

**MOTIVATION AND THE BRAIN:
HOW DO APPETITIVE VERSUS AVERSIVE STATES RELATE
TO ELECTROENCEPHALOGRAPHIC ACTIVITY?**

DISSERTATION

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Bei der Auswahl und Auswertung folgenden Materials haben mir die nachstehend aufgeführten Personen in der jeweils beschriebenen Weise unentgeltlich geholfen.

1. Markus Quirin hat als Koautor an Manuskripten 1-3 mitgewirkt und Feedback zur Struktur der Einleitung und der allgemeinen Diskussion dieser Dissertation gegeben.
2. Thomas Gruber hat als Koautor an Manuskripten 1-3 mitgewirkt.
3. Benjamin Schöne (geb. Kuhr) hat als Erstautor des ersten Manuskripts, sowie als Koautor von Manuskript 2 (geteilte Erstautorenschaft) und Manuskript 3 fungiert. Zudem hat er bei der Erhebung der Daten und der Stimulenauswahl mitgewirkt. Die Datenanalyse für alle drei Studien haben Herr Schöne und ich gemeinschaftlich durchgeführt.
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Weitere Personen waren an der inhaltlichen materiellen Erstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die entgeltliche Hilfe von Vermittlungs- bzw. Beratungsdiensten (Promotionsberater oder anderen Personen) in Anspruch genommen. Niemand hat von mir unmittelbar oder mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

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*Die Fragen eines Kindes sind schwerer zu beantworten als die Fragen eines
Wissenschaftlers.*

Alice Miller (1923-2010)

Psychologin und Autorin

Ich widme diese Dissertation meinen Kindern, Noah und Lilli Schomberg, in der
Hoffnung, dass ihr nie aufhört Fragen zu stellen.

General Abstract

Approach and Avoidance motivation are two of the oldest psychological concepts of behavior. Whereas approach motivation corresponds to the strong urge to come close to an object, state or person (e.g., during states of sexual attraction), avoidance motivation corresponds to the strong urge to avoid a specific situation (e.g., evade a dangerous situation). This dissertation deals with the electroencephalographic (EEG) markers of approach and avoidance motivation, assessed using event-related-potentials and brain oscillations in a low frequency band (alpha band).

The first manuscript shows a left hemispheric processing advantage for approach-related stimuli. Specifically, we report a reduction in the alpha band (as an inverse marker for cortical activity) for erotic, but not for control pictures. Notably, we are the first to report alpha-asymmetries using an event-related design.

In the second manuscript we describe evidence (a) for separating approach motivation from the affective dimensions of valence and arousal and (b) for an enhanced attention-related early EEG amplitude (P1 component) only for approach-related but not for control pictures. Up to our knowledge, we are the first to associate the P1 component with approach motivation.

In the third manuscript we report an enlarged P1 component for increased avoidance motivation, as measured by the negative affect scale of the German Positive and Negative Affect Schedule (PANAS; Krohne, Egloff, Kohlmann, & Tausch, 1996). In more detail, state negative affect correlated positively with the P1 component, as a marker of increased selective attention. As far as we know, no study ever showed that state negative affect has an influence on attention. Therefore, we consider these findings regarding previous findings on trait negative affect, specifically on anxiety and phobia.

All findings are discussed in the context of established views and models, such as Personality Systems Interaction (PSI) theory, hypervigilance theory, wanting versus liking and are also integrated into the findings from neuroimaging studies.

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1 Introduction

1.1 Approach and Avoidance Motivation

Approach and avoidance motivation are two of the oldest discussed concepts of behavior. The distinction among these two motivational dimensions even goes back to the Greek philosopher Democritus of Abdera, who lived around 400 B.C. (Elliot, 2008b). Democritus discussed that approaching pleasurable states (via approach motivation) and avoiding dangerous and painful situations (via avoidance motivation) is central for human life: “The best thing for a man is to pass his life so to have as much joy and as little trouble as may be” (Copleston, 1946). This view towards the importance of approach and avoidance motivation is prevailing up to modern times. Leknes and Tracey (2008) consider these types of motivation vitally important for successful adaptation. Avoidance motivation alerts the human being in order to assure survival by evoking withdrawal reactions, which facilitate defense, flight, and general protection. Approach motivation evokes appetitive reactions by facilitating thriving and reproduction, as in the case of sexual approach motivation (Bradley, Codispoti, Cuthbert, & Lang, 2001; Elliot, 2008b; Schneirla, 1959). This distinction in motivation has been studied intensively, among others concerning their neural functions (Spielberg et al., 2011), neuroanatomy (LeDoux, 1995), psychophysiology (Bradley, Codispoti, Cuthbert, et al., 2001), alpha band oscillations (Harmon-Jones, Gable, & Peterson, 2010), event-related brain potentials (Schupp et al., 2007), personality (Elliot & Thrash, 2002), and behavior (Seibt, Neumann, Nussinson, & Strack, 2008).

Despite the agreement on the importance of these two motivational concepts, different views on the nature of approach motivation have developed during the last few decades, which have caused an ongoing debate on its definition. According to an established model of Bradley and Lang’s lab (Bradley, 2000; Bradley, Codispoti, Cuthbert, et al., 2001) approach and avoidance motivation are based on the dimensions

of (a) hedonic valence (pleasantness vs. unpleasantness) and (b) arousal (the degree of motivation, e.g., high versus low activation). In this model, the valence dimension specifies which motivational system (approach vs. avoidance) is active and arousal indicates the intensity of the motivational activation (Bradley, Codispoti, Cuthbert, et al., 2001).

However, whereas this widely accepted view indicates that approach motivation can only be triggered by a positively valenced stimulus (see also Elliot & Covington, 2001; Lang & Bradley, 2008), E. Harmon-Jones and colleagues argue that approach motivation can also be elicited by negative stimuli (Harmon-Jones, Harmon-Jones, & Price, 2013). The authors review findings in which high approach motivation can be caused by anger, which is (a) triggered by a negatively valenced stimulus and (b) experienced as a negatively valenced feeling. Furthermore, trait measurements of temperament towards approach motivation (measured via the Behavioral Inhibition and Behavioral Activation Scales; BISBAS; Carver & White, 1994) correlate positively with both, trait (Harmon-Jones, 2003a) and state anger (Carver, 2004). Additionally, neural correlates associated with high approach motivation (i.e., larger left frontal than right frontal activations) were found for states of anger (Harmon-Jones, Sigelman, Bohlig, & Harmon-Jones, 2003).

Notably, anger does not seem to be the only negative emotion associated with approach motivation. Larger left frontal brain activations were also found for feelings of guilt when persons make amends (Amodio, Devine, & Harmon-Jones, 2007). Besides, addictive behavior also indicates that strong approach motivation must not necessarily be induced by positive stimuli or be experienced as a positive state. Addicts yearn for addiction-related objects or states, which themselves do not give them pleasure anymore, for example during compulsive gambling (Berridge, Robinson, & Aldridge, 2009).

This collection of research reveals that approach motivation and affect (negative versus positive) must not be necessarily confounded. However, there is also empirical evidence for an existing link between approach motivation and positive affect (see also Kuhl, 2009). A reaction time study (Wentura, Rothermund, & Bak, 2000) showed that reaction times were slower for positively ('honest') than negatively valenced words ('depressive'), when they became larger once the participant pressed a key (approach condition). Vice versa, reaction times were slower for negative words than positive words, when they became smaller once the participant released a key (avoidance condition). Thus, in contrast to the above reviewed findings, these effects favor the view that approach motivation and positive affect as well as avoidance motivation and negative affect are at least partially confounded.

The nature of avoidance motivation is less controversial. Various researchers concordantly agree that strongly negative and high-arousing stimuli, like pictures showing death and mutilation, engage avoidance motivational reactions (Bradley, Codispoti, Cuthbert, et al., 2001; Elliot, 2008a; Hillman, Rosengren, & Smith, 2004; Lang, 2000). Furthermore, negatively valenced emotions, like fear and anxiety, have consistently been linked to avoidance motivation (Elliot & Thrash, 2002; Gray, 1987). Therefore, high negative valence is positively related to avoidance motivation. Consequently, measuring negative affect, for example via the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988), is likely to be a valid measurement of avoidance motivation since it also covers emotions like anxiety and distress. In this dissertation, I will interpret our results concerning negative affect in the context of avoidance motivation.

1.2 Electroencephalographic Markers of Approach and Avoidance Motivation

Motivational reactions (approach vs. avoidance) go along with specific neural mechanisms, which can be detected via electroencephalography (EEG). The present

dissertation addresses these EEG correlates of approach and avoidance motivation.

Before I describe the detailed research questions I want to introduce the discussed EEG markers by giving an overview about the components and frequency waves reported in the manuscripts of my dissertation.

According to a well-established view, neural reactions associated with approach and avoidance motivation should occur very early and automatically after a given incentive (Elliot & Covington, 2001; Zajonc, 1998), because approach and avoidance motivation are described as the initial and most fundamental response to stimuli on which all subsequent reactions are based (Zajonc, 1998). Therefore, the differentiation between stimuli eliciting either approach or avoidance motivation has to happen very rapidly, which should be reflected in early ERP components. Indeed, negative stimuli eliciting strong avoidance-motivated reactions (e.g., pictures showing mutilations) trigger very early brain processes associated with attention allocation (N. K. Smith, Cacioppo, Larsen, & Chartrand, 2003; N. K. Smith et al., 2006). This effect is often referred to as a negativity bias, as the early attentional bias was only found for strongly negative but not for positive pictures (for a review see Olofsson, Nordin, Sequeira, & Polich, 2008).

