16) = 6.9, $p<0.0001$).

Cycle phase and behaviour

The results of this analysis are summarised in Table 1. The 2 x 2 x 2 ANOVA with repeated measures factors cycle phase (follicular, menses), visual half-field (LVF, RVF) and lag (2, 7) revealed a significant main effect of visual field ($F(1,16) = 9$, $p<0.01$), indicating better performance in LVF (75.9%, SEM = 2.9) than RVF (65.7%, SEM = 3.5). Moreover, the interaction between visual half-field and lag was significant ($F(1,16) = 9.3$, $p<0.01$). The interaction was followed up by paired t-tests that revealed that in the LVF, lag 7 (80.9%, SD = 11.4) was significantly more accurate than lag 2 (71%, SD = 16.1) ($t(16) = 2.85$, $p<0.05$). This difference was not present in the right visual field ($t(16) = 0.47$, $p = 0.64$). It also revealed that in lag 7, significantly more targets were identified in the LVF (80.9%, SD =

11.4) compared to the RVF (66.4%, SD = 17.3) (t(16) = 4.05, p = 0.001). This visual field difference was not observed in lag 2 performance (t(16) = 1.5, p = 0.14). Unexpectedly, no main effect of cycle phase (F(1,16) = 0.6, p= 0.4), nor any interaction between cycle phase and visual half-field (all F (1,16) = 0.25, p = 0.63) was observed.

Table 1. Behavioural Results.

Phases		**Menstrual**	**Phase**			**Follicular**	**Phase**	
Lag	**Lag 2**		**Lag 7**		**Lag 2**		**Lag 7**	
Visual field	**LL**	**RR**	**LL**	**RR**	**LL**	**RR**	**LL**	**RR**
T2|T1								
Mean	70.96	64.7	77.63	65.0	71	65.6	84.1	67.7
SD	4.9	3.7	4.3	4.6	3.9	4.4	2.5	4.2

Contrary to our expectations, but corresponding to the findings in the ANOVA, no significant correlation was seen between estradiol concentrations in either cycle phase and LVF T2-performance (follicular estradiol: $r(15)= -0.27$, p = 0.304; menses estradiol: $r(15)= 0.22$, p = 0.40).

<u>Estradiol and alpha activity: Rest</u>

(a) <u>ANOVA</u>

During rest, the 2 x 5 ANOVA with cycle phase (follicular, menses) and electrode pairs (F3/F4, C1/C2, P3/P4, T5/T6, O1/O2) as repeated measures, revealed main effects of cycle phase (follicular mean asymmetry -0.18 μV^2, SEM = 0.014; menses menses mean asymmetry 0.01 μV^2, SEM = 0.019) (F(1,16) = 99.1 , p<0.0001). It also revealed a significant main effect of electrode pairs (F(4, 64) = 164.9, p<0.0001), where asymmetry was largest for F3/F4, followed by C1/C2, P3/P4, T5/T6 and O1/O2, with asymmetry indices of -0.95, 0.85, 0.42, -0.38 and -0.37 respectively. Subsequent T-tests indicated that the differences between the pairs collapsed over cycle phase were significant for all possible combinations of electrode pairs (all t(16)>±8.6, all p<0.0001) except temporal and occipital (t(16) = -0.14, p = 0.89). A significant interaction between phase and electrode pairs was also found (F(4,64) = 95, p<0.0001). This interaction was followed up by paired t-tests for each of the pairs in the two cycle phases. They revealed that in all pairs asymmetry was significantly smaller during follicular phase than during menses (frontal (t(16) = 4.8, p<0.0001), central (t(16) = -15.6, p<0.0001), parietal (t(16) = -12.8, p<0.0001), temporal (t(16) = 4.6, p<0.0001), occipital (t(16) = 3.9, p<0.001) indicating reduced alpha asymmetries across all electrode pairs during the follicular phase.

(b) Correlations

Alpha asymmetry and power during rest were compared with estradiol levels using correlation analysis. The concentration of estradiol during the follicular phase correlated significantly with alpha asymmetry in two of the five pairs after FDR correction (central: *r*(15)= 0.5, p<0.05 and occipital: *r*(15)= -0.51, p<0.05; FDR threshold was 0.05). The negative correlation found in the occipital electrode pair is in contrast with the expected direction seen in the ANOVA results. The positive correlation found in the central electrode pair could reflect that the region is differently affected by estradiol concentration compared to the posterior regions. The concentration of estradiol during the follicular phase also correlated significantly after FDR correction with the alpha log power of right frontal (*r*(15)= 0.58, p<0.05), left central (*r*(15)= 0.6, p<0.05), and right occipital (*r*(15)= 0.65, p<0.01) electrodes. The FDR threshold here was at 0.005. These correlations indicate which electrode of the pairs contributes most to correlations between pair differences and estradiol concentration. Estradiol concentration during the menses phase did not correlate significantly with any pair difference or electrodes.

