Conscious and unconscious somatosensory perception and its modulation by attention

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Dekan: Prof. Dr. Tilo Pompe
Gutachter: Prof. Dr. Matthias M. Müller
Prof. Dr. Felix Blankenburg
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Norman Forschack

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Our brains handle vast amounts of information incoming through our senses. Continuously exposed to sensory input, the sense of touch, however, may miss tactile stimuli, no matter how much attention we pay to them. In four empirical studies, this thesis tested (1) the feasibility of investigating *undetectable* stimulation by electrical finger nerve pulses, (2) how its neural correlates dissociate from *detectable* stimulation and (3) whether and how selective somatosensory attention nevertheless affects the neural representation of *undetectable* stimuli. The first two studies showed that there is a natural range of electrical stimulation intensities that cannot be detected. A rigorous statistical evaluation with Bayes factor analysis indicated that the evidence of chance performance after *undetectable* stimulation reliably outweighed evidence of above-chance performance. A subsequent study applying electroencephalography (EEG) revealed qualitative differences between the processing of *detectable* and *undetectable* stimulation, which is evident in altered event-related potentials (ERP). Specifically, *undetectable* stimulation evokes a single component that is not predictive of stimulus detectability, but lacks a subsequent component, which correlates with upcoming stimulus detection. The final study showed that attention nevertheless affects neural processing of *undetectable* stimuli in a top-down manner as it does for detectable stimuli and fosters the view of attention and awareness being two separate and mostly independent mechanisms. The influence of the pre-stimulus oscillatory (~10 Hz) alpha amplitude—a putative marker of attentional deployment—on the ERP depended on the current attentional state and indicats that both processes are interacting but not functionally matching.

“[…] Die Theorie ist das Netz das wir auswerfen, um ‘die Welt’ einzufangen, - sie zu rationalisieren, zu erklären und zu beherrschen. Wir arbeiten daran, die Maschen des Netzes immer enger zu machen.“ (Karl Popper, p. 31 in *‘Logik der Forschung’*, Tübingen, 1973)

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Norman Forschack, Leipzig, February 2019

Contents

1 Touch, Consciousness, And Attention – Theoretical Considerations

The sense of touch is the most intimate link to everyone's environment and, from an evolutionary point of view, of utmost importance. We can shut our eyes, close our mouth, cover our ears, or hold our nose. However, "silencing" touch may not be achieved as easily (cf. Low, 2009). E.g., it requires considerable mental effort to not withdraw a finger from a needle perturbating the skin. Signaling proximate and potentially harmful interactions with the external world is of central importance for the survival of an individual and the species as a whole.

Moreover, this perpetual immediacy constitutes our feeling of an integrated, i.e., unitary self and thereby enables us to distinguish ourselves consciously from our surroundings (Grunwald, 2008). Given its unmatched heterogeneous structure comprised of a variety of mechano-, chemo-, thermoreceptors as well as noci- and proprioceptors, we will easily miss many somatic sensations if we do not pay attention to them: the touch of the clothes that we are wearing while reading a book, the body position or gesticulation during an intense discussion, just to mention a few. Under optimal conditions, however, humans may consciously perceive skin indentations of the fingertip as small as 11 µm (Johansson & Vallbo, 1979). Here, this thesis examines the possibility of sensory events escaping conscious access and the puzzling question whether there are correlates of such unconscious sensations in the brain. What do these neural markers—or the absence of those that are present during conscious perception—tell us about the mechanisms precluding awareness and what is the role of cognitive factors, foremost attention, in modulating such perceptual processes.

After a short introduction into the empirical study of consciousness (section 1.1), detection thresholds (section 1.3) and selective attention (section 1.4), this dissertation is comprised of four studies, first investigating the validity of undetectable electrical stimulation in touch through psychophysics (section 2.2). Next, suitable central neural markers related to these sensations will be identified (section 2.3). The final study (section 2.4) utilizes those neural correlates to investigate their potential modulation by attention and supports our understanding of a general neural signature for attentional deployment that is independent of conscious perception (Koch & Tsuchiya, 2007).

1.1 A Neural Account To (Un-) Consciousness

Contrary to the collective intuition of experiencing a unitary consciousness, the meaning of the term varies broadly in its scientific study. In order to address the results of the current thesis adequately, one has to define those aspects of consciousness, to which the studies explicitly refer. Unless stated otherwise, this thesis confines the meaning of consciousness to two aspects. First, in distinguishing between global states of arousal ranging from coma to alertness (Kiefer, 2002), this thesis is exclusively concerned with fully awake participants that can communicate in an experimental environment. Various states of this aspect not only pose the necessary condition to perceptual awareness, but they may additionally gate, which objects (Brentano, 1874) or contents our cognitive system might represent (Bayne, Hohwy, & Owen, 2016). That is, investigations on conscious and unconscious perception of external somatosensory stimulation have to control for the participant's global state of arousal. Awake participants that are engaged in an experimental situation can perceive externally driven excitation. This capacity, however, might be absent or degraded for other states of arousal, in which we nevertheless experience a feeling of having a unitary consciousness (e.g., in lucid dreaming).

The second constriction to the term of consciousness builds on an operational definition of what happens when we are aware of specific content or when we are not.