In my dissertation, I will present results from two studies, in which an enlarged early ERP component was found in response to positive stimuli. I will discuss these results in the context of both approach (manuscript 2) and avoidance motivation (manuscript 3). Furthermore, I will link these findings with how approach and avoidance motivation modulate attentional processes. In addition to the ERP findings, I will also report differences in alpha band oscillations and connect them to approach motivation (manuscript 1). For a better understanding of the motivational implications, I will now give a short introduction of the EEG markers discussed in the manuscripts of this dissertation.

1.2.1 Event-related potentials.

Ever since Hans Berger (1929) discovered the possibility of measuring human brain potentials by placing electrodes on the scalp, the interest in the EEG has been unbroken. Until today, heaps of research have been conducted by investigating the relationship between EEG activity and psychological processes, such as learning (Gruber, Müller, & Keil, 2002; Miltner, Braun, Arnold, Witte, & Taub, 1999), memory (Klimesch, 1999), emotion (Olofsson et al., 2008), and also motivational processes (Harmon-Jones et al., 2010; Spielberg, Stewart, Levin, Miller, & Heller, 2008). Because EEG recordings provide a precise temporal resolution, they are highly suitable for measuring early and automatic processes, as they are supposed to occur in both, avoidance and approach motivation (N. K. Smith et al., 2003; Zajonc, 1998).

1.2.1.1 P1 component.

The P1 component is an early positive amplitude peaking at around 110 ms after visual stimulus onset. It is measured via occipital electrodes accessing brain activity over visual areas. The P1 originates in the extrastriate visual cortex which contributes to the visual areas V2-V5 and is a direct index for automatic allocation of visual attention (Clark & Hillyard, 1996; Gomez, Clark, Fan, Luck, & Hillyard, 1994). Regarding affective dimensions, the P1 has been found to be highest for negative arousing but not for positive arousing or neutral stimuli (negativity bias; Crawford & Cacioppo, 2002; Olofsson et al., 2008; N. K. Smith et al., 2003). In this work, I connect enhanced P1 components to both, approach (manuscript 2) and avoidance (manuscript 3) motivational processes.

1.2.1.2 N1 component.

The N1 component is the first negative amplitude peaking at about 170 ms after visual stimulus onset and is also measured over occipital electrodes. The N1 is larger for

attended than for unattended stimuli (Vogel & Luck, 2000) and a marker of feature processing (Itier & Taylor, 2004). Regarding affective and motivational processes, the N1 was reported to be modulated by valence, arousal and also by motivation (Gable & Harmon-Jones, 2011; Keil et al., 2001; Olofsson et al., 2008; Schupp et al., 2007). In this work, I will show how approach motivational processes are related to N1 activity (manuscript 2).

1.2.1.3 Late potentials.

Later ERP components such as the P3a, P3b and late positive potentials (LPP), start to occur 300 ms after stimulus onset. They represent higher and cognitive perceptual functions, such as object recognition, evaluation, and memory processes (for reviews see Polich, 2007; Polich & Criado, 2006). There is a considerable body of evidence for a modulation by participants' motivational relevance (for a review, see Olofsson et al., 2008) of these components. In particular, the P3 was found to be modulated by tasks' monetary reward (Kleih, Nijboer, Halder, & Kübler, 2010) and the LPPs were found to be higher for emotional relevant pictures (positive or negative in valence) and highest for erotic primes (Feng, Wang, Wang, Gu, & Luo, 2012; Schupp et al., 2004; Schupp et al., 2000). In my dissertation I aim to replicate the effect of erotic pictures on late potentials.

1.2.2 Hemispheric asymmetries and the alpha band.

Asymmetries in the hemispheric function of the brain have been studied for over a century and a half. First evidence that the brain hemispheres differ in their function came from the French physician Paul Broca in the 1860s. By examining brains of deceased aphasic patients, Broca (1861) detected the language dominance of the left hemisphere (for a review see Springer & Deutsch, 1985). Concerning emotional processes, Charles Mills was one of the first to describe hemispheric differences. Based

on his observations, he reported that patients with right-hemispheric lesions seem to exhibit reduced emotional expression in comparison to patients with left-hemispheric lesions (Mills, 1912). These initial observations led to an increased interest in studying hemispheric asymmetries during emotion processing, which continues until the present day.

In particular there is extensive current literature about what kind of affective or motivational states modulate hemispheric asymmetries over frontal areas (for a review, see Spielberg et al., 2008). The theories range from valence (pleasantness vs. unpleasantness; R. J. Davidson, 1984a; Heller, 1990), to approach versus avoidance motivation (Harmon-Jones et al., 2010), behavioral inhibition versus behavioral activation (BIS/BAS; Wacker, Chavanon, Leue, & Stemmler, 2008) and social motives (affiliation versus power motive; Quirin, Gruber, Kuhl, & Düsing, 2013; Quirin, Meyer, et al., 2013). A more detailed overview about the different models is given in the introduction section of the first manuscript (section **Fehler! Verweisquelle konnte nicht gefunden werden.**).

Frontal hemispheric asymmetry in motivational and affective neuropsychology is mainly assessed by comparing alpha activity in the left frontal hemisphere with alpha activity in the right frontal hemisphere. They are neural oscillations, measured by EEG, in the frequency range of 8 – 13 Hz. Alpha waves are pronounced in states of wakeful relaxation (Klimesch, 1999) and have been found to be inversely related to cortical activation (e.g., I. A. Cook, O'Hara, Uijtdehaage, Mandelkern, & Leuchter, 1998). It is assumed that higher alpha reduction indicates higher activity of the specific cortical area (Laufs et al., 2006; Laufs et al., 2003).

A large body of research reports frontal asymmetries in the alpha band based on measurements of resting state alpha. Thereby, alpha oscillations are recorded over several minutes and afterwards correlated with personality dimensions (for a review, see

Harmon-Jones et al., 2010; Quirin, Gruber, et al., 2013). Using this method, a relation between frontal alpha asymmetry and approach motivation was found. Until now, motivational alpha asymmetries effects were not found when using an event-related design. In his review, Harmon-Jones and colleagues (2010) conclude that event-related designs are not suitable to track motivational effects since these are too weak when induced by using a randomized picture presentation design. However, in manuscript 1 of this dissertation, my colleagues and I aim to give evidence that frontal alpha asymmetries can indeed be tracked by using an event related paradigm.

1.2.3 Research Questions of the Present Dissertation

One of the three manuscripts of this dissertation has been published (Kuhr, Schomberg, Gruber, & Quirin, 2013; shared first authorship) and two have been recently submitted for publication (Schomberg, Schöne, Gruber, & Quirin, 2015; Schöne, Schomberg, Gruber, & Quirin, 2015). In the first and second manuscript, I will show electroencephalographic correlates of approach motivation and appetite, respectively. In particular, the first manuscript discusses whether hemispheric differences, tracked by changes in the alpha band, can be elicited by manipulating approach motivation in an event-related picture paradigm. The second manuscript presents first evidence for very early attentional effects of appetite, as indexed by an enlarged P1 component (Kuhr et al., 2013). Additionally, the first and second manuscripts both intend to constitute approach motivation as a distinct dimension, which does not arise out of the affective dimensions valence and arousal. The third manuscript deals with avoidance motivation on the state level and its representations on event-related-potentials. In particular, we investigate EEG markers of increased avoidance motivation, as measured by the negative affect scale of the PANAS (Krohne et al., 1996; Watson et al., 1988).

1.2.4 Disambiguation of Terms Associated with Approach and Avoidance Motivation

In the literature different terms for approach and avoidance motivations are used. Bradley and colleagues (Bradley, Codispoti, Cuthbert, et al., 2001) use the term “appetitive system” and “defensive system”, connecting these terms to the positive and negative valence of the desired or dreaded object, respectively. Harmon-Jones and colleagues use the terms “approach motivation” and “avoidance motivation” (Harmon-Jones et al., 2013). In contrast to Bradley and colleagues, Harmon-Jones’s lab aims to dissociate these motivational states from the valence of a focused object. An interesting overview about the different terms used is given in Elliot and Covington (2001).

In Manuscript 2 of this dissertation, we use the term “appetence” for a positive approach motivation, which can be characterized as a strong urge to come near to a desired object or person. We decided to refer to the term appetence, since we showed erotic pictures of nude women and our participants explicitly rated the pictures as desirable.

In manuscript 1, however, we use the term “approach motivation”, although we also showed erotic pictures and assessed appetitive motivation. But since a central point of the manuscript relates to Harmon-Jones’s assumption (Harmon-Jones et al., 2010) that states of approach motivation are not strong enough to be reflected by alpha asymmetries when they are measured by an event-related paradigm, we decided to also use the superordinate term Harmon-Jones used.

In manuscript 3, by using the term “state negative affect”, I refer to avoidance motivation, as I already discussed above in section 1.

2 Approach Motivation and Alpha asymmetries

Schöne, B., Schomberg, J., Gruber, T., Quirin, M. (2015). Event related frontal alpha asymmetries: Electrophysiological correlates of approach motivation. *Accepted for publication in Experimental Brain Research*. doi:10.1007/s00221-015-4483-6.

Abstract

Over the last decades, frontal alpha asymmetries observed during resting state periods of several minutes have been used as a marker of affective–motivational states. To date, there is no evidence that alpha asymmetries can be observed in response to brief affective–motivational stimuli, as typically presented in event-related designs. As we argue, frontal alpha asymmetry might indeed be elicited by brief events if they are salient enough. In an event-related design, we used erotic pictures, i.e., highly salient incentives to elicit approach motivation, and contrasted them with pictures of dressed attractive women. As expected, we found significant alpha asymmetries for erotic pictures as compared to control pictures. Our findings suggest that the highly reactive reward system can lead to immediate, phasic changes in frontal alpha asymmetries. We discuss the findings with respect to the notion that high salience of erotic pictures derives from their potential of satisfying an individuals' need by mere visual inspection, which is not the case for pictures showing other types of motivational stimuli such as food.