Estradiol and alpha activity: Pre-T1

(a) ANOVA

During the task in the pre-T1 period, the same 2 X 5 ANOVA with cycle phase (follicular, menses) and electrode pairs (F3/F4, C1/C2, P3/P4, T5/T6, O1/O2) as repeated measures revealed main effects of cycle phase (follicular mean asymmetry -0.13 μV^2, SEM = 0.022; menses mean asymmetry 0.01 μV^2, SEM = 0.03) (F(1,16) = 9.2 , p<0.01), and pairs (F(4, 64) = 82.1, p<0.0001), where asymmetry was largest for F3/F4, followed by C1/C2, T5/T6, P3/P4, and O1/O2, with asymmetry indices of -0.62, 0.56, -0.28, 0.24, and -0.19 respectively. Subsequent t-tests indicated that the differences between the pairs collapsed over cycle phase were significant for all possible combinations of electrode pairs (all t(16)>±5.24, all p<0.0001) except temporal and occipital (t(16) = -0.99, p = 0.339). A significant interaction between phase and electrode pairs (F(4,64) = 30.1, p<0.0001) was also found. The interaction was followed up by paired t-tests for each of the pairs in the two phases. They revealed that the frontal, central, parietal and temporal pairs showed a significantly reduced asymmetry during follicular phase, (frontal (t(16) = 2.58, p<0.05), central (t(16) = -11.06, p<0.0001), parietal (t(16) = -7.12, p<0.0001), temporal (t(16) = 2.52, p<0.05). The occipital pair did not show this difference (t(16) = 1.37, p = 0.19).

(b) Correlations

Alpha asymmetry and power during task were correlated with estradiol levels. The concentration of estradiol during the follicular phase correlated significantly after false discovery rate (FDR) correction with alpha asymmetry in the temporal pair (*r*(15)= -0.49, p<0.05) suggesting that as estradiol concentrations increased, the asymmetry between the temporal electrode pair reduced. During the menses phase a correlation between occipital pair asymmetry and estradiol concentration was found (*r*(15)= 0.51, p<0.05) suggesting that as estradiol concentrations increased, asymmetry in this region also increased during task. This is in contrast to the findings at the occipital region during rest. This finding is illustrated in Figure 9. No significant correlations were observed between individual electrode alpha power and estradiol concentration.

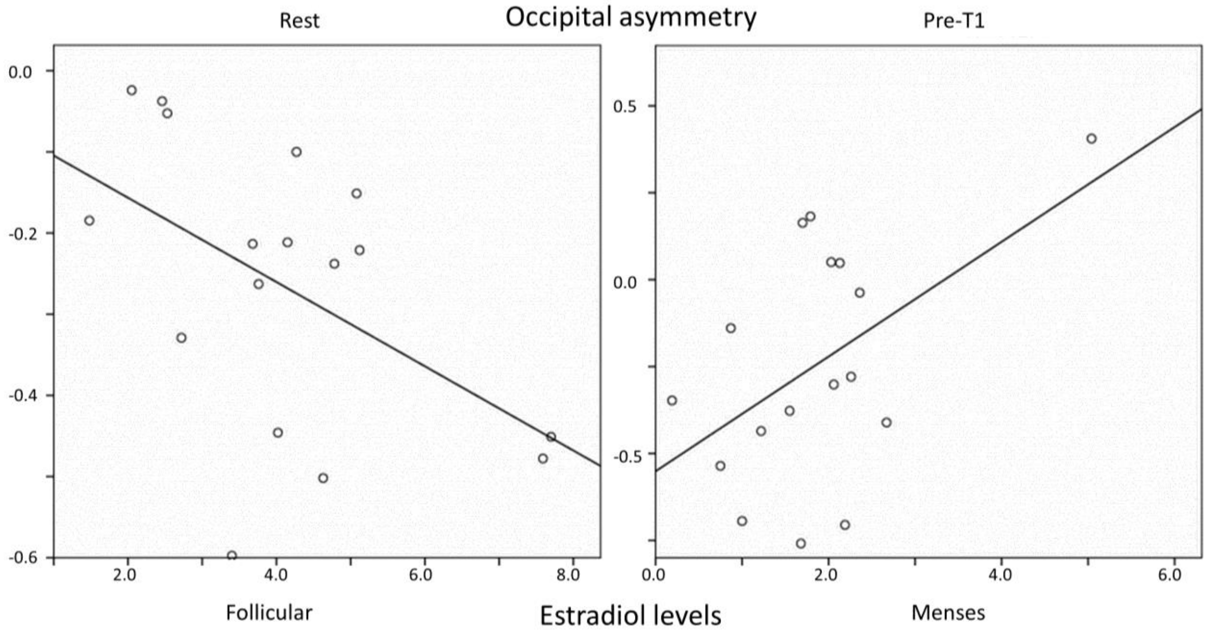

Figure 9. Correlations between estradiol levels and asymmetry in the occipital electrode pair are the opposite in Rest and Pre-T1 task conditions.