> *"Using a broad definition, conscious information can be considered any stimulus, either externally- or internally-generated, which we are aware of at any given time - thus, these items are 'in mind'. In contrast, unconscious stimuli are those items, which are currently not in awareness, and have no reportability."* (Gilchrist & Cowan, 2010)

Such an assessment will allow revealing the description of what underlies a conscious or unconscious percept but importantly does not provide any explanation the sort of "what is it like to be a bat?" (Nagel, 1974). The former is sometimes referred to as being the easy problem in consciousness research (Chalmers, 1996) and is related to the study of the neural correlates of consciousness (NCC, Mormann & Koch, 2007) that we will address more thoroughly below. The latter—referred to as the hard problem (Chalmers, 1996)—reflects the first-person-perspective of having a private and subjective experience about something. Having a first-person-perspective—e.g., coined by mental content like “I think” or “I perceive”—implicitly requires a model of one’s mental self (Craig, 2002; Park & Tallon-Baudry, 2014; Prinz, 2017a, 2017b). Cognitive neuroscientists argued that only a self-model allows a subjective perspective on external (e.g., sensory) and internal (e.g., thoughts) representations (Metzinger, 2007) and that representations representing the self therefore pose a necessary condition for being conscious at all (Metzinger, 2004; Prinz, 2017b). Although empirical approaches to the study of selfhood are feasible and actually undertaken (Blanke & Metzinger, 2009; Prinz, 2017b), most literature in the field of consciousness research is focusing on descriptions of neural substrates and processes correlating with conscious and unconscious perception, memory and behavior (Aru, Bachmann, Singer, & Melloni, 2012; Baars, 1997; Crick & Koch, 1990, 2003; Dehaene & Naccache, 2001; Victor A. F. Lamme, 2006; Ruhnau, Hauswald, & Weisz, 2014; Samaha, 2015; Silverstein, Snodgrass, Shevrin, & Kushwaha, 2015a; Tononi & Koch, 2015). The studies of the present thesis build on an already developed first-person-perspective of the studied participants and ask the question, which brain processes add to their subjective, self-referential experience when they report an external stimulus, as compared to the subjective experience of an external stimulus reported being absent.

Indeed, both invasive and non-invasive brain imaging techniques as, first of all, electroencephalography (EEG) and later magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI) uncovered a wealth of finely resolved brain responses related to perceiving and acting human subjects since 1929 (Berger, 1929). None so far, however, has identified a unique neural correlate of conscious content everyone agrees on (for an overview see Aru et al., 2012; Verleger, 2010). An intricate difficulty arising when identifying NCCs comes with the requirement for any report with which the participant has to indicate his or her awareness of something (Hesselmann, Hebart, & Malach, 2011). Genuine markers of conscious content—the so-called NCC proper (Aru et al., 2012)—therefore appear to be conflated with other brain processes either preceding or following conscious perception, such as expectation, attention or decision-related processes. For example, Hillyard and colleagues (Hillyard, Squires, Bauer, & Lindsay, 1971) presented college students weak tones embedded into white background noise in a way that these tones were perceived on one trial but not on the other. Students’ task was to indicate after each trial whether they detected the tone or not. Because of concurrently measuring EEG, Hillyard et al. (1971) identified a positive deflection in the event-related potential (ERP) about 300ms after tone presentation—a so-called P300 (see section 2.1.4 and 2.1.5 for further details)—that showed an increased amplitude when students detected the tone as compared to when they reported it to be absent. This increase indicates that the P300 component relates to conscious content. To reflect a proper marker of consciousness, however, it must also be present when participants are not engaged in a task and nevertheless experience the tone consciously. The P300, though, vanished utterly, when participants were passively receiving those tone intensities that they previously detected. Thus, the P300 seems to reflect decisional processes that rely on a conscious percept and does not resemble a proper NCC but rather a consequence of it (Aru et al., 2012). Another obstacle for distinguishing proper markers of consciousness concerns the type of report, with which participants are asked to respond. Observers may report having nothing perceived but still perform better than chance (Adams, 1957). Accordingly, one distinguishes between subjective and objective measures of behavioral responses, where the former might be not sensitive enough to grasp partial consciousness, and the latter may be too conservative to allow it (Haynes, 2013). Experiments applying stimulation at the objective threshold belong to this latter kind, and we will discuss them more closely in the next section (1.2).

The bottom line of this short excursion is that, in the current thesis, I will circumnavigate the quest of identifying proper NCC by shedding light on processes arising without the smallest sign of conscious perception, i.e., without partial conscious awareness, and trying to recognize those neural substrates that probably do not reflect the NCC (Aru et al., 2012). Such markers might be necessary for conscious perception but do not pose a sufficient condition. Specifically, investigating unconscious perception may reveal neural phenomena that may keep us from conscious perception and thereby showing qualitative distinctions between the neural processing of detectable and undetectable stimuli (Merikle & Daneman, 1998). The first step, however, is to identify a suitable procedure that allows stimulating reliably at the objective detection threshold or below, which is the topic of the next section.

1.2 Controlling detectability of external stimulation

There are two common ways to render stimuli undetectable. One is stimulus masking, of which the so-called backward masking is probably the most prominent (Breitmeyer

& Ogmen, 2007; Enns & Lollo, 2000; Meador, Ray, Day, Ghelani, & Loring, 1998; Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006) and the other is by restricting the stimulation energy as a function of stimulus intensity and duration (Iliopoulos, Nierhaus, & Villringer, 2014; Shevrin, 2001). When applying backward masking in vision, for example, a briefly presented target stimulus turns invisible when followed by a non-target stimulus within tens of milliseconds (Enns & Lollo, 2000). Electrophysiological studies explained this effect by assuming interrupted cortical processing of the target stimulus by the processing of the mask and indeed, provided evidence for suppressed neural activity in early sensory areas after masked compared to unmasked stimulation (Fahrenfort, Scholte, & Lamme, 2007; Lamme, Zipser, & Spekreijse, 2002; Schubert et al., 2006). Thus, masking may preclude observations unique to neural processes below consciousness elicited by unmasked but undetectable stimulation. This difference seems highly relevant especially concerning early responses in the EEG evoked by the stimulus. Backward masking paradigms obscure early ERP modulations since the masking stimulus is applied only after the onset of those early components that were shown to be related to conscious perception (Auksztulewicz & Blankenburg, 2013; Auksztulewicz, Spitzer, & Blankenburg, 2012; Palva, Linkenkaer-Hansen, Näätänen, & Palva, 2005; Schubert et al., 2006). Importantly, stimulus masking may not allow revealing any qualitative differences between conscious and unconscious perception during early phases of stimulus processing.