Keywords: Appetence, Approach motivation, Frontal alpha asymmetries, EEG

3 Approach Motivation and the early ERP-component P1

*Kuhr, B., *Schomberg, J., Gruber, T., Quirin, M. (2013). Beyond pleasure and arousal: appetitive erotic stimuli modulate electrophysiological brain correlates of early attentional processing. *NeuroReport*, 24, 246-250.

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Abstract

Previous studies investigating affective reactions to pictures, which elicit a specific affect, have mainly focused on the dimensions valence and arousal. Using an event-related picture-viewing paradigm in electroencephalogram (EEG), we investigated whether erotica, i.e. appetitive, evolutionarily relevant stimuli, have effects on early stages of attentional processing that are distinct from other positive and arousing stimuli. Seventeen male students viewed arousing photos of erotic, nude women or extreme sport scenes, as well as control pictures of attractive, dressed women or daily activities. Erotic pictures differed from extreme sport pictures not only in late but also in early attentional processes as indicated by event-related potentials (ERPs) appearing as from 130ms after stimulus onset (P1). The findings suggest a) that the dimension of appetite should be considered in addition to valence and arousal when investigating psychophysiological reactions to affective-motivational stimuli and b) that early attentional processing as mirrored by the P1 can be influenced by motivational systems.

Keywords: EEG, ERP, motivated attention, approach, appetite, valence, arousal, negativity bias

4 Avoidance Motivation and the early ERP-component P1

Schomberg, J., Schöne, B., Gruber, T., Quirin, M. (2015). Emotion and Hypervigilance: Negative Affect Predicts Increased P1 Responses to Non-Negative Pictorial. *Accepted for publication in Experimental Brain Research*. doi:10.1007/s00221-015-4544-x.

Abstract

Previous research has demonstrated that negative affect influences attentional processes. Here, we investigate whether pre-experimental negative affect predicts a hypervigilant neural response as indicated by increased event-related potential amplitudes in response to neutral and positive visual stimuli. In our study, seventeen male participants filled out the German version of the Positive and Negative Affect Schedule (PANAS; Watson et al. 1988; Krohne et al. 1996) and subsequently watched positive (erotica, extreme sports, beautiful women) and neutral (daily activities) photographs while electroencephalogram was recorded. In line with our hypothesis, low state negative affect but not (reduced) positive affect predicted an increase of the first positive event-related potential amplitude P1 as a typical marker of increased selective attention. As this effect occurred in response to non-threatening picture conditions negative affect may foster an individual's general hypervigilance, a state that has formerly been associated with psychopathology only.

Keywords: hypervigilance, selective attention, negative affect, anxiety, event-related potentials, P1 amplitude

5 General Discussion of All Manuscripts

The manuscripts of my dissertation identified electroencephalographic correlates of approach (manuscripts 1 and 2) and avoidance motivation (manuscript 3) by investigating both, alpha band oscillations (manuscript 1) and event-related potentials (manuscripts 2 and 3). More specifically, in the first manuscript my co-authors and I reported reduced left hemispheric alpha activity after the elicitation of high approach motivation by showing pictures of nude women in erotic poses to heterosexual men. This finding is insofar notable as we seem to be the first to find changes in the alpha band after motivational priming using an event-related picture priming paradigm.

The findings of the second manuscript were (a) that the early ERP-component P1, associated with selective attention, is modulated by approach motivation and (b) that approach motivation is independent of the affective dimensions valence and arousal but rather reflects an independent dimension. In more detail, the P1 component was larger for erotic pictures (high approach motivation, high valence, high arousal) than for control pictures (low approach motivation, high valence, high arousal) leading to the conclusion that motivational systems are active even during very early visual processing stages.

In the third manuscript, we found evidence that avoidance motivation leads to an enhanced selective attention towards all kind of new stimuli. More specifically, we found a positive correlation between participants' high state negative affect and the P1 component. This effect was irrespective of the valence, arousal, or appetite content.

The single findings are comprehensively discussed in the context of recent research in the corresponding discussion sections of the manuscripts (sections **Fehler! Verweisquelle konnte nicht gefunden werden., Fehler! Verweisquelle konnte nicht gefunden werden.** and **Fehler! Verweisquelle konnte nicht gefunden werden.**). I therefore proceed directly with an integration of these findings into different theories

and findings, among others PSI theory (section 5.3), social motives (section) wanting versus liking (section 5.6.4), and neuroimaging findings (section 5.6.3).

5.1 Affect versus Approach and Avoidance Motivation

No consistent definition of affect exists in the literature. Sometimes, it is confounded with emotion and mood (Batson, Shaw, & Oleson, 1992). Frequently, affect is referred to as the superordinate concept of emotion, which is focused on a specific event and is more distinct, and mood, which is more diffused and unfocused (Gross, 2010; Kuhl, 2009). However, there is a general consensus that affective states express the fulfillment and the frustration of needs or indicate dangerous situations (Kuhl, 2001; Schwarz & Clore, 1983, 2003). Whereas high positive affective states reflect the fulfillment of a need, high negative affective states reflect the presence of a need waiting for fulfillment. Overall, needs show the discrepancy between a desired state and an actual state on an implicit level (Elliot, 2008a; Kuhl, 2001); e.g., during hunger states the blood glucose level is low. The term *needs*, compared to the term *motivation*, is generally used for basal and non-cognitive processes, which specify the basic supplies an individual needs for an individual's well-being (Kuhl & Koole, 2008). In contrast to approach motivation, avoidance motivation does not necessarily promote the satisfaction of needs (Kuhl & Koole, 2008). Rather, it prevents or exits aversive states and regenerates safety (Bischof, 1985).

Positive and negative affect, as assessed via the PANAS, are dimensions reflecting two basic and distinct systems of activation, whereas positive affect reflects states of alertness, enthusiastic activeness and negative affect mainly reflects states of fear and anxiety (Watson & Tellegen, 1985). The developers of the PANAS even argued for relabeling their constructs from positive and negative affect to positive and negative activation (Watson, Wiese, Vaidya, & Tellegen, 1999). It is a central research interest to find out whether approach motivation is independent of positive affect (for

reviews see Bradley, Codispoti, Cuthbert, et al., 2001; Harmon-Jones et al., 2010; Harmon-Jones et al., 2013). As already mentioned in the introduction, approach motivation was suggested to be not related to valence (Harmon-Jones et al., 2013). Also in this dissertation (see manuscript 1), I was able to disentangle high states of appetitive motivation from high states of valence and arousal (for further information see the discussion section of manuscript 1, section **Fehler! Verweisquelle konnte nicht gefunden werden.**).

5.2 Approach versus Avoidance Motivation

Approach and avoidance motivation, similar to positive and negative affect, are independent of each other and therefore are best illustrated by a two-dimensional model, rather than by a one-dimensional model (Kuhl, 2009). Whereas approach motivation, as shown in this thesis, is associated with an enlarged relative activation of the left hemisphere (Harmon-Jones et al., 2010; first manuscript of this dissertation), avoidance motivation is associated with an enlarged relative activation of the right hemisphere (R. J. Davidson, Ekman, Saron, Senulis, & Friesen, 1990; Jones & Fox, 1992).

Further evidence for the two-dimensional model comes from findings on the neurotransmitter-systems involved in the neural processes linked to approach and avoidance motivation. Whereas serotonin is involved in the inhibition of the reward system (and therefore the inhibition of approach motivation; cf. below and section 5.6), acetylcholine is involved in the excitation of neural functions linked to avoidance motivation (Hoebel, Avena, & Rada, 2008). However, there is also fundamental evidence linking the dopaminergic system to both, increased approach and increased avoidance motivated behavior (for a review paper see Hoebel et al., 2008; Salamone, 1994). Although, dopamine release is widely accepted to increase approach-related behavior (Berridge, 2007; Ikemoto & Panksepp, 1999; see also section 5.9), the administration of dopamine antagonists has also been found to be associated with the

discontinuation of active avoidance behavior (L. Cook & Weidley, 1957; A. B. Davidson & Weidley, 1976; Hoebel et al., 2008).

Besides the dopaminergic evidence, there is research confounding approach- and avoidance-related behavior. It has been suggested that approach and avoidance-related reactions are strongly related to each other and that avoidance behavior is a form of approach motivation, namely an approach to safety (Ikemoto & Panksepp, 1999). Also, sometimes individuals use negative affect for approach behavior, although negative affect was originally used to facilitate avoidance behavior (Kuhl & Koole, 2008). This phenomenon, referred to as “functional crossovers” (Kuhl & Koole, 2008), is discussed in more detail below in section 5.3.

5.2.1 EEG-evidence against the lateralization model of approach and avoidance

Research contradicting the traditional left frontal hemispheric dominance for approach motivation and the right hemispheric frontal dominance for avoidance motivation connection comes from Wacker and colleagues (Wacker et al., 2008; Wacker, Heldmann, & Stemmler, 2003). The authors showed activation of left frontal brain regions, generally associated with approach motivation – as also done in this work – for participants experiencing strong avoidance motivation (Wacker et al., 2008). In this study, participants imagined themselves in fear-provoking situations (e.g., coming across a gang of rowdies in the night) and afterwards rated the intensity of the elicited aversive feelings. These ratings correlated positively with activity over left frontal brain regions, as indexed by changes in the alpha band. According to the authors’ interpretation, left frontal brain activation is therefore not elicited by approach motivation per se. Rather they explain their findings in the context of the behavioral activation system and the behavioral inhibition system (BIS/BAS; Carver & White, 1994; Gray & McNaughton, 2000).