Estradiol and alpha activity: Rest vs. Task

To compare the rest and pre-T1 conditions, a 2 x 2 x 5 ANOVA was run with cycle phase (follicular, menses), condition (rest, pre-T1) and electrode pairs (F3/F4, C1/C2, P3/P4, T5/T6, O1/O2) as repeated measures. Effects including the factor condition were a two-way interaction between pairs and condition (F(4,64) = 17.7, p<0.0001) and a three-way interaction between phase, pairs and condition (F(4,64) = 3, p<0.05). To further explore this three-way interaction, we ran separate 2 x 2 ANOVAs for each of the electrode pairs with cycle phase and condition as repeated measures. As before, in all pairs, a main effect of phase was present (all $F(1,16) \geq 7.2$; all $p \leq 0.05$). The main effect of condition was present in all but the temporal electrode pair ($F(1,16) = 3.8$, $p<0.68$); all others ($F(1,16) \geq 10.2$, $p \leq 0.01$). Two-way interactions were found for the central ($F(1,16) = 13.9$, $p<0.01$) and parietal ($F(1,16) = 8.1$, $p<0.05$) electrode pairs. For the central pair, t-tests indicated significant differences between rest and task in the follicular ($t(16) = 3.2$, $p<0.01$) as well as the menstrual phases ($t(16) = 5.5$, $p<0.0001$). For the parietal pair too, t-tests indicated significant differences between rest and task in the follicular ($t(16) = 3.7$, $p<0.01$) as well as the menstrual phases ($t(16) = 3.6$, $p<0.01$). In sum, with the exception of the temporal electrode pair, alpha asymmetries were generally more pronounced during rest.

Alpha activity and behavioural performance

To explore the relationship between alpha activity and behaviour, we correlated LVF performance with alpha asymmetry as well as the power in each electrode of interest. At rest, not in accordance with the hypothesis, significant correlations were found for alpha asymmetry in the occipital electrode pair in the menses phase ($r(15)= -0.69$, $p<0.01$) implying that LVF performance dropped with increased rest asymmetry. FDR threshold was at 0.017. This relationship was also reflected in a significant correlation between performance in the LVF in the menses phase and the power of the right occipital electrode ($r(15)= -0.55$, $p<0.05$) (see Figure 10), indicating that performance suffered with increased alpha power at right occipital electrode during rest. This is in alignment with prior literature (MacLean et al. 2012) which reported stronger alpha power linked to larger AB.

During the task in the pre-T1 time window no significant correlations were found between behavioural performance and asymmetry in the occipital or other electrode pairs in the follicular or menses phases. However, in parallel to the rest data an FDR checked significant correlation was found between performance in the LVF in the menses phase and the power of the right occipital electrode ($r(15)= -0.52$, $p<0.05$).

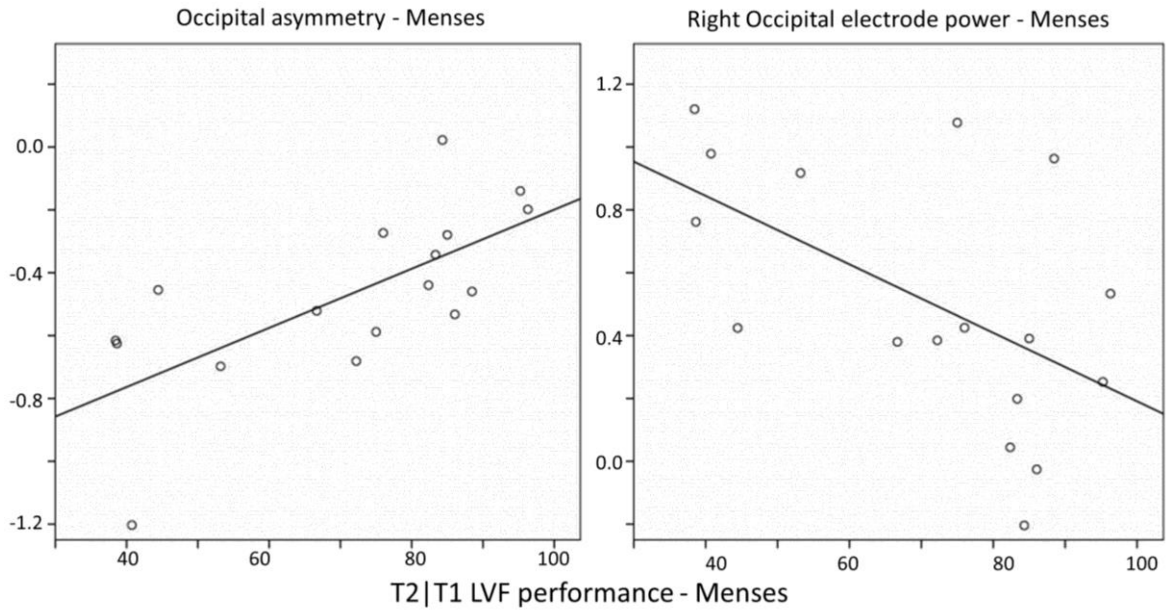

Figure 10. Correlation plots (a) between performance T2|T1 in LVF during menses and the occipital asymmetry and (b) between performance T2|T1 in LVF during menses and right occipital electrode power.