Accordingly, in the current thesis, I controlled detectability of somatosensory events by manipulation of stimulus energy. The question then is, "is it possible to tune the energy of stimulation in such a way that observers are unaware of it even without a backward mask?" Physiological studies showed that Meissner corpuscles—one type of principal mechanoreceptors in the glabrous skin—respond to fingertip skin indentations as small as 11 μm and, furthermore, that a single action potential of an isolated axon innervating receptive fields of the hand might suffice for detection (Goodwin & Wheat, 2008; Johansson & Vallbo, 1979; Vallbo & Johansson, 1984). In other words, the absolute threshold for stimulus detection appears to be identical to the sensory threshold of the receptor. On the other hand, different studies applied transcutaneous electrical nerve stimulation either to a finger or the median nerve, for which participants were reported to be completely unaware (Baumgarten, Königs, Schnitzler, & Lange, 2017; Blankenburg et al., 2003; Ferrè, Sahani, & Haggard, 2016;

Iliopoulos et al., 2014; Klostermann et al., 2009; Libet, Alberts, Wright, & Feinstein, 1967; Ray et al., 1999a; Taskin, Holtze, Krause, & Villringer, 2008). These studies defined undetectable stimulation magnitudes proportional to the intensity of the individually assessed detection threshold—typically 10 to 20% below the threshold and termed these either “subliminal” or “subthreshold.” However, the term threshold is mostly not described at all. In the psychophysical literature, a "threshold" defines a point on a psychometric function that satisfies a statistical criterion, i.e., the stimulus intensity required for 50% correct performance. Thus, any stimulus intensity below the threshold is considered "subthreshold." Stimulus intensities below the 50% threshold, therefore are still perceived consciously on a portion of the trials.

Furthermore, the mentioned studies did not rigorously test—at least they did not report it—whether applied intensities below detection threshold were reliably undetectable. If any, retrospective subjective reports or a small number of test trials were acquired to validate the usage of a specific subthreshold intensity (Ferrè et al., 2016; Taskin et al., 2008). As discussed above, subjective reports such as the presence of a signal or the rating of its magnitude (for an overview see Sandberg et al., 2010) are inappropriate for the investigation of unconscious stimulus processing as they might be insensitive to the availability of partially conscious information (Haynes, 2013).

In contrast, objective reports refer to forced-choice procedures, where the observer is required to discriminate at least between two randomly presented stimulus conditions (Reingold, 1988), e.g., target-present and target-absent, resulting in four possible behavioral outcomes regarding correct and incorrect classification. To show the relevance of the distinction between subjective and objective reports neurally, Hesselmann et al. (2011) recently could dissociate blood-oxygen-level-dependent (BOLD) activation patterns of subjective visibility ratings and discrimination performance either in higher-order visual areas or in early visual areas, respectively. Importantly, although rated as invisible, observers’ performance was above chance (>25%) when asked to discriminate, in which of the four possible locations the target appeared.

Thus, investigations on neural processes below conscious perception must prove objective performance being at the chance level for a specific stimulus claimed to be undetectable. However, objective measures of awareness (as subjective measures) might be susceptible to response biases, i.e., the observer’s contingent tendency to prefer a particular response category often called "criterion." In a forced-choice detection task, for example, an observer may be overly lenient in reporting the presence of a stimulus in order to increase stimulus detection probability. Conversely, a somewhat conservative response strategy would decrease false positives when in fact no stimulus is presented. In both cases, the observer's sensitivity to a specific stimulation intensity could be the same, though the response strategy, i.e., the bias, is different. Signal detection theory (SDT) provides means to keep these factors apart, which influence observers' decisions. Developed in the 50s and 60s by Tanner, Swets and Green (Green & Swets, 1966; Swets, 1964; Tanner & Swets, 1954) SDT is, until today, recognized as one of the most influential theories in basic Psychology (Macmillan & Creelman, 2004). Its notion of a perceptual continuum cast doubt on the existence of thresholds (Goldstein, 2009). Nevertheless, the term threshold is still widely used throughout the literature (Haynes, 2013; Kingdom & Prins, 2009). Therefore, the next section dedicates a few hopefully clarifying thoughts to the use of the term threshold under signal detection theory.

1.3 Thresholds in the light of signal detection theory

In SDT the process leading to the decision about presence or absence of a sensory stimulus, i.e., the signal, rests—apart from sensory sensitivity—on the internal, i.e., psychological, evaluation of a chosen decision criterion. If the stimulus—or more precisely the internal activation it produces—exceeds the criterion, the observer confirms its presence and vice versa. Importantly, another stimulation condition, e.g., without any stimulus, will be evaluated on the same grounds. Despite stimulation absence, the observer reports the detection of a "stimulus" due to baseline activity of the sensory system—often referred to as being noise—if this activity exceeds the criterion. Thus, the report of the presence or absence of a stimulus varies with the strategy or criterion the observer adopts in order to cope with the experimental situation.

Classical psychophysics researchers noted the variability of behavioral reports, too, and proposed a statistical definition of a threshold being an "arbitrary point within a range of variability" (Stevens, 1951). However, whereas SDT assumes perception to happen on a continuum (Macmillan & Creelman, 2004), threshold theory conceives an in-built limit within the observing system that divides experience into different discrete states, in one of which we consciously perceive sensory stimuli and in the other we do not have conscious access. Discredit for the usage of the term threshold mainly comes from the latter. For threshold theory, i.e., more specific “high-threshold theory,” undetected signals directly correspond to the state below the threshold and “yes”-responses to stimulus absent trials (catch trials)—false alarms in SDT—are treated as guesses. Sensitivity threshold then is merely the proportion of detected signal trials corrected for guessing (Macmillan & Creelman, 2004). A threshold defined in this way implies chance performance below that very threshold because behavioral responses here may only arise from the state below consciousness. However, in a rating experiment, in which Swets (1961) presented both stimulus and catch trials and asked observers to indicate the likelihood of stimulus presence on a six-point scale. High-threshold theory predicts that below threshold no ordering regarding the likelihood of stimulus presence should be possible. Nevertheless, in Swets study (1961) classifications of stimulus likelihood did predict the proportion of detection even below the threshold. On the contrary, a continuous perception proposed by SDT explains this ordering very well, because there is no internal state not capable of perceptual processing.