Whereas BIS reflects a neuropsychological system predicting an individual's response to avoidance-related cues, BAS reflects a neuropsychological system predicting an individual's response to approach-related cues (Gray, 1987). Wacker et al. (2008) connect the observed correlation between left frontal alpha reduction and the intensity of aversive feelings to behavioral activation (associated with flight). Vice versa, the authors did also find evidence for the connection between right frontal activation and behavioral inhibition. Those participants, who associated the imagined situation more with behavioral inhibition (freezing) than with behavioral activation (flight), showed a stronger activation in right frontal brain regions.

Altogether, these findings discussed in this section illustrate that the neural markers of approach and avoidance motivation are not yet fully understood and that further research needs to be done to clarify to what extent state approach and motivation mediates frontal hemispheric asymmetries.

5.3 Approach and Avoidance Motivation in PSI Theory

In this section, I will connect my findings about the neural correlates of approach and avoidance motivation to the Personality Systems Interaction (PSI) Theory, which integrates different theories of personality by assigning them to different levels of personality functioning (Kuhl, 2000, 2001; Kuhl & Koole, 2008). I will first give a very short summary of PSI theory and afterwards discuss my findings in terms of PSI theory.

Understanding personality and finding explanations for human behavior have been central aims for psychologists during the last decades. Thereby, various different psychological theories and schools emerged. Personality and human behavior was explained by differences in habits and conditioning (Hull, Skinner), arousal (H.-J. Eysenck), affect (Freud, Gray), social motives (Atkinson, Murray, McClelland), cognition and perception (Kelly, Jung) and the self / free will (Rogers, Deci). PSI theory is not in conflict with any of these theories but integrates them by assigning each of

these six schools to a separate level of personality functioning, with one additional level which supposedly mediates and integrates processes on the lower levels. These seven PSI levels are:

- (1) *Low-level Cognition*: intuitive behavior control (habits) and object recognition
- (2) *Temperament*: motor activation and sensory arousal
- (3) *Affect*: Positive affect (facilitation) and negative affect (inhibition)
- (4) *Progression versus Regression*: mediating level
- (5) *Motives*: instrumental (e.g., power) and experiential (e.g., affiliation) social needs
- (6) *High-level Cognition*: analytical thinking and holistic feeling
- (7) *Agency*: intention memory (self-control) and extension memory (self-maintenance)

As this overview illustrates, the levels range from very basic and basal processes (Level 1) to higher-order systems, supporting self-control and intentional actions (Level 7). The lower levels are onto- and phylogenetically older than the higher levels, which developed in the course of human evolution. Each level on its own suffices to explain the corresponding findings of the above mentioned psychological schools but in order to understand complex human behavior, it is central to allow for an interaction between the levels. In this context, four different cognitive macro systems and their interactions are of particular importance, two of which operate at the lowest level of personality and two which operate at the highest level. These systems are *intuitive behavior control*, *object recognition system*, *intention memory*, and *extension memory* (Kuhl, 2001). I will briefly introduce them below. For a more detailed description of the four macro systems, I refer the reader to Kuhl (2000, 2001).

Intuitive behavior control is represented at Level 1 and thus closely related to habits and classical learning theories, which do not necessarily occur consciously. Examples for the involvement of this system are the intuitive exchange between mother and child (Papoušek & Papoušek, 1987) or small talk (Kuhl, 2001). Overall, intuitive behavior control is associated with automatic behavior, holistic perception and linked to activation of the right hemisphere.

The object recognition system, which is also represented at Level 1, is responsible for the conscious perception of isolated objects, independently of the context in which the objects occur. The disengagement of a single object out of the context becomes especially important for danger detection. Object recognition is associated with activation of the left hemisphere.

Intention memory (represented at Level 7) is the system in which conscious intentions are stored. It works analytically and sequentially and is thus directly linked to thinking and planning. Intention memory is decoupled from emotion and supported by the left (and more logical) hemisphere.

Extension memory, which is also represented at Level 7, can be seen as an extensive network, comprising and integrating the individual's experiences, goals, needs and preferences. It works holistically, parallel, primarily unconsciously and is mainly supported by the right hemisphere.

These four systems and the seven PSI levels are proposed to interact with each other in seven different modulation assumptions. An explanation of these assumptions goes beyond the scope of this short introduction to PSI theory (for more information see also Kuhl, 2001). However, it is central for this dissertation that affect is responsible for a dynamic interaction between the systems and the levels, respectively. In particular, negative versus positive affect modulate the relationship between the four macro systems either by dampening or facilitating the specific affect. A very pronounced

relationship exists between intuitive behavior control and intention memory, as well as between object recognition and extension memory. Especially noteworthy for this work is the modulation assumption about negative affect activating the object recognition system, in order to facilitate a sensibility towards danger cues.

After this short introduction to PSI theory (for an more in-depth view see Kuhl, 2000; Kuhl, 2001), I will integrate my findings concerning approach and avoidance into PSI theory. According to Kuhl and Koole (2008), approach- and avoidance related tendencies can be located in every level of PSI theory's hierarchical model of personality (see Table 32.1. in Kuhl & Koole, 2008), although some personality systems are more strongly linked to approach and others are more strongly related to avoidance motivation. But importantly, although a certain system is more linked to approach or avoidance motivation, respectively, it does not mean that it is not compatible to the other type of motivation. PSI theory allows for exceptional cases referring to them as *functional crossovers*. Kuhl and Koole (2008) explain functional crossovers in the context of exaptation. For example, horror movie loving individuals evaluated a horror movie more positively and state to watch it again (approach motivation), only when they experienced fear (avoidance motivation) while watching the movie (Martin, Abend, Sedikides, & Green, 1997). This example illustrates that human beings learned to use negative affect for approach motivation, although evolution presumably connected it to avoidance behavior. Kuhl and Koole (2008) make clear that approach and avoidance are not only restricted to basic motivational reactions (e.g., fight versus flight) but can also be regulated by more complex motivational phenomena such as self-control or self-regulation.

In our manuscripts we reported neural correlates of appetence towards erotic stimuli (Manuscript 1 and 2) as well as neural correlates of avoidance motivation towards neutral and positive stimuli (Manuscript 3). The enlarged ERP components

(Manuscript 2) and alpha asymmetry (Manuscript 1) for enhanced appetite can be attributed to an involvement of PSI theory's basic levels, as I will discuss below. The erotic pictures were rated high in valence (involvement of Level 3) and arousal (involvement of Level 2). However, the neural markers we observed for approach motivation (or appetite) cannot be ascribed to the dimensions of valence or arousal, because the ratings for these dimensions were constant also for the control condition, which were pictures showing extreme sports. Therefore, another level has to be involved, which accounts for the differences between appetite and the control condition, which I suppose to be low-level cognition (Level 1). As outlined above, low-level cognition differentiates between intuitive behavior control and object recognition. Although, object recognition is mainly associated with avoidance behavior (Kuhl & Koole, 2008), I connect it to appetite towards erotic stimuli by using functional crossover. The following findings speak for a connection between appetite and object recognition. Appetitive stimuli (pictures or film clips showing desserts) were shown to narrow the attentional focus as indexed by a perceptual global-local task (Gable & Harmon-Jones, 2008) and EEG-correlates (Harmon-Jones & Gable, 2009). Furthermore, an eye-tracking study revealed that men (we likewise included only men in our studies) do not focus on the environment and contextual information when viewing erotic pictures (Rupp & Wallen, 2007, 2008). Evidence from our studies comes from the reported left-hemispheric advantage for appetite in Manuscript 1, which indicates an involvement of the object recognition system, as this system is also represented in the left brain hemisphere (Kuhl, 2000). Most importantly, the increased P1 component we found after our participants viewed appetite pictures reflects enhanced selective attention, which corresponds strongly to object recognition. Appetite seems to be linked to selective attention in order to shut out irrelevant information, perception, and cognition during the attempt to acquire the desired object (Harmon-Jones & Gable,

2009). Therefore I highly assume the object recognition system to be involved during the perception of erotic stimuli. However, eroticism can also be linked to intuitive behavior control, for instance sexual intercourse. During the sexual act, our behavior should come intuitively, without the involvement of high-level-cognition or intention memory, similar to the intuitive interaction between lovers or family members (Kuhl, 2001).

After the integration of the approach-related findings of my dissertation into PSI theory, I turn to my findings concerning avoidance motivation, for which we found a more pronounced early ERP component (P1 component) associated with selective attention. As already discussed above, we assessed avoidance motivation using the negative affect scale of the German Version of the PANAS (Krohne et al., 1996; Watson et al., 1988) and found a positive correlation between reported state negative affect and the neural markers of selective attention. Because the scales of the PANAS do not directly refer to positive versus negative valence but also comprise the level of activation (Watson et al., 1988; Watson et al., 1999), it is not explicitly clear if PSI Level 2 (referring to sensory arousal), Level 3 (referring to negative affect) or both are involved. But most definitely, the object recognition (Level 1) system is activated. Participants' negative affect triggers the object recognition system in order to detect threatening and survival-critical objects (Kuhl, 2001). By doing so, it is most probably that participants' selective attention is enhanced, leading to an enlarged P1 component. This explanation is also in line with findings on phobia patients, which respond to new stimuli, irrespective of the phobia-relevance, with enlarged P1 components (Kolassa, Kolassa, Musial, & Miltner, 2007; N. K. Smith et al., 2003). Most probably, the experienced phobia, as a kind of trait negative affect, leads to enlarged selective attention in order to detect dangerous cues as fast as possible.