6.5 Discussion

In the present study we aimed to investigate whether estradiol-related modulations in asymmetry of the AB performance are mediated by modulations in alpha activity. The paradigm was validated by ensuring that there was a significant difference in estradiol concentrations between the follicular and menstrual phases. In the analysis of the behavioural data, the expected right hemisphere advantage was seen irrespective of cycle phase (Verleger, Smigasiewicz & Moeller 2011), along with the typical AB phenomenon which impacts T2 detection at lag 2 but not at lag 7 (Chun 1997; Kranczioch et al. 2003; Kranczioch et al. 2005).

<u>Relationship between alpha and estradiol</u>

We could not replicate the previously suggested effect of estradiol on LVF performance in the behavioural measures of the AB task (Holländer et al. 2005), however we found a very clear electrophysiological effect of estradiol on alpha asymmetry. That is, alpha asymmetry was generally lower in the follicular phase than during menses, both during rest and during RSVP stimulation. This is also supported by the correlation analysis during rest which showed, as estradiol levels increase in the follicular phase, asymmetry decreased in the occipital region.

A similar relationship was seen in the task condition between the temporal electrode pair and estradiol levels.

Additionally, the finding of a positive correlation between the alpha in the right frontal electrode during and estradiol levels follicular phase is similar to the results found in the study by Hwang et al. (2008) which also found higher right frontal alpha activity during high-estradiol ovulation.

<u>Relationship between alpha and LVF performance</u>

In spite of the lack of relationship between estradiol and LVF performance, a relationship was observed between occipital alpha asymmetry and LVF performance. Correlations indicated that during menses and the follicular phase, higher LVF performance was linked to reduced asymmetry at rest, and that the reduction in asymmetry was due to reduced right occipital power. This is in line with previous research that finds a right occipital dominance in visual processing (Verleger et al. 2011).

Thus, overall, our data imply a link between alpha asymmetry and behaviour on the one hand, and alpha asymmetry and estradiol on the other hand. This provides evidence for the impact of estradiol on neural asymmetry by modulating interhemispheric cross-talk as postulated by updated hypothesis of the sex hormone-modulated cortical interaction (Hausmann et al. 2013). As alpha asymmetry is a reflection of neural activity in either hemisphere, this finding also extends the current understanding of hemispheric asymmetry. Future studies on cerebral asymmetry may find it useful to control for phase of the cycle phase of their female participants to account for the impact of estradiol. The findings presented here also support the idea that alpha oscillations directly influence the attentional performance as shown in several previous studies and reviews (Janson & Kranczioch 2011; Klimesch 2012; Thut et al. 2006). Overall, they provide evidence for the idea that cycle-related modulations in asymmetry in the AB may be mediated by alpha activity.

It is possible to speculate that the reason we don’t see the direct physiological relationship between estradiol and behaviour is that the effect of estradiol on alpha may be complementing this cycle related fluctuation. Another possible reason that though, as found in the study by Holländer et al. (2005), estradiol is the main modulatory hormone of this effect, perhaps there is an interactive or additive effect between estradiol and progesterone which is necessary to cause the change behavioural performance without which only the effect on alpha is apparent. This is speculative but can be tested by running a similar experiment at both the follicular as well as the mid-luteal phases to compare the behavioural effects seen in both with the respective alpha asymmetries. This would provide a clearer picture of the mechanism behind the behaviour fluctuations.

Comparing rest and task conditions

During the task at the pre-T1 interval, just as during rest, we found a clear effect of estradiol on alpha asymmetry. Lower alpha asymmetry was found in the follicular phase than during menses in all pairs in the rest condition, and in all but the occipital electrode pair in the task condition. During menses, as estradiol levels decrease, in the task condition an decrease in occipital pair asymmetry was seen. This is the opposite relationship to what is found during rest. This contrast may be explained by the opposite relationship found between endogenous and RSVP-induced alpha with respect to attention performance (Janson et al. 2014). We further explored the difference between the rest and task conditions to find that the differences in the level of change in asymmetry were clearer at rest than during the task. It is possible that the RSVP-induced alpha created an entrainment that diminished this effect somewhat during the task condition (Janson et al. 2014).

In conclusion, relationships between alpha asymmetry and estradiol, as well as between alpha asymmetry and behavioural performance were seen in both rest and task conditions. These relationships provide evidence for the role of alpha as a possible neural mediator of the impact of estradiol on attention performance. This provides the first evidence of the role of alpha asymmetries in relation to the fluctuation of attention over the menstrual cycle. The contrast between rest and task condition findings seems to support their contrasting influence on attention found in other recent studies.

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6. General Discussion

6.1 Summary

Selective attention is known to be affected by many factors. In this thesis, three of these factors: 1) positive and negative affect state, 2) personality factors such as neuroticism and extraversion, and 3) estradiol concentrations that fluctuate over a menstrual cycle, were explored to get a better understanding of how they impact the distribution of selective attention.