Alongside this internal threshold definition, researchers often operationally assess the relation between stimulus intensity and psychological detection, so-called psychometric functions. Along with such functions, one may define any threshold magnitude about an arbitrarily chosen, preselected performance level (Macmillan & Creelman, 2004). As we have seen, SDT provides a measure for the observer’s response criterion that is independent of the empirical threshold measure. SDT, therefore, controls for decision-related processes occluding inferences on sensory sensitivity from overt behavior, which was not possible in classical psychophysics (Dixon, 1971; Swets, 1961). Thus, throughout the thesis, I will *empirically define* any subthreshold stimulation to exert zero sensitive responses that are independent of observer’s response criterion (see also section 2.1.3 for the statistical proof of zero sensitivity). I.e., the terms absolute detection threshold and subthreshold stimulation refer exclusively to the ability or inability of observers to detect, i.e., report, stimuli without their decisional tendency to prefer one answer over the other.

1.4 Selective attention in touch

In the previous section, we have seen that the observer's chosen response criterion determines the behavioral report irrespective of actual stimulus presence. On the other hand, it is clear that the probability of detecting a "true" stimulus depends on how well its elicited activity within the observer separates from neural baseline activity (noise). Long before the advent of neuroimaging techniques, William James' imposing phenomenal description of selective attention, pointed to its involvement in improving detection by sharpening sensory percepts to "catch an impression of extreme faintness" or "discriminate a sensation merged in a mass of others that are similar" (James, 1890). Extensive empirical research on this topic ever since conjectured two complementary, i.e., mutually non-exclusive, mechanisms serving selective attention. First, enhancement of signal activation that can be observed in psychophysical experiments by a reduced contrast threshold (Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010) or, in the brain, by an activity gain in the neural response of the stimulus coding population (Carrasco, 2011). Second, the reduction of noise—external, i.e., sensory, or internal noise, i.e., neural activity unrelated to the task—that has been shown to sharpen neural response tuning curves, e.g. in feature-based attention (David, Hayden, Mazer, & Gallant, 2008; Ling, Liu, & Carrasco, 2009). Thus, selective attention may play a crucial role in dissociating relevant sensory input from noise (Carrasco, 2011). For a distracted observer, a stimulus might pass by undetected if the stimulus' neural response is small and close to baseline activity. However, the very same stimulus could be consciously perceived if the observer pays attention to it.

A large body of neurocognitive research illustrates the selective prioritization of those neural responses that are most relevant for the current behavioral goals (Buschman & Kastner, 2015). For now, we will focus on work studying attention in touch (for an overview see Gomez-Ramirez et al., 2016). Studies showing enhanced activity of single cells in primary and secondary somatosensory cortex (SI and SII; Hsiao et al., 1993), increased neural population responses in the EEG (Forster & Eimer, 2004), and whole neural network modulations (Goltz et al., 2015; Goltz, Pleger, Thiel, Villringer, & Müller, 2013) during attention agree with a signal gain mechanism. Furthermore, in an ERP study Forster and Eimer (2005) observed—relative to a neutral cue condition, in which participants had no information about the location of an upcoming vibrotactile target—an increased N140 amplitude after the target when it appeared at the cued hand, however, a reduction of N140 when it appeared at the uncued side. This points to the co-occurrence of signal gain at attended locations and suppression of irrelevant information coming from unattended locations mediating the effect of attention (Forster & Eimer, 2005).

Another potential marker for noise suppression is oscillatory neural activity in the alpha-band (~10Hz; Foxe & Snyder, 2011). Neural oscillations are thought to emerge from the rhythmic firing of neural populations and may coordinate distributed network activity (Buschman & Kastner, 2015; Buzsaki, 2011). The advantage of firing in synchrony is increasing the effectiveness of neurons (in influencing others) without changing their firing rate (the so-called temporal synchronization hypothesis, Singer & Gray, 1995). In a MEG study, Jones and colleagues (2010) observed less rolandic alpha amplitudes (i.e., mu, alpha oscillatory activity over somatosensory regions) in somatotopically localized hand area in primary somatosensory cortex (SI) after cueing attention to the hand compared to when cueing attention to the foot. Furthermore, in a simple detection task, they found pre-stimulus mu power negatively correlated with the detection probability of a small tap to right-hand fingertips. Other studies also suggest a close relationship between mu-activity and both performance and attention (Haegens, Händel, & Jensen, 2011; Haegens, Luther, & Jensen, 2011) leading to the hypothesis that attention suppresses irrelevant or distracting stimuli by up-regulating alpha activity (Foxe & Snyder, 2011; Gomez-Ramirez et al., 2016). However, as we will discuss later (section 2.4), this view is not always supported by empirical data.

In summary, this thesis takes advantage of the EEG method—specifically by analyzing the ERP and mu-alpha (i.e., sensorimotor or rolandic alpha or simply mu) amplitudes, respectively—in order to study signal enhancement and noise suppression in stimulus perception.

Concerning the tight relationship of attention and consciousness, the unmatched William James already noted that "but without it [attention] the consciousness of every creature would be a gray chaotic indiscriminateness, impossible for us even to conceive" (James, 1890). Without selective attention, we are dazed and "the foreground of consciousness is filled, if by anything, by a sort of solemn sense of surrender to the empty passing of time" (p. 404, ibid.). However, interrelatedness does not imply a strict dependence of attention on conscious percepts or vice versa (Koch & Tsuchiya, 2007).

So-called blindsight patients suffering from a lesion within primary visual cortices give one of the most intriguing examples of attention without consciousness (for an overview see Kiefer (2002) and Weiskrantz (2007)). Those patients are not aware of stimuli occurring in the affected visual field but can point towards them, discriminate targets among other stimuli, and show shorter reaction times to targets that match the location indicated by a previous but unseen cue (Kentridge, Heywood, & Weiskrantz, 1999). This phenomenon has been observed in touch as well (Rossetti, Rode, & Boisson, 1995), however, instead emerging from a thalamic lesion. The existence of blindsight or blind touch shows that selective attention may operate without the presence of conscious percepts and therefore does not represent a sufficient condition for conscious detection. A full dissociation of both concepts, leading to a four-way classification scheme, is not subject to the current work. This is discussed at length in the review by Koch and Tsuchiya (2007), who enlist empirical findings for all four combinations of the alleged different processes: attention with consciousness (e.g. verbal reportability), no or minimal attention without consciousness (e.g. negative afterimages), attention without consciousness (see blindsight example above) and consciousness without attention (gist extraction of unattended peripheral scenes).