In this section, I briefly summarized PSI theory and wrote that approach and avoidance motivational tendencies are represented in all seven layers of PSI theory. Nevertheless my findings correspond to the more basal representation of approach and avoidance, which can be explained by using PSI theory's lower Levels 1-3. Notably, I provided evidence for the involvement of the object recognition system in both, approach and avoidance motivation.

5.4 Distinct Emotions versus Affective Dimensions

In this dissertation I only reviewed research characterizing human affective phenomena using a two-dimensional model. However, there is large part of emotion research dealing with the discussion about whether two affective dimensions (negative vs. positive affect) suffice to describe affective phenomena or whether it is more fitting to use distinct emotions. In this context, the central question arose about whether the so-called "basic emotions" exist, which can be understood and expressed by people all around the world and are hard-wired into our brains by evolution (Ekman & Friesen, 1971; Ekman et al., 1987; LeDoux, 2012). These basic emotions should be essential for preparing the organism for specific actions facilitating survival and also serve as a communication function (e.g., via facial expressions) to other individuals (Panksepp, 1998). Depending on the specific theory, four to eight distinct basic emotions have been proposed (for a review see Ortony & Turner, 1990). For example, broadly accepted model by Ekman (1972) identifies six distinct basic emotions: fear, anger, happiness, sadness, disgust, and surprise.

If human affective phenomena can indeed be divided into basic emotions, then these basic emotions should have consistent and specific neural correlates. In line with this assumption, a meta-analysis of 83 neuroimaging studies provided evidence that discrete basic emotions (which were happiness, fear, sadness, anger, and disgust) indeed have consistent and discriminable neural correlates (Vytal & Hamann, 2010). Another

meta-analysis of 105 fMRT-studies comes to a similar conclusion by demonstrating distinct regions in the neural network for the same five basic emotions (Fusar-Poli et al., 2009). However, unlike the former meta-analysis the distinct emotions were not represented by entirely distinct neural networks, even though the different components of the networks were at least partially separable. For example, happy, fearful, and sad primes activated the amygdala, but angry and disgusting primes did not. However, amygdala activation was highest for fearful primes.

Since one central premise of basic-emotion theories is that these emotions can be universally expressed and understood, analyzing facial expression became another established method for studying emotions. A very recent report on the separation of universal facial expressions differentiated four basic emotions, which were happy, sad, afraid/surprised, and disgust/anger (Jack, Garrod, & Schyns, 2014). The authors conclude that these four emotions underlie our biologically based facial signals and that the distinction between anger and disgust as well as between surprise and fear developed later, more for social than survival reasons.

In line with the other theoretical view, namely that emotions are only separable using the dimensions valence (degree of pleasantness or unpleasantness) and arousal (emotional strength), two meta-analyses concluded that the basic emotion theories cannot be fully supported by neuroimaging studies (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002). Another very recent meta-analysis strengthens this evidence by finding the neural correlates of negative versus positive affect (Lindquist, Satpute, Wager, Weber, & Barrett, 2015). However, the results do not support the hypothesis that positive versus negative affect correspond to spatially separable and distinct brain systems. Rather, the authors found functional preferences for positive over negative affect and vice versa for some brain regions. For example, whereas amygdala and left anterior insula activation was highest for negative

affect, the ventromedial prefrontal cortex and anterior cingulate cortex were highest for positive affect (for an extensive listing of regions preferring positive versus negative affective processing see Table 2 in Lindquist et al., 2015).

At a first glance, the two-dimensional theory of emotion, as also discussed in this work, contradicts the theory of distinct and basic emotions. However, there are also theories connecting these different models. For example, Barrett (2006) postulates, that distinct emotions only exist as situation-specific interpretations of lower-level “core affect”. Also, PSI theory (discussed above in section 5.3) helps to integrate these supposedly contradictory findings, by assuming that distinct theoretical views are represented at different levels of personality functioning. Whereas the two-dimensional distinction between negative and positive affect is represented in PSI Level 3, the discrete distinction of the basic emotion is represented at Level 6 (Kuhl, 2001). Thereby, the differentiation between positive and negative valence happens at a more basic stage of processing and experiencing than the distinction between the basic emotions (Kuhl, 2009).

5.5 About the Ambiguous Use of Vigilance in the Literature

In Manuscript 3, we discuss our found enlarged P1 component in the context of (hyper)vigilance. However present literature is not concise about the usage of the term “vigilance”. Broadly, vigilance (coming from the Latin word *vigilare* = to watch, to be awake) is used in the context of alert preconscious automatic processing in order to detect and prevent dangerous situations (Bargh, 1989). Based on this broad definition, various researchers assign different meanings to the term vigilance. Whereas Kuhl, Quirin, and Koole (2015) use the term for broad attention integrating holistic perception by simultaneously paying attention to heaps of additional information (see also Kuhl, 2001), other research papers use vigilance in the context of threat-related and selective attention (Kolassa et al., 2007). This latter view is consistent to M. Eysenck’s

hypervigilance theory, which associates vigilance with the narrowing of perception in order to identify possibly dangerous stimuli as soon as possible (Eysenck, 1992, 1997).

In more detail, Eysenck states that individuals high in trait anxiety have an exceedingly vigilant attentional system, to which he refers as a hypervigilant attentional system. This hypervigilance manifests in different ways, one of which corresponds to increased early and selective attention while processing salient stimuli in order to evaluate the threat the detected stimuli might pose as early as possible.

EEG studies support Eysenck's hypervigilance theory for individuals with spider and social phobia (as a form of trait negative affect or rather anxiety; Kolassa et al., 2007; N. K. Smith et al., 2003). In the respective studies, phobia patients reacted towards all kind of stimuli (phobia-relevant and phobia-irrelevant) with an enhanced P1 component (as a marker of narrowed and selective attention), most probably because their organisms are constantly on alert. In this context, we found continuously increased early attention, marked by the P1 component, for individuals experiencing state negative affect (Manuscript 3). In the discussion section of our paper (section **Fehler! Verweisquelle konnte nicht gefunden werden.**) we explain this effect also with an increased degree of vigilance. However, this view of vigilance must not be confounded with the meaning (Kuhl, Quirin, & Koole, 2015) ascribed to vigilance.

5.6 Neural Brain Mechanisms of Approach and Avoidance Motivation

5.6.1 Is Love Right? – An Alternate Hypothesis on Hemispheric

Lateralization

Up to this point I mainly reviewed findings showing associations between relative left frontal activation for approach motivation (Harmon-Jones et al., 2010; see also manuscript 3) and relative right frontal activation and avoidance motivation (R. J. Davidson et al., 1990; Jones & Fox, 1992). However, recent research supports right-frontal processing of a specific kind of approach-related stimuli, namely primes with

affiliation content (Kuhl & Kazén, 2008; Quirin, Gruber, et al., 2013; Quirin, Meyer, et al., 2013). These studies do not aim to investigate hemispheric lateralization on the basis of broader dimensions like approach versus avoidance motivation (see above), or negative versus positive affect (Heller, 1990) but aim to differentiate different approach motivational states from each other. The authors therefore discriminate between the two approach related social motives affiliation and power. The affiliation motive refers to the disposition of an individual to engage, maintain or regain a positive relationship to another person (Atkinson, Heyns, & Veroff, 1954), whereas the power motive refers to the disposition to gain influence and control over other persons (Veroff, 1957).

Although both, the affiliation and the power motive, are more related to approach than avoidance motivation, they differ in their behavioral, hormonal, and cognitive correlates (for an exhaustive overview, see Schultheiss & Brunstein, 2010). Kuhl, Quirin, and their co-workers indeed established first evidence for differences in hemispheric lateralization, with a left-hemispheric processing advantage for power-related stimuli and a right-hemispheric processing advantage for approach-related stimuli. They spotted motive-specific lateralization effects in various behavioral experiments using the dot probe task (Kuhl & Kazén, 2008), by accessing alpha oscillations using EEG (Quirin, Gruber, et al., 2013) and by using neuroimaging techniques (Quirin, Meyer, et al., 2013). Despite the found motivational state effects, the authors also detected an involvement of trait motivation, by showing that the hemispheric effects were stronger for individuals with a high disposition than for individuals with a low disposition in the specific motive (Kuhl & Kazén, 2008).

It is not straightforward how these findings can be explained in relation to the traditional view on a right-hemispheric advantage of avoidance motivation versus a left-hemispheric advantage of approach motivation. Whereas the left-hemispheric preference for the power motive can be explained in terms of a strong approach

motivation experienced during high states of power motivation (Kuhl & Koole, 2008), the right-hemispheric preference for affiliation motivation is worth discussing. In this context, the relationship between right-hemispheric activation and empathy must also be considered (Tullett, Harmon-Jones, & Inzlicht, 2012). It is possible that the right-hemispheric dominance of affiliation stimuli is related to the stronger empathic abilities of affiliation motivated individuals (Quirin, Gruber, et al., 2013). Thus, future studies should focus on controlling for empathy.

Additionally, the affiliation motive, similar to positive affect, is linked to broad attentional processing (Gasper & Clore, 2002; Kuhl & Kazén, 2008) and is associated with the release of oxytocin (Carter, 1998) and opioids (Depue & Morrone-Strupinsky, 2005), which are both more linked to liking than wanting (see section 5.6.4). Therefore, it is possible that the right-hemispheric advantage for affiliation goes back to the positive affective experience of being together with someone else rather than to an appetitive motivation, which is more associated with wanting than liking (Quirin, Gruber, et al., 2013).