In the first study, the influence of short-lived emotion states on attention was explored. A double RSVP doughnut paradigm similar to that used in Müller and Hübner (2002) was used in combination with emotional manipulation. The emotional manipulation was carried out between groups where one group was exposed to positive and neutral sets of pictures and the other was exposed to negative and neutral sets of pictures. The power modulations of the ssVEP elicited by the affective pictures were predicted to reveal the neural underpinnings of the fluctuations in spatial attention that we expected based on the positive affect hypothesis postulated by Olivers and Nieuwenhuis (2006). When the spotlight of attention was diffused using positive affect, the power distribution was expected to be more evenly distributed between the two streams, resulting in less of a power difference between the two streams. When attention was more focused by a negative affect state, more attentional resources, as reflected by ssVEP power, were expected in the attended stream, resulting in a more dissimilar ssVEP response between the two streams. In the results we found that the attention effect, that is, the increase of power of the ssVEP frequency that was being attended to, was present in all affect states. The emotional manipulation was also validated using SAM ratings, and performance data confirmed that participants attended the stream they were instructed to. Negative affect was found to modulate attentional resources compared to the neutral affect condition in the negative group. No effect of affect manipulation was found in the positive group. But although there was an increase of attentional resources with negative affect, the spatial interpretation of the diffuse mental state was not supported by the results. It is possible that the attentional demands of the task attenuated any effect of emotion manipulation (Schupp et al. 2007); however, given the validation of the affect manipulation by the SAM ratings, it is more likely that the spatial interpretation of the diffuse mental state idea itself should be called into question. Perhaps the neural mechanism of the diffuse mental state could be found using an alternative interpretation. This was investigated in the second study.

Based on the conclusions of the first study, in the second study we viewed the diffuse mental state as being related to improved cognitive flexibility (MacLean et al. 2010). Thus a focused cognitive style of those individuals with higher neuroticism would result in difficulty in disengaging from an irrelevant, perhaps salient, stimulus. We used the same dual-stream RSVP paradigm (Müller & Hübner 2002) in combination with measures of negative emotionality, including the PANAS and NEO-FFI questionnaires, to study the distribution of attention as it changed with negative emotionality. We expected that a more focused cognitive style linked with higher neuroticism would result in an overinvestment of attention in the irrelevant stream, especially when it was more salient than the relevant stream. As the larger RSVP stream, flickering at a slower rate, was more salient than the smaller stream, flickering at a faster rate, individuals with higher negative emotionality were expected to show more difficulty in switching attention from the larger stream to the smaller stream. This expectation was fulfilled by the results. As expected, a negative correlation was found between neuroticism and the difference in power evoked by the attended small stream and the unattended large stream. The negative correlation with neuroticism was consistent with the suggestion that the neuroticism trait is linked to difficulty in disengaging from a salient stimulus after attention capture. This link would also explain why no correlation was found between negative emotionality and the difference in power evoked by the attended large and unattended small stream. Alongside the confirmation of the hypothesis relating to neuroticism, we also found that extraversion behaved in the opposite manner to neuroticism with respect to the attention difference, that is, there was a positive correlation between the difference in power evoked by the attended small stream and unattended large stream, and the extraversion factor as measured by NEO-FFI. This finding was supported by existing research that contrasts the effect of neuroticism and extraversion as being opposite to each other and adds support to the idea that the diffuse mental state is closely related to cognitive flexibility, enhanced by traits such as extraversion. Extraversion is associated with positive affect (Carver et al. 2000; Nemanick Jr & Munz 1997; Rusting & Larsen 1997) and forms the opposite personality disposition to a trait such as neuroticism that, in combination with avoidance, is associated with a negative personality disposition (Elliott R. 2002).

From the first two studies which examined the concept of overinvesting attention in a negative emotion state or as a personality trait, in the third study, we ventured to understand how varying levels of estradiol impacted women's attentional performance. This departs from the question of distribution of attention into the realm of exploring how changes in attention performance can be elicited by fundamental biological processes such as the female menstrual cycle. RSVPs with an AB task were presented in either the left or the right visual field following the paradigm used by Holländer et al. (2005). The AB task measured behavioural performance while EEG data, collected both during the task and at rest, assessed the alpha band asymmetries that we suspected mediated estradiol's impact on behaviour. Hausmann and Güntürkün (2000) proposed that higher estradiol levels would lead to a decoupling of the two hemispheres leading to more independent activity of the two during follicular phase. We expected that with the rise in estradiol, ABs in the left visual field would also increase and alpha band asymmetry would decrease. Results showed that alpha band asymmetries did change with estradiol concentrations, and alpha activity was also related to the behavioural performance. These relationships provide evidence for the role of alpha as a possible neural mediator of the impact of estradiol on attention performance. The report of this study is in preparation.

Put together, the first and second studies contribute to the first uncovering of the physiological mechanisms underlying the diffuse mental state indicating that, rather than a spatial phenomenon, it is related to cognitive flexibility and control. This flexibility seems to be strongly linked to positive affect state as well as personality factors such as extraversion. A more focused cognitive style, on the other hand, is a result of both negative affect as well as negative personality factors such as neuroticism.

While the first two studies focused on primarily psychological phenomenon such as affect and personality, the third focused on a biological phenomenon present in women. The study endeavoured to contribute detail to a complex picture of how estradiol influences alpha band activity and attention performance. By addressing three distinct forms of influence on attention, we have gained greater insight into the fundamental physiological workings of selective attention and attention distribution.