With stimulus intensities producing chance performance (see section 1.2), manipulation of top-down selective attention, and concurrently measuring EEG responses, the current thesis quantifies attentional processes in the absence of conscious perception in healthy human participants. Contrary to the proposition of representing selective attention and subthreshold perception as endpoints on a continuum of information handling (Dixon, 1971), this work exploits and compares neural processing of both attended and ignored detectable stimulation as well as sensory perturbations that may never become consciously perceived.

1.5 Research questions

In this thesis, I set out to investigate neural processes related to undetectable somatosensory stimuli and examined mechanisms precluding conscious awareness. Furthermore, I asked whether attentional modulation is limited to consciously perceivable stimuli, or also applies to undetectable stimulation that is empirically defined to exert objective performance at the chance level, independent of observer's response criterion. For this, two psychophysical (n=22) and two electrophysiological (n=80) studies explored perception for various stimulation intensities along the individual psychometric function in an overall sample of 102 participants.

The primary research questions are: (1) Is it possible to adjust the intensity of unmasked electrical somatosensory stimulation in a way that observers' behavioral performance is reliably at the chance level? Study I (section 2.2.1) establishes a fast and reliable, manual threshold assessment procedure in order to estimate observers' absolute detection thresholds (ADTH) below which they produce a chance-level performance. Study II (section 2.2.2) validates this threshold assessment procedure by applying a one-alternative-forced-choice (1AFC, i.e., yes-no detection) task for stimuli ranging from intensities below absolute detection threshold to intensities clearly above it, but still below the pain threshold. Importantly, the design includes trials without any stimulation (catch trials) to allow for the estimation of perceptual sensitivity (*d*-prime) and response bias (criterion) according to signal detection theory and statistically proves the chance performance of stimulation intensities below ADTH by Bayes factor null-hypothesis testing (see section 2.1.3 for details).

Section 2.3 asks (2) whether there are measurable neural correlates of subthreshold stimulation intensities. If so, are there qualitative differences between stimulation below and above ADTH concerning the stimulus-evoked response and oscillatory activity that may prevent access to conscious experience in the case of subthreshold stimulation? Furthermore, (3) which features of the earliest neural responses (amplitude and latency of the somatosensory evoked potential, SEP) after somatosensory stimulation are predictive of its detection and do these post-stimulus features interact with pre-stimulus intrinsic oscillatory activity in the alpha-band that has been surmised to regulate the excitability of sensory cortices awaiting stimulus input? Study III (section 2.3.2) was therefore designed as an EEG adaptation of study II and investigates these neural stimulus-locked responses for various stimulation intensities.

As discussed in section 1.4, selective attention plays a crucial role in stimulus detection by increasing the target signal response and suppressing task-irrelevant noise. Furthermore, attention affects both SEPs and alpha-band activity. Thus, study IV (section 2.4) investigates the modulatory role of selective spatial attention in somatosensory stimulus processing across awareness conditions by its relation to early SEPs and oscillatory mu-alpha activity. Precisely, (4) does attention modulate neural processing of subthreshold somatosensory stimuli and (5) what is the role of sensorimotor alpha-band activity to the effect of attention?

2 Empirical Evidence

2.1 General methods

This chapter summarizes the most important methods used throughout the empirical investigations. It is not meant, however, only to collect facts about the experiments but, importantly, also contains central reasoning within this thesis: the direct proof of unconscious stimulus processing, the topic of section 2.1.3 and 2.1.4. So, dear reader, please keep on reading. The method sections of the specific studies hold additional methodological details.

2.1.1 Stimulation

All studies used constant-current stimulators (DS7/DS7A, Digitimer, Welwyn Garden City, Hertfordshire, United Kingdom) for electrical finger nerve stimulation. Single current pulses (quantified in milliampere, mA) are adjusted to have a monophasic square wave shape with duration of 200µs consistent with previous studies (Blankenburg et al., 2003; Iliopoulos et al., 2014; Taskin et al., 2008). The experimenter adjusted stimulation magnitudes directly at the device and triggered pulses manually during threshold assessment (see next section) or automatically during the main experiments by custom scripts running in the stimulation software "Presentation" (Neurobehavioral Systems, San Francisco, U.S.A.). A pair of steel wire ring electrodes attached to the middle (anode) and the proximal (cathode) phalanx of the left (and for the attention study of section 2.4 right) index finger delivered the stimulator output.

2.1.2 Threshold assessment procedure

All studies defined the absolute detection threshold (ADTH) empirically as the lowest current intensity at which participants just reported a sensation. ADTH was assessed manually by the experimenter employing a two-step procedure that involves one trial method of limits with ascending intensities for a rough estimation followed by a one-alternative-forced-choice task (1AFC, i.e., yes-no detection) for fine adjustment. In the former task, the experimenter gradually increases stimulation intensity until the participant verbally reports a conscious percept. The latter task involves a semi-random presentation of stimulation intensities around the previously estimated rough threshold. The participant has to respond (forced-choice) either having detected a stimulus ("yes") or not ("no"). Importantly, the experimenter applies trials without any stimulation ("catch trials"), too, in about 20% of all trials (usually 30–60). These catch trials allow estimating the participant's tendency towards responding with "yes" despite no stimulation ("false alarms" or simply fA). ADTH is then the smallest stimulus magnitude for which the participant's detection rate ("hit-rate") exceeds the fA-rate of the catch trials, which is equivalent to calculate stimulus sensitivity in signal detection theory that is independent of the individual response bias (see next section). This procedure is relatively fast, as, in each trial, stimulation and verbal response require roughly five seconds.