Although a vast amount of research still has to be done in order to disentangle the diverse hemispheric lateralization findings, they clearly suggest that it seems promising to consider sub-categories of approach motivation in the future.

5.6.2 Left-Hemispheric Preference for Processing of Sex-Related Content

In this work, I also provide further evidence for left-hemispheric processing advantage for approach-related stimuli by using appetitive stimuli with erotic content (Manuscript 1). Besides the already discussed findings linking the left hemisphere to approach motivation per se, a considerable body of research associates sex-related stimuli with left-hemispheric processing. These findings come from behavioral (Förster, Epstude, & Özelsel, 2009) and endocrinal (Herrero, Gadea, Rodríguez-Alarcón, Espert, & Salvador, 2010), as well as from neuroimaging studies (Kühn & Gallinat, 2011).

In particular, a recent meta-analysis of functional magnetic resonance imaging (fMRI) studies showed that sexual arousal in response to erotic stimuli triggers activities in the hypothalamus, thalamus, left amygdala, anterior cingulate cortex, left anterior insula, left precentral gyrus, parietal cortex, and bilateral medial occipital cortex (for a discussion of the involved regions, see section 5.8; Kühn & Gallinat, 2011). Very notably, the majority of these activated clusters are located in the left hemisphere, corresponding to the idea of a left hemispheric advantage for processing erotic content.

Endocrinal evidence comes from findings on the hormone testosterone, which is known as a hormonal correlate of sexual motivation. It modulates sexual arousal as well as the activity of brain structures important for sexuality (Alexander & Sherwin, 1991; Strüber & Roth, 2009). Herrero et al. (2010) found a relationship between left-hemispheric processing and testosterone. The authors increased participants' testosterone level via anger induction (as measured via saliva samples) and afterwards conducted a dichotic listening task. An increased right ear advantage, that is left hemispheric processing advantage, was found after the anger induction (increased testosterone level) in contrast to before the anger induction (baseline testosterone level). This result does not only support the relationship between the left hemisphere and sexual arousal but does also strengthen the connection between the left hemisphere and power motivation, as testosterone is also increased after power induction (Schultheiss, Campbell, & McClelland, 1999). That testosterone is involved in both, sexual need and power motive, is not unexpected, since both needs stand in strong relation to each other (Bischof, 1985; Schultheiss, Dargel, & Rohde, 2003).

Further evidence for the connection between sexual arousal and the left hemisphere comes from an attention experiment using a global local task, in which sex primes were found to support a local attention focus (Förster et al., 2009). In more detail, participants responded faster to the local features of a figure showing local as

well as global objects (Kimchi-Palmer task; Kimchi & Palmer, 1982) after they were subliminally confronted with sex-related words versus love-related words or neutral non-word strings. Fitting the line of reasoning of this section, local attentional processing is commonly associated with activation of the left hemisphere (Fink et al., 1996; Kuhl, 2001; Van Kleeck, 1989), so that the above described study provides a further link between sexual arousal and left hemispheric lateralization.

In sum, our reported result linking sexual appetitive motivation to left lateralized activation fits in with previous findings on hemispheric lateralization of sexual motivation. This is probably the case because sexual motivation resembles a very strong appetitive motivation.

5.6.3 Neuroimaging Studies: Brain Mechanisms of Approach and Avoidance Motivation

In my dissertation I used EEG to access the neural correlates of approach and avoidance motivation. EEG has a precise temporal resolution but only little spatial resolution. Because the EEG is measured at the scalp, the signal mainly is caused by cortical activity. Subcortical activity, on the other hand, such as activity in the basal ganglia or amygdala contribute only slightly to the EEG signal (Attal, Maess, Friederici, & David, 2012). Therefore, neuroimaging techniques are better suited than EEG in order to explore the motivational pathways, which consist of both, cortical and subcortical brain structures. In this paragraph, I will outline the spatial correlates of approach and avoidance motivation. For this purpose, I will review neuroimaging studies using fMRI and positron emission topography (PET), but also refer to animal studies using genetic manipulation, brain lesions, and single unit recordings (for an overview regarding these methods see the review by Cain & LeDoux, 2008).

Avoidance and approach motivation are guided by a motivational brain network including both, subcortical structures, such as the amygdala and the striatum, and

regions of the prefrontal cortex, such as orbitofrontal regions (Craig, 2002; Haber & Knutson, 2010). However, brain processes for avoidance- and approach-motivated behavior seem to differ. Whereas the amygdala was found to play a more pronounced role in avoidance motivational behavior (Adolphs, Tranel, Damasio, & Damasio, 1995; Davis, 1992), the striatum was reported to be involved in approach motivational behavior (Izuma, Saito, & Sadato, 2008; Schultz, Tremblay, & Hollerman, 2000). Motivation was further reported to be modulated by regions of the prefrontal cortex, such as dorsolateral prefrontal regions (Spielberg et al., 2012), as well as by regions in the orbitofrontal cortex (Tremblay & Schultz, 1999). As for the subcortical regions, these cortical prefrontal regions show different activation patterns for approach and avoidance motivation. Whereas the medial orbitofrontal cortex is involved in approach motivation (Grabenhorst & Rolls, 2011), the lateral orbitofrontal cortex was found to be activated during avoidance motivation (O'Doherty, Critchley, Deichmann, & Dolan, 2003). This distinction in neural underpinnings which I shortly introduced seems to be plausible when we think of approach and avoidance motivation as two independent motivations (see also section 5.2). In the following section I will first give a summary on the neural underpinnings on approach motivation and then I will review the neural correlates of avoidance motivation.

5.6.3.1 Approach motivation.

As already mentioned, approach motivation is strongly linked to the obtainment of reward. Reward is central for survival, since it serves as an automated program to approach valuable objects (S. Kim, 2013). Therefore, it induces positive emotions and increases the frequency of approach-related behavior (Schultz, 2004). However, reward mechanisms are not as simple as this sounds, since several sub processes are underlying them, such as encoding the value of the reward, associating it with behavior, planning on how to receive it, and many more (S. Kim, 2013). As such, diverse brain regions are

involved during reward pursuit and obtainment, resulting in a highly complex neural pathway. The main brain regions associated with reward are part the dopamine pathway, which is also known as the reward pathway.

Dopamine is a neurotransmitter, which is produced in the ventral tegmental area, passes through the globus pallidus and is then released into the nucleus accumbens, which is a part of the ventral striatum. This pathway can be further divided into the (a) mesolimbic pathway and (b) the mesocortical pathway. In the mesolimbic pathway, the ventral tegmental area connects to the nucleus accumbens, the amygdala, and the hippocampus. This pathway is responsible for storage of experienced reward, the learning of motivated behavior, and reward anticipation (Hoebel et al., 2008).

The nucleus accumbens was found to be activated when viewing stimuli depicting persons engaging in activities favored by the participants, like social activities or falling in love (Aharon et al., 2001; Aron et al., 2005; Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003). Thus, the nucleus accumbens is often referred to as the “pleasure center” (Dallman, Warne, Foster, & Pecoraro, 2007). In the mesocortical pathway, the ventral tegmental area connects to medial prefrontal regions, the anterior cingulate cortex, and the perirhinal cortex. In this pathway, the value of the reward is judged and goal-directed behavior is formed (S. Kim, 2013). The prefrontal regions are central for the reward pathway when it comes to executive functions in order to obtain the reward, such as planning or encoding the predicted reward value (Miller & Cohen, 2001; Spielberg, Heller, & Miller, 2013; Walter, Abler, Ciaramidaro, & Erk, 2005).

5.6.3.2 Avoidance motivation.

FMRI experiments revealed activation in the amygdala, insula, striatum, and in fronto-cortical regions after inductions of avoidance motivation (e.g., via avoiding financial loss during a gambling task; Schlund, Hudgins, Magee, & Dymond, 2013). Many of these regions overlap with the neural system of approach motivation. However,

as discussed below, many studies identified the amygdala as a region uniquely involved during avoidance motivation. Thereby, the amygdala was recognized as the center of avoidance motivation, where learning, storage and expression of avoidance behavior take place (for reviews see Hoebel et al., 2008; LeDoux, 2000).

Activation in the amygdala was reported to correlate with avoidance behavior, but not with approach behavior (Schlund & Cataldo, 2010; Schlund et al., 2010). Non-human studies on aversive conditioning identified the amygdala to be crucial to threat processing (for a review see Cain & LeDoux, 2008). Studies on children and adults further support the involvement of the amygdala in human aversive learning behavior (Schlund & Cataldo, 2010; Schlund et al., 2010). However, research also revealed the amygdala as being intensity-sensitive instead of valence-sensitive (Anderson et al., 2003; Small et al., 2003). Via an olfactory experiment in the magnet resonance imaging scanner amygdala activation was associated with the intensity and not the valence of odors (Anderson et al., 2003). Similarly, amygdala activation was also found to correlate with taste intensity and not with the affective valence of the taste (Small et al., 2003).

The insula was found to be activated under conditions involving very risky decisions, e.g. in gambling tasks (Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003). Additionally, increased state anxiety was found to be correlated to increased insula activation (Schlund, Magee, & Hudgins, 2011). However, there is also evidence linking the insula to the formation of approach - avoidance decisions (Craig, 2002; Tops & De Jong, 2006).