6.2 Future Work

It is important to note certain shortcomings of scientific work in order to improve upon it in one's future work and note what more can be explored from this point on. In the first study, the method of affect manipulation could have been more effective. Though IAPS pictures have been tried and tested successfully by many studies before (e.g. Dreisbach & Goschke 2004; Olivers & Nieuwenhuis 2006), other studies have used music of the participants' choice to induce positive affect effectively enough to eliminate spatial neglect (Soto et al. 2009) and to widen the breadth of attention selection (Rowe et al. 2007). Eliciting a stronger positive affect state in the first study would have strengthened the conclusion that the diffuse mental state is not a spatially-oriented phenomenon. Also, there was a difference between our use of the IAPS pictures and that of previous studies. In order for the affective content to be more fully processed and to create a more intense affect change, we used twice as many pictures, 20 instead of 10, and exposed the pictures for a full second rather than for only 250 ms (Olivers & Nieuwenhuis, 2006; Dreisbach & Goschke, 2004). It is possible that overexposure weakened the effect of each picture. Future experiments would benefit from taking these points into account.

In the second study the condition in which the participants attended the large stream and ignored the small stream yielded no particular insight on its own. It was only useful as a control for the effects found when participants attended the smaller stream. Perhaps fewer trials could have been devoted to this condition in the experiment to optimise the design.

The first study was well followed up by the second. The natural next step in this line of research would be to design a study in which the AB is also incorporated into the double ssVEP paradigm. It is possible that this paradigm, combined with affect manipulation and personality scores, would lead to more answers about how the relevant and irrelevant stimuli of differing size and salience are processed in different mental states. Another interesting next step to the second study would be to investigate the somewhat surprising result found when individuals with low neuroticism scores were contrasted with those with higher scores. This test was done to find out whether the higher scorers attended more to the irrelevant stimuli (i.e. with higher power to unattended stimuli) or paid less attention to the relevant stimuli (i.e. with lower power to attended stimuli). The current understanding is that individuals with higher neuroticism scores tend to pay more attention to the irrelevant stimulus; however our result contradicts this assumption by noting that individuals with higher neuroticism actually paid less attention to the attended stream rather than more attention to the irrelevant stream. Though this finding only approached significance, another study with a paradigm more suited to explore this difference that is, where size is not the salience-related factor, would be of great interest to this subfield.

This research could also have implications in understanding disorders associated with high neuroticism levels such as dysphoria or depression, or those relating to emotion regulation in general, because the information from the surroundings that an individual selects to process often gives direction to their subsequent thoughts and feelings. For example, if more studies show that it is salience rather than negativity that individuals with higher negative emotionality attend more to, it may be possible to use this implicitly in clinics to help people with depression focus more on salient positive information. If it is understood with further research that individuals with depression tend to attend less to relevant information, rather than attending more to irrelevant information, depression may start to be seen more as a symptom of an attention disorder rather than as a primarily emotional disorder. This may even help improve the classification of certain disorders in the Diagnostic and Statistical Manual of Mental Disorders (DSM). Attention strategies are already being used in therapy techniques such as cognitive behavioural therapy where patients are asked to keep count of their blanket negative statements in order to be better able to spot them. For example, patients may be asked to recount five positive things that happened to them that day and keep journal entries in order to train their mind to better attend positive information and 'look on the bright side of life'. Understanding how emotion states and traits influence selective attention will only add to the potential of inventing new strategies that may help patients cope with or recover from depression.

The third study dealt with the potential link between estradiol-related modulations of FCA in the AB and modulations in the symmetry of alpha activity. It may have been useful to include the mid-luteal phase to the comparison as well as to measure progesterone along with estradiol levels in order to contrast the findings with previous literature that has explored both hormones. This may have helped make a stronger case for estradiol being the primary hormone modulating asymmetry. Understanding the influence of estradiol on brain asymmetry will also help in controlling for the menstrual phase of women in future studies of hemispheric asymmetry of the brain. A possible next step could be to integrate these findings with studies on hormone replacement therapies to investigate cognitive side effects of the drugs in postmenopausal women. It could also be useful in extending current research on hormone-related contraceptive pills with regard to their side effects on attention performance.

6.3 Outlook

In the sea of factors that affect visual selective attention, the studies reported in this thesis explored short lived emotion states that disappear over seconds, long term personality factors that are stable over a lifetime, and estradiol which fluctuates over the menstrual cycle of women. The evolutionary significance of negative stimuli has fundamentally altered the way we process the outside world. In the words of Mark Antony,

"The evil that men do lives after them;
The good is oft interred with their bones."
- Act 3 Scene 2, Julius Caesar, Shakespeare

We are programmed to perceive and remember the negative but we speedily habituate to the positive sources. When this tendency is taken to an extreme it can make an individual susceptible to affect disorders such as depression and anxiety. It has been shown that individuals with both of these disorders are reported to focus more on the negative affect stimuli and those with depression tend to report disengagement from pleasurable activities and stimuli (Watson et al. 1988). Perhaps our deepening understanding of how visual stimuli are differently selected based on these factors will help us to better understand such disorders and contribute to more effective treatment options.