In most of the current studies, a stimulation intensity above ADTH (i.e., suprathreshold) but well below pain threshold was directly estimated during threshold assessment either depending on the participants' subjective reports of experiencing a clear (i.e., conscious) percept or by applying the method of constant stimuli. For the latter, the experimenter presented several different stimulation intensities and participants responded according to the 1AFC scheme (see above). The suprathreshold stimulus (STH) then refers to the smallest intensity that exerts (close to) perfect detection performance, i.e., hit-rates of roughly 100%.

2.1.3 Behavioral analysis

All studies report the hit- and false alarm rates (HR, FAR), i.e., the probability of responding "yes" when a stimulus was presented or responding "no" when there was no stimulation, respectively. Both measures are affected by the observer's perceptual sensitivity to a stimulation intensity and an individual response tendency towards reporting or not reporting a signal, independent of its actual presence (Green & Swets, 1966; Kingdom & Prins, 2009; Macmillan & Creelman, 2004; Swets, 1961, 1964). Therefore, in those studies that include catch trials, perceptual sensitivity is calculated as D-prime (Macmillan & Creelman, 2004):

$$d' = z(HR) - z(FAR),$$

where the function z(x) is the inverse-normal transformation and converts hit and false alarm rates ranging from 0 to 1 to *z* scores having zero mean and a standard deviation of one. D-prime is then the distance between the two *z*-scores representing the observers' internal response to a signal and noise, respectively. This distance is mathematically independent of a possible response tendency of the observer being either lenient (bias towards saying "yes") or stringent (bias towards saying "no"). With *d'* values of zero, observers are not able to discriminate a stimulus at all, i.e., HR = FAR. A stimulus that exerts zero perceptual sensitivity, i.e., a detection probability that is no different from "yes" responses to null events, therefore satisfies the condition of escaping conscious perception, because objective performance is at the chance level. This situation, though, is hard to meet, since a satisfying precision for the statistical estimate of the true value would require an impractical amount of data.

Furthermore, testing the null hypothesis (NH), i.e., proving chance performance, cannot be accomplished by classical test theoretic procedures. Frequentist statistics are designed to reject the null and to be sensitive for the alternative hypothesis (AH, Rouder et al., 2009). This sensitivity for the AH is, e.g., evident for the simple *t* statistic of a one-sample *t*-test, which—despite constant mean difference and variance—increases by ramping up the sample. Conversely, if the null hypothesis is true, *p*-values are equally likely and may take on any value between 0 and 1 (Rouder et al., 2009). Unconsciousness in this framework, therefore, cannot be proven. Although this led the research field to propel productive questions of qualitative differences on the consequence of unconscious perception from the consequences of conscious perception (Merikle & Daneman, 1998), also methodologically motivated alternatives to classical test theory have been suggested (Rouder, Morey, Speckman, & Pratte, 2007; Rouder et al., 2009). However, these are almost unnoticed in the core field of unconscious perception research (Haynes, 2013; Kiefer, 2012; Peters & Lau, 2016; Silverstein et al., 2015a; Soon, Brass, Heinze, & Haynes, 2008; Wiens, 2008).

Bayes factors, instead, evaluate probabilities of at least two hypotheses conditional on observed data (Rouder et al., 2009). In the case of comparing the evidence for the NH against the evidence for the alternative, a Bayes factor calculates the posterior odds ratio of the probability of the NH given the data against the probability of the alternative hypothesis (AH) given the data:

$$\Omega = \frac{\Pr(H_0 \,|\text{data})}{\Pr(H_1 \,|\text{data})},$$

where H_0 and H_1 denote null and alternative hypothesis, respectively (Rouder et al., 2009). An odds ratio of two means in this case that the NH is two times more likely than the alternative. A convention by Lee and Wagenmakers (2013) classifies odds ratios of more than three as moderate and more than ten as strong evidence in favor of the hypothesis in the nominator. In order to calculate the probabilities of the competing hypotheses, prior information about the hypotheses' parameters have to be incorporated. Under the null hypothesis, i.e., chance performance, the true standardized difference between the perceptual sensitivity to a stimulus intensity is assumed to be zero. Under the alternative, a distribution of different weights on different effect sizes expresses this prior information. For an objective statistical proof of chance performance exerted by subthreshold stimulation in the current thesis, we need priors with minimal assumptions about the range of effect sizes under the alternative. Therefore, I rely on the Cauchy distribution (one degree of freedom *t* distribution) of effect sizes together with the Jeffreys prior on variance (Jeffreys, 1961). The zero-centered Cauchy does not favor a direction of effect sizes in the two-sided test case and further assumes them to be normally distributed (Rouder et al., 2009). The so-called JZS prior, i.e., the combination of the Cauchy distribution on effect size and Jeffreys prior on variance (ibid.), might be scaled when smaller or larger effect sizes are expected a priori (ibid.). However, the Bayes factor analysis in this thesis considers a range of scales, *r*, to relax strong expectations about the effect size.

The computational implementation of the above procedures, I mainly realized in two software packages: 1) Matlab (Mathworks, Natick, MA, USA, RRID: SCR_001622) for the basic statistical comparisons of experimental conditions, e.g., condition contrasts with *t*-test statistics and 2) the R environment (R Core Team, 2014) for more advanced modeling, like Bayesian statistical inference.