In the section above, I reported the ventral striatum to be involved in reward processing. However, the ventral striatum was found to be activated in anticipation regardless of whether harmful stimuli can be avoided or whether a reward can be anticipated (Jensen et al., 2003). Additionally, the nucleus accumbens, as being part of

the ventral striatum and concordantly identified as playing a central role in the reward pathway, was also associated with avoidance behavior (McCullough, Sokolowski, & Salamone, 1993). A review indicated substantial similarities between the characteristics of dopaminergic involvement in appetitive and aversive motivation (Salamone, 1994). Altogether, administration of dopamine antagonists or localized interference with the nucleus accumbens dopamine system was shown to disturb ongoing avoidance-motivated behavior.

Overall, the motivational neural circuits underlying approach and avoidance behavior are very complex. A central research interest is to detect brain regions responding exclusively to approach or avoidance motivation, respectively (Spielberg et al., 2012). Several brain regions are believed to be unique for approach or avoidance, such as nucleus accumbens (Aharon et al., 2001; Aron et al., 2005) and the amygdala (Schlund & Cataldo, 2010), respectively. However, I also reviewed evidence for overlapping neural underpinnings in these regions. In the literature, these overlapping neural correlates are speculated to refer to the fact that escaping or avoiding a dangerous situation is rewarding itself (H. Kim, Shimojo, & O'Doherty, 2006).

In this dissertation, I also present first evidence for associating approach motivation to a neural correlate, which has been linked to only avoidance motivation in the previous literature. An enlarged P1 component, a marker of early selective attention, was reported to be only modulated by states of high negative valence (Olofsson et al., 2008), an indicator of high avoidance motivation. However, we were the first to show an enhanced P1 component for a high positive approach-related state towards erotic pictures. Thus, much has still to be investigated to spot approach- and avoidance related correlates, using both, neuroimaging techniques as well as EEG.

5.6.4 Wanting Versus Liking

Our findings concerning sexual approach motivation as discussed in Manuscript 1 and 2 can also be reviewed in terms of “wanting” and “liking”. Wanting, often also labeled “incentive salience”, refers to a state of active incentive motivation that promotes approach towards a specific reward before it is processed (Berridge et al., 2009). The sexual appetite measured in the manuscripts of this dissertation refers to wanting (Georgiadis & Kringelbach, 2012). Liking, also labelled “hedonic impact”, refers to a passive state in which the quality of the processed stimulus is evaluated (Berridge et al., 2009). Research has established that liking and wanting are distinct components of reward. For example, although a professional soccer player might have a strong intrinsic motivation to play soccer, he may not always feel pleasure during exhausting training (S. Kim, 2013). The discrimination between wanting and liking has been also found on the anatomical and neurobiological level (for a review see Berridge et al., 2009). Whereas opioid, endocannabinoid, and GABA-benzodiazepine neurotransmitter systems are central for generating liking reactions (R. J. Davidson, 1984b; Peciña, 2008; Peciña & Berridge, 2005), dopamine is central for generating wanting reactions (Robinson, Sandstrom, Denenberg, & Palmiter, 2005). More specifically, liking can occur without wanting when lesions or dopamine antagonists suppress the release of dopamine. In this case, individuals showed no wanting behavior towards a specific reward, but still reported to like the processed reward (Berridge & Robinson, 2003). Thus, dopamine plays a central role in generating wanting reactions, but it does not affect the liking and enjoyment of the gathered reward.

Evidence for distinct involved neuroanatomy comes from research on microinjections of mu opioid antagonist, which increases the wanting and liking of food in the nucleus accumbens (Peciña & Berridge, 2005). But whereas wanting is increased in very widely distributed regions of the nucleus accumbens, liking is only increased in

a very specific sub region of it. Further anatomical distinctions were found in sub regions of the ventral pallidum (for more details see Berridge et al., 2009; K. S. Smith & Berridge, 2005).

Altogether, these findings demonstrate that liking and wanting underlie distinct psychological, anatomical and neurobiological mechanisms. Whereas liking refers to the positively valenced-emotional state, wanting refers to the strong urge to experience this state. Also in our studies, we were able to differentiate a pleasurable state (indicated by high positive valence) from a appetitive state (Manuscript 1 and 2). We found several distinct neural markers (e.g., P1 component, alpha asymmetries) for pictures eliciting both high valence and high approach motivation (erotic pictures) in contrast to pictures eliciting high valence but no approach motivation (extreme sport pictures). By that, I assume that we also found EEG correlates for the distinction between wanting and liking.

5.6.5 Source Localization of the Alpha Band

In this section I will report findings from source localization algorithms we executed in order to locate the generators of the alpha asymmetry reported in the first manuscript, which underlies the sexual approach motivation. Oscillations, for example alpha waves, recorded at the scalp using EEG are generated by the sum of excitatory and inhibitory post-synaptic pyramidal cells (Spekman, Elger, & Altrup, 1993). These contributing cells do not necessarily have to be located where the oscillations are recorded by the EEG. Thus, the alpha asymmetries can originate from regions elsewhere as the recorded signal (Pizzagalli, 2007). In order to detect these generators of the oscillations, source localization algorithms are used. In the past, diverse algorithms have been developed, each of them differing in their advantages and disadvantages (for an detailed overview see Pizzagalli, 2007). All of them try to compute, on the basis of the measured electric potential (μV) at different positions on the scalp, the generators that

fit best to the measured data. Unfortunately, this method has been widely disregarded in motivational neuroscience. Up to now, there is only one published study assessing the brain sources of approach motivation, which is, however, already ten years old (Pizzagalli, Sherwood, Henriques, & Davidson, 2005). In this paper, the authors report left dorsolateral and medial orbitofrontal regions as the generators of motivational alpha activity. In line with the above reported findings in section 5.6.3 these regions were associated with strong approach motivation by neuroimaging studies (Spielberg et al., 2012; Tremblay & Schultz, 1999).

Additionally to the research questions reported in Manuscript 1, our aim was to locate the generators of the alpha asymmetry underlying sexual approach motivation. For that purpose, we applied the source localization algorithm VARETA (variable resolution electromagnetic tomography, Bosch-Bayard et al., 2001) of the alpha asymmetry data reported in the first manuscript. VARETA applies the inverse solution (Pascual-Marqui, 1999) by using the Lead-Field-Matrix, in which different properties of the brain structure are stored. Our research aim was to find out whether the generators of frontal alpha asymmetry lie in frontal areas and are asymmetrical.

In contrast to Pizzagalli et al. (2005) we found no generators of the alpha asymmetry in frontal regions. Rather, we detected widely distributed generators in the parietal and occipital lobe for a contrast of erotic pictures versus sports pictures (see Figure 1).

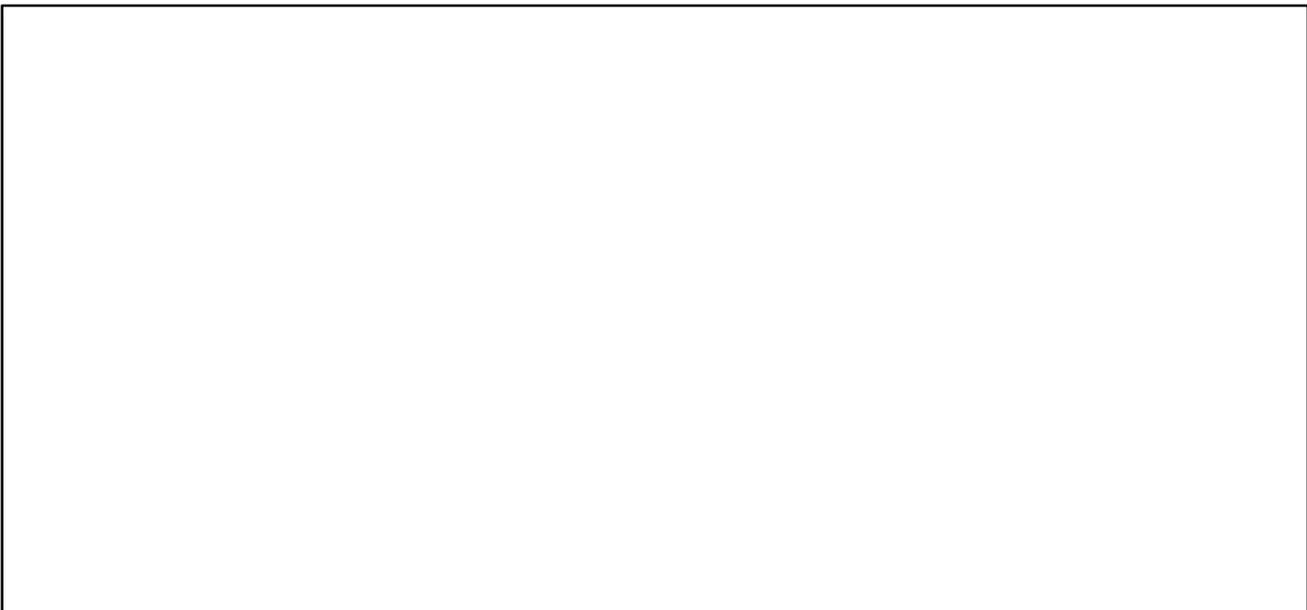
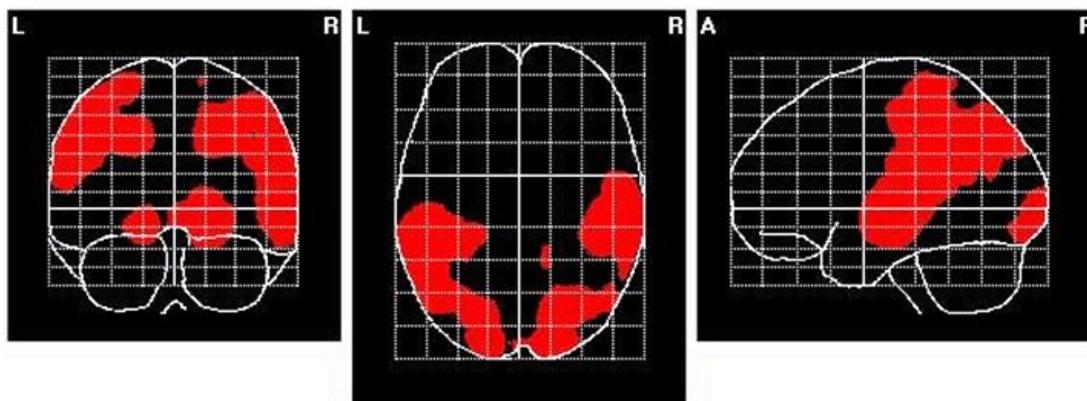


Figure 1. Calculated generators of the alpha activity of the difference for erotic pictures minus extreme sport pictures, $p < .01$.