Although one cannot ascribe an evolutionary explanation to how attention is modulated by the menstrual cycle because menstruation is a far more fundamental non-psychological phenomenon, these findings offer a springboard from which to speculate about where future studies will take us in terms of insights into the inner workings of visual attention. Currently, finer details that will disentangle one's own natural alpha rhythms from those evoked by external RSVP and the influence each of these have on the AB performance are being explored (Janson et al. 2014); the role that primary visual characteristics such as hue, lightness and saturation have on spatial selective attention is being investigated (Stuart Barsdell, & Day 2014); and the influence of blindness on spatial attention in the auditory modality is being uncovered (Lerens & Renier 2014).

What we have been able to glean using EEG is temporally rich information. Combined with an imaging technique such as functional magnetic resonance imaging (fMRI), near infra-red spectroscopy (NIRS), MEG or perhaps even diffuse tensor imaging (DTI), we may be able to define neural networks with high spatial resolution that would shed more light on the parts of the brain involved in attention. Perhaps, with more advanced studies on attention, we may even be able to step closer to understanding the elusive idea of consciousness.

With the increased development of BCI, selective, spatial, and sustained attention will become more useful even at a commercial level for clinical, entertainment-based, and industrial uses. Clinically, BCI can be applied in designing machines that both aid the giving of voice to those who are unable to speak and aid movement for paralysed patients using their event related potentials. In terms of entertainment, the technology of interfacing the brain with computers will expand rapidly into areas such as gaming where it currently has a modest presence. In a few decades BCI technology may even assist in driving a car hands-free, operating dangerous machinery from a safe location, or controlling space equipment such as robots from earth. This technology would dramatically reduce the expense of several industrial processes and aid in space exploration. This would in turn feed other waves of research that will make the classifiers of brain activity more individualised and trainable using uniform or adaptable strategies. The better we are able to understand how visual selective attention works, the more effectively these areas will grow.

My contribution to this field is but to investigate three of the many factors that influence attention. I hope that these studies will enrich further enquiry into attention.

Declarations

Statement of the part of all authors on the scientific work of this Cumulative Dissertation according to § 8 paragraph 3 of the doctoral regulations of the Faculty of Mathematics and Natural Sciences at the Carl von Ossietzky University of Oldenburg

Study 1

Janani Dhinakaran and Cornelia Kranczioch developed the study concept and design. Testing, data collection and analysis were performed by Janani Dhinakaran. Cornelia Kranczioch, Maarten De Vos, Jolanda Janson, and Niclas Braun were involved in data analysis. Jeremy D. Thorne significantly supported programming of the experiment. Janani Dhinakaran drafted the paper with the support of Cornelia Kranczioch and critical revisions of Maarten De Vos, Jolanda Janson, Niclas Braun, Jeremy D. Thorne. All authors approved the final version of the paper for submission. This research was supported by grant KR 3433/2-1 of the German Research Foundation to Cornelia Kranczioch. Maarten De Vos was supported by the Humboldt Foundation.

Study 2

Janani Dhinakaran and Cornelia Kranczioch developed the study concept and design. Testing, data collection and analysis were performed by Janani Dhinakaran. Cornelia Kranczioch, Maarten De Vos and Jeremy D. Thorne were involved in data analysis. Jeremy D. Thorne significantly supported programming of the experiment. Janani Dhinakaran drafted the paper with the support of Cornelia Kranczioch and critical revisions of Maarten De Vos and Jeremy D. Thorne. All authors approved the final version of the paper for submission. This research was supported by grant KR 3433/2-1 of the German Research Foundation to Cornelia Kranczioch. Maarten De Vos was supported by the Humboldt Foundation. The authors would also like to thank the reviewer for the insightful and constructive comments on an earlier version of the manuscript.

Study 3

Janani Dhinakaran and Cornelia Kranczioch developed the study concept and design. Niclas Braun helped significantly in programming the experiment. Data collection was done by Janani Dhinakaran and Anja Lindig. Data analysis was performed by Janani Dhinakaran with the guidance of Cornelia Kranczioch and Jeremy D. Thorne. Janani Dhinakaran is drafting the paper with the support of Cornelia Kranczioch and critical revisions of Markus Hausmann, Jeremy D. Thorne and Jolanda Janson. This research was supported by grant KR 3433/2-1 of the German Research Foundation to Cornelia Kranczioch.

Statement for the intended doctoral degree according to § 10 paragraph 2a, 2b and 2c of the doctoral regulations of the Faculty of Mathematics and Natural Sciences at the Carl von Ossietzky University of Oldenburg

I hereby declare that this work is towards the doctoral title of Dr. rer. nat.

I have completed the work independently and used only the indicated facilities. This dissertation is my own work. All the sources of information have been acknowledged by means of complete references.

This dissertation has neither as a whole nor in part been published or submitted to assessment in a doctoral procedure at another university.