2.1.4 Electrophysiological measurement

To analyze the rapid changes (<500 milliseconds) underlying the processing of sensory events supposed to distinguish conscious from unconscious perception, a temporally exemplary resolved method is required. Non-invasive electroencephalography (EEG) measures little potential changes by placing many small electrodes over the (human) scalp. These scalp potentials are generated by synchronized and spatially aligned current dipoles in the brain and propagate through the insulating, anatomical layers of the brain, cerebral spinal fluid (CSF), dura and scalp (Jackson & Bolger, 2014)—the so-called volume conduction. Coherently oriented pyramidal dendritic trunks form cortical macro-columns that are thought to contribute to EEG signals (Pizzagalli, 2007) mainly. Synchronized input to these macro-columns by excitatory and inhibitory post-synaptic potentials (EPSP and IPSP) sums up and composes the signal that the scalp electrodes measure. The polarity of these scalp potentials depends on the depth of the post-synaptic potentials relative to the Pyramidal cells (soma or apical dendrite) and the position of the scalp electrode relative to the radially or tangentially oriented dipoles. Neural source modeling of sensory evoked responses showed that EEG may be both sensitive to the initial feedforward sweep from thalamus to granular layers (4/5) of SI as well as feedback connections from either local or distant brain areas like secondary somatosensory cortex (SII) frontal cortex (FC) or posterior parietal cortex (PPC; Auksztulewicz & Blankenburg, 2013; Auksztulewicz et al., 2012; Jones et al., 2009; Jones, Pritchett, Stufflebeam, Hämäläinen, & Moore, 2007).

Either 32-channel caps (study section 2.4) or 62-channel caps (study section 2.3.2) realized EEG recordings using the BrainAmp amplifier (Brain Products, Munich, Germany) together with the Brain Vision Recorder to record the signals of active Ag/AgCl electrodes arranged according to the international 10-20 system or its extended version, respectively. The midfrontal electrode (FCz) served as an online reference and a sternum electrode as ground. Impedances were checked at the beginning of each session and reduced below five kΩ for all channels. The method sections of the EEG studies (section 2.3.2 and 2.4) detail all information of the specific EEG acquisition. In the following two sections, I describe the general analysis procedures behind the central EEG measures investigated in the current thesis: event-related potentials (ERP, section 2.1.5) and the time-frequency response (TFR, section 2.1.6).

2.1.5 Analysis of event-related potentials

An event-related potential captures neural activity that is generally phase- or time-locked to a specific event, be it the onset of a stimulus or the onset of a behavioral response. In the remainder, I will refer to stimulus-related potentials exclusively. The ERP in a single trial is overlaid by steadily varying background activity (see next section), whereas the event-related response, i.e., the transmission of electrical current after transducing an incoming stimulus by the receptor (sometimes called evoked potential, see Luck, 2005), is thought to be relatively invariant with respect to time. To distill the evoked response, averaging many trials will cancel the time-varying components (background and induced activity) in the signal and leave the stimulus-locked components. Early components, i.e., roughly up to 100ms following stimulus onset, usually have a marked peak either in the positive or negative direction and mainly depend on external factors like stimulus magnitude ("exogenous components"; Luck, 2005). Endogenous components, instead, depend on internal factors like awareness of stimulation, attentional deployment or reporting related activity (Pitts, Metzler, & Hillyard, 2014; Silverstein et al., 2015a). Potential amplitudes across time for a specific channel or group of channels illustrate such evoked components where zero marks the onset of the stimulus. Complementary, one calculates the potential amplitude at a specific time, e.g., at the peak of a specific component, for all channels as a topographic map. Because this thesis investigates event-related potentials to somatosensory stimulation, topographic maps show maximum component peak distributions close to central gyrus, i.e., at midline EEG channels. As a convention, I will call these ERPs "somatosensory evoked potentials" (SEP).

2.1.6 Spectral Analysis resolved over time

As mentioned in the previous section, EEG also captures activity that is not strictly phase-locked to the onset of an external stimulus. Simply averaging single trials would suppress such signal variations. Often these variations show a certain periodicity over time. Hans Berger (1929) gave the first record of a ten times per second (i.e., 10 Hz) waxing and waning human EEG, the so-called alpha rhythm. One way to extract such rhythms is by convolving the single trial data with so-called morlet wavelets (MW). Morlet wavelets are complex valued sinusoids of the frequency of interest (f) multiplied by a Gaussian window. Convolution of the single trial signal with the MW results in a time-frequency response of the trial that enhances frequency components that are similar to the MW and suppresses others (Cohen, 2014). The TFR is a smoothed representation of *f* localized in time (*t*), i.e., it depends on neighboring time points and frequencies. This smoothing—or the precision of the TFR—can be controlled by adjusting the width of the Gaussian window with $\sigma = c \; / \; (2\pi * f)$, where *c* is the number of cycles of *f* the MW should "look for" in the signal. With a wider Gaussian window, i.e., more frequency cycles, more sustained oscillatory effects can be extracted. Accordingly, narrow Gaussian windows track more transient changes. Importantly, this comes with a trade-off with respect to frequency precision: the more localized in time, the broader the smoothing across frequencies and vice versa. The following formula constructs a complex morlet wavelet for a discrete time period *t* and the just introduced parameters:

$$m(t) = e^{-t^2 / 2*\sigma^2} \; * \; e^{-i*2\pi*f*t}$$

The first part of the formula is the Gaussian window that is multiplied by a complex sinusoid, indicated by the *i*, of the second part. The literature discusses at length some further details to the method (e.g., Cohen, 2014). The point here was to illustrate why averaging of single-trial TFRs may not suppress activity that is not phase-locked. Depending on the amount of temporal smoothing it is less critical whether an oscillatory activity appears several milliseconds earlier or later across the to-be-averaged trials as long as the time window of the MW can capture it.

If the oscillatory activity is related to the onset of a stimulus but not strictly phase-locked to it, one often refers to as induced time-frequency response (iTFR). iTFR amplitudes in the alpha (8–14 Hz) and beta band (15–30 Hz) are known to decrease upon stimulus presentation with respect to a pre-stimulus baseline (van Ede, Szebényi, & Maris, 2014), which has been attributed to serve different functions ranging from processing of the incoming stimulation to higher cognitive processes (Neuper & Klimesch, 2006; Nierhaus, Schön, Becker, Ritter, & Villringer, 2009; Pfurtscheller & Lopes da Silva, 1999; Sauseng et al., 2005).