This contrast corresponds to the elicited appetitive motivation and controls for the affective dimensions valence and arousal. Activations in these brain areas are broadly linked to attentional processes and visual processing. In order to check the reliability of the calculated generators, we applied the forward solution for calculating alpha asymmetries. By that, only the activity arising from the found generators is used for reconstructing the alpha asymmetries. In Figure 2 the comparison between the forward solution and the real solution (as reported in the first manuscript) of computed alpha can be seen. As a result, the alpha asymmetries get much smoother and more pronounced. Thus, we strongly assume that the detected generators contribute to the found alpha asymmetries.



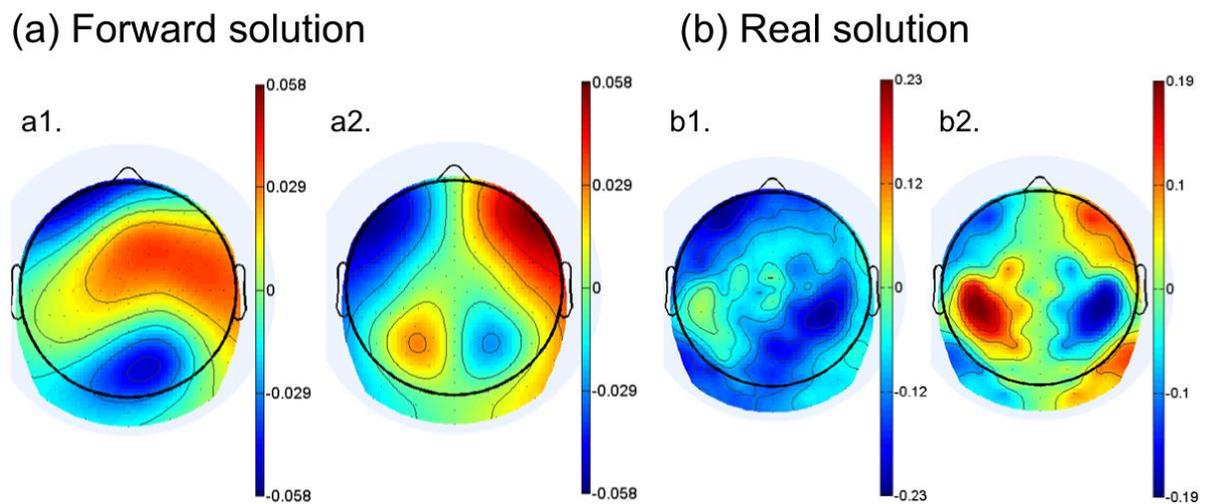


Figure 2. Comparison between the forward solution (a) and the real solution (b) of calculating alpha asymmetry. The asymmetries were calculated by subtracting the alpha band of the extreme sport pictures from the alpha of the erotic pictures using the forward solution (a1) and the real solution (b1). Additionally, the calculated difference scores for left minus right hemisphere for the forward solution (a2) and the real solution (b2) are depicted.

However and as already discussed above, these findings do not match the very sparse previous research on generators of motivational alpha asymmetries (Pizzagalli et al., 2005). In order to replicate and manifest our detected sources of the approach-related alpha asymmetry, we are currently running a follow-up study. Yet, source localization is a very powerful tool, which has been widely neglected in motivation research (for exceptions see Pizzagalli et al., 2005; Quirin, Gruber, et al., 2013) and deserves much more attention.

5.7 Is There Another Dimension Besides Approach and Avoidance?

A pioneering study gives first evidence that the two dimensions approach and avoidance do not suffice to understand human affect, behavior and cognition (McCall & Singer, 2012). The authors suggest that organisms are also able to experience other states than just approach and avoidance. According to their view, a third motivational state, quiescence, exists, which is related to a homeostasis, referring to a calm and digestive state after goal achievement. It is further described how quiescence and approach motivation differ according to neurochemical and behavioral attributes. Whereas quiescence is associated with parasympathetic activity and activity of the opioid system (linked to liking, see section 5.6), approach is associated with sympathetic activity and activity of the dopaminergic system (linked to wanting, see section 5.6). From the behavioral view, the authors connect approach motivation with readiness for action and quiescence with the absence of any action. Yet, the conceptualization of an additional motivational state, such as quiescence is still in its infancy and much research still needs to be conducted to confirm its existence, especially using EEG and brain imaging measurements (Hillman et al., 2004) .

5.8 Limitations and Future Research

In this section, I first indicate limitations of our studies examining EEG correlates of approach motivation (manuscript 1 and 2) and afterwards discuss the restrictions of the study examining avoidance motivation (manuscript 3).

Regarding our approach motivational effects, only male participants contributed to the results. Therefore, I can make no generalizing statements about similar effects in women. Previous reviews report differences between the sexes, especially when investigating appetitive reactions towards erotic stimuli (Chivers, 2005). Men show greater appetitive reactions to erotic content than women (Bradley, Codispoti, Sabatinelli, & Lang, 2001) and seem to differ in their processing styles of erotic content (for a review see Rupp & Wallen, 2008). Future studies should investigate approach motivation towards erotic stimuli on both, men and women in order to come to a generalizing conclusion of the EEG correlates of sexual appetite.

In order to access state avoidance motivation, we used the negative affect scale of the PANAS. In the literature, high negative affect was consistently linked to avoidance motivation (Bradley, Codispoti, Cuthbert, et al., 2001; Elliot & Thrash, 2002; Gray, 1987; Kuhl, 2009; Lang, 2000). However, the negative affect scale of the PANAS includes the items *hostile*, *upset* and *guilty*, which at least partly refer to concept of anger and guilt. Both emotional states were associated with approach motivation in previous literature (Amodio et al., 2007; Harmon-Jones & Allen, 1998; Harmon-Jones et al., 2003). Therefore, three items of the 10-item NA scale of the PANAS are at least likely to activate the approach rather than the avoidance system. The other words, which are *distressed*, *scared*, *irritable*, *ashamed*, *jittery*, *nervous*, and *afraid* relate to the concepts of fear and stress, which relate to avoidance motivation (Gray, 1987). Therefore, it is up to speculation if the negative affect scale of the PANAS is suitable for measuring avoidance motivation. However, no other valid questionnaire for

assessing state avoidance motivation has been developed. In order to assess avoidance motivation previous research performed either psychophysiological (Bradley, Codispoti, Cuthbert, et al., 2001; Harmon-Jones, 2003b) or behavioral measurements (Chen & Bargh, 1999; Seibt et al., 2008). Whether and how state avoidance motivation (and also approach motivation) can be validly assessed using questionnaire method is still up to future research.

5.9 Conclusion

In this dissertation, I presented evidence for EEG markers of approach and avoidance motivation, accessed using event-related-potentials and alpha band oscillations. Some of the found EEG markers were in line with previous research, such as left frontal alpha asymmetries and enhanced LPP for high-approach related stimuli. Besides, I also presented evidence not considered in previous research before, such as an enhanced P1 component (standing for increased selective attention) for approach-related stimuli. Until now, the P1 component was only connected to the processing of aversive pictures. Additionally, we found a modulation of state negative affect on the P1 component in response to non-negative pictures. So far, such a modulation was only found for negative pictures or for trait forms of negative affect, such as phobia. Moreover, the found alpha asymmetry in response to approach pictures was detected using an event-related design. By that, we demonstrated that the underlying reward system is extremely reactive - contrary to common notion. In the previous literature, alpha asymmetries were only reported by using a resting state paradigm.

In this general discussion of all manuscripts I discussed these findings in terms of existing models, e.g. PSI theory, distinct emotions, diverse theories of hemispheric lateralization as well as previous research on neuroimaging studies.

6 References for General Introduction and Discussion of all Findings

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7 Appendix

Positive and Negative Affect Schedule (PANAS)
nach Krohne, Egloff, Kohlmann, & Tausch (1996)

Wie fühlen Sie sich im Moment?

	überhaupt nicht	etwas	einigermaßen	ziemlich	sehr
interessiert	①	②	③	④	⑤
bekümmert	①	②	③	④	⑤
freudig erregt	①	②	③	④	⑤
verärgert	①	②	③	④	⑤
stark	①	②	③	④	⑤
schuldig	①	②	③	④	⑤
erschrocken	①	②	③	④	⑤
feindselig	①	②	③	④	⑤
begeistert	①	②	③	④	⑤
stolz	①	②	③	④	⑤
gereizt	①	②	③	④	⑤
wach	①	②	③	④	⑤
beschämt	①	②	③	④	⑤
angeregt	①	②	③	④	⑤
nervös	①	②	③	④	⑤
entschlossen	①	②	③	④	⑤
aufmerksam	①	②	③	④	⑤
durcheinander	①	②	③	④	⑤
aktiv	①	②	③	④	⑤
ängstlich	①	②	③	④	⑤