Janani Dhinakaran

Erklärungen und eidesstattliche Versicherungen

Darlegung der Anteile aller Autoren an den wissenschaftlichen Einzelarbeiten der kumulativen Dissertation gemäß § 8 Abs. 3 der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg

Studie 1

Janani Dhinakaran und Cornelia Kranczioch entwickelten gemeinsam das Konzept und die Ausrichtung der Studie. Die Austestung, Datenaufnahme und Datenanalyse wurde durch Janani Dhinakaran durchgeführt. Cornelia Kranczioch, Maarten De Vos, Jolanda Janson und Niclas Braun waren an der Datenanalyse beteiligt. Herr Jeremy D. Thorne half wesentlich bei der Programmierung des Experiments. Janani Dhinakaran verfasste das Manuscript unter Mitwirkung von Cornelia Kranczioch und mit Hilfe der Korrekturvorschläge von Maarten De Vos, Jolanda Janson, Niclas Braun und Jeremy D. Thorne.

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Studie 2

Janani Dhinakaran und Cornelia Kranczioch entwickelten gemeinsam das Konzept und die Ausrichtung der Studie. Die Austestung, Datenaufnahme und Datenanalyse wurde durch Janani Dhinakaran durchgeführt. Cornelia Kranczioch, Maarten De Vos und Jeremy D. Thorne waren an der Datenanalyse beteiligt. Herr Jeremy D. Thorne half wesentlich bei der Programmierung des Experiments. Janani Dhinakaran verfasste das Manuscript unter Mitwirkung von Cornelia Kranczioch und mit Hilfe der Korrekturvorschläge von Maarten De und Jeremy D. Thorne. Alle Autoren stimmten der Veröffentlichung der finalen Manuscript-Version zu.

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Studie 3

Janani Dhinakaran und Cornelia Kranczioch entwickelten gemeinsam das Konzept und die Ausrichtung der Studie. Niclas Braun half wesentlich bei der Programmierung des Experiments. Die Datenaufnahme erfolgte durch Janani Dhinakaran und Anja Lindig. Die Datenanalyse erfolgte durch Janani Dhinakaran unter wesentlicher Mithilfe von Cornelia Kranczioch und Jeremy D. Thorne. Janani Dhinakaran verfasst dieses Manuskript unter Mitwirkung von Cornelia Kranczioch und unter Berücksichtung der Korrekturvorschläge von Markus Hausmann, Jeremy D. Thorne und Jolanda Janson.

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Erklärung zum angestrebten Doktorgrad gemäß § 10 Abs. 2a der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg

Hiermit erkläre ich, dass ich eine Promotion zum Dr. rer. nat. anstrebe.

Erklärung zum angestrebten Doktorgrad gemäß § 10 Abs. 2b der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg

Hiermit versichere ich, dass ich die vorliegende Dissertation selbständig verfasst und nur die angegebenen Quellen verwendet habe. An den aufgeführten Manuskripten trug ich wie oben dargelegt, den Hauptteil bei.

Erklärung zum alleinigen Vorliegen der Dissertation an der Carl von Ossietzky Universität Oldenburg gemäß § 10 Abs. 2c der Promotionsordnung.

Hiermit versichere ich, dass die vorliegende Dissertation weder in ihrer Gesamtheit noch in Teilen in einer anderen wissenschaftlichen Hochschule zur Begutachtung in einem Promotionsverfahren vorliegt oder vorgelegen hat.

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2000 - 2006	High school at The Valley School (KFI), Bangalore, India
1995 - 2000	Primary school at Holsworthy Public School, Sydney, Australia

Other courses

2011, 2012	EEGLab workshop
2012	Introduction to Cognitive Neuroscience
2012	Neurocognitive Development
2012	Multivariate Statistics
2012	Computer-Controlled Experimentation
2012	Introduction to Scientific Programming
2011	MATLAB beginner's course
2011	Psychological Assessment and Diagnostics
2011	Neurophysiology – EEG analysis with MATLAB
2011	Entrepreneurship course for scientists
2010	fMRI-EEG course
2010	SPM8 course
2010	Postgraduate Program Review Training Course
2010	Science and Media course
2007-08	A certificate course in Journalism-printed media
2006-07	A certificate course in Neuro-linguistic Programming

Awards

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Article Publications

Dhinakaran J, De Vos M, Thorne JD, and Kranczioch C (2014). Neuroticism focuses Attention: Evidence from ssVEPs. *Exp. Brain Res.*

Dhinakaran J, De Vos M, Thorne JD, Braun N, Janson J and Kranczioch C (2013). Tough doughnuts: Affect and the modulation of attention. *Front. Hum. Neurosci.*

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Conference Abstracts

K. Davidson-Kelly, S. Hong, J. Dhinakaran, J. Sanders, C. Gray, E. J. van Beek, N. Roberts, and K. Overy. Middle Frontal Gyrus as a Potential Neural Indicator for Musical Imagery. ISMRM 2011.

Posters

K. Davidson-Kelly, S. Hong, J. Dhinakaran, J. Sanders, C. Gray, E. J. van Beek, N. Roberts, and K. Overy. An fMRI study of expert musical imagery: To what extent does imagined and executed performance share the same neural substrate? ISPS 2011