However, oscillatory rhythms may also fluctuate spontaneously, i.e., without being evoked or induced by a stimulus, e.g., in the resting state (Papo, 2013) or the period before a stimulation (the “baseline”), the so-called background activity (Nierhaus et al., 2009). There are at least three different background rhythms in the 8–14 Hz range related to the brain area processing the sensory modality: the occipital alpha rhythm (visual alpha), the Rolandic alpha rhythm (somatosensory alpha or mu) and the tau rhythm (auditory alpha, Nierhaus et al., 2009). The mu rhythm amplitude, which is central to the current thesis, has been shown to inversely correlate with BOLD signal activity (Ritter, Moosmann, & Villringer, 2009; Yin, Liu, & Ding, 2016) and reduced amplitude values to be predictive for upcoming stimulus detection (Schubert, Haufe, Blankenburg, Villringer, & Curio, 2008) and greater attentional deployment (van Ede et al., 2014).

2.2 Psychophysical assessment of subthreshold stimulation

In this chapter, means for assessing the individual threshold are explored and validated. The goal was to derive a practical assessment procedure that is both fast in the application (section 2.2.1) and reliable in its estimation of an absolute detection threshold (section 2.2.2).

2.2.1 A method for assessing the individual absolute detection threshold (ADTH)

It is known that longer stimulation of cortical areas increases the probability of reporting a sensation (Libet et al., 1967; Ray et al., 1999a), which suggests the duration of neuronal activation to be an essential factor determining conscious and unconscious experience. E.g., Ray and colleagues (1999) reported the lowest (cortical) absolute detection thresholds for stimulus trains lasting ≥ 1000ms resulting from averaged trials of ascending and descending electrical current intensities (method of limits, see section 2.1.2). Shorter stimulation trains resulted in increased ADTH, i.e., the more electrical current had to be applied in order to exert a conscious percept. This result is congruent with our experience from the laboratory for ADTH assessment with healthy volunteers. It is usually much easier (and faster) for participants to get an idea of the perceptual quality of electrical stimulation presented with longer stimulus durations (e.g., 1sec of 7 Hz monophasic current stimulation) rather than irregular sub-Hz single pulses, especially for untrained participants. Thus, manipulating the duration of peripheral electrical stimulation may lead to lower ADTH for longer stimulation trains than for single pulses; however, no one, so far, reported a systematic assessment with such stimuli.

Furthermore, the primary concern with stimulation intensities below ADTH is whether they are indeed "subthreshold," i.e., whether those stimuli exert chance performance or, more precisely, observers do not respond more often with "yes" (hit-rate) than for trials without any stimulation (false-alarm-rate, fA-rate). Comparing response rates is straightforward if the fA-rate is greater than zero indicating that the individual criterion is placed within the internal noise distribution (see also section 1.3 and 2.1.3). However, both measures—hit-rates to subthreshold stimulation and false-alarm-rates—being zero might blur a true sensitivity to subthreshold stimulation if the observer rather tends to respond with "no" (overly conservative response bias). Thus, despite showing chance performance to subthreshold stimulation, internal signal and noise distribution might be separated. Assessing ADTH with longer stimulation durations than applied during the main experiment would, at least partly, account for this problem when an observer's criterion is low (i.e., overly conservative).

In order to test stimulation duration effects on ADTH, we ran a psychophysics experiment comparing the estimates of our manual DS7 threshold assessment procedure (section 2.1.2) conducted with either 7 Hz stimulation or irregular single pulse stimulation (roughly around 0.5 Hz).

Methods

Participants

Eight participants (age range 22–29 yrs, mean 25.4 ± 2.6 yrs S.D.; 7 females) volunteered and gave their informed consent to take part in the study. The local ethics committee at the medical faculty of the University of Leipzig approved the study.

Experimental Procedures

Somatosensory Stimulation and Task Design

The Experimenter manually assessed ADTH of the left index finger as described in section 2.1.2 via electrical stimulation through a pair of steel wire ring electrodes controlled by a constant current stimulator (DS7). The electrical current step size for the fine adjustment was 0.05 mA. Participants underwent a threshold assessment two times for two different stimulation conditions: 7Hz pulse trains and single irregular pulses (ISP). Repetition of threshold assessment allowed estimating threshold stability over time. The order of stimulation conditions alternated after, an across participants, randomized starting condition. Stimulation duration within a trial was 2–3 seconds to allow at least two pulses in the ISP condition triggered at a stimulation rate of roughly 0.5Hz, i.e., every two seconds on average with a pseudo-random jitter of ±300ms. Each threshold assessment took about 5 minutes, which makes up 20 minutes per participant for the whole experiment.

Behavioral Analysis

ADTH values (in mA) for all conditions were statistically analyzed in a 2 by 2 within-subject repeated measurement analysis of variance (ANOVA) with the factors "stimulation frequency" (7Hz, ISP) and "measurement" (1,2) using the "ez-package" (Lawrence, 2013) in R, as well as post hoc *t*-tests for condition contrasts. The visualization was produced with a custom Matlab script.

Results

Threshold assessment resulted in lower current values (in milliampere) for the 7Hz condition (*M*=1.6 mA; *SD*=0.38 mA; range: 1.1–2.08 mA) as compared to the ISP condition (*M*=1.88 mA; *SD*=0.44 mA; range: 1.2–2.25 mA). We found a small but significant interaction effect between stimulation frequency and measurement ($F(1,7)=7$, $p=0.033$, $\eta^2_G=0.0003$) indicating that a threshold shift within the sample after roughly 10 minutes depends on stimulation frequency. Furthermore, there was a significant main effect of stimulation frequency ($F(1,7)=7.81$, $p=0.027$, $\eta^2_G=0.11$), whereas factor measurement was not significant ($F(1,7)<1.2$). Threshold assessment with 7Hz stimulation consistently resulted in lower ADTH values than stimulation with single irregular pulses at a rate of 0.5Hz. 7Hz ADTH current values were lowest for all participants as can be observed in *figure 1*. Post hoc *t*-tests for the measurement factor contrasts of 7Hz and 0.5Hz irregular single pulse stimulation did not reveal a significant effect ($t(7)=-0.36$, $p=0.7$ and $t(7)=-1.67$, $p=0.14$, respectively). Descriptively, ADTH for 7Hz stimulation on average increased by 0.006mA and for ISP by 0.03mA from the first to the second measurement (time difference ~10 minutes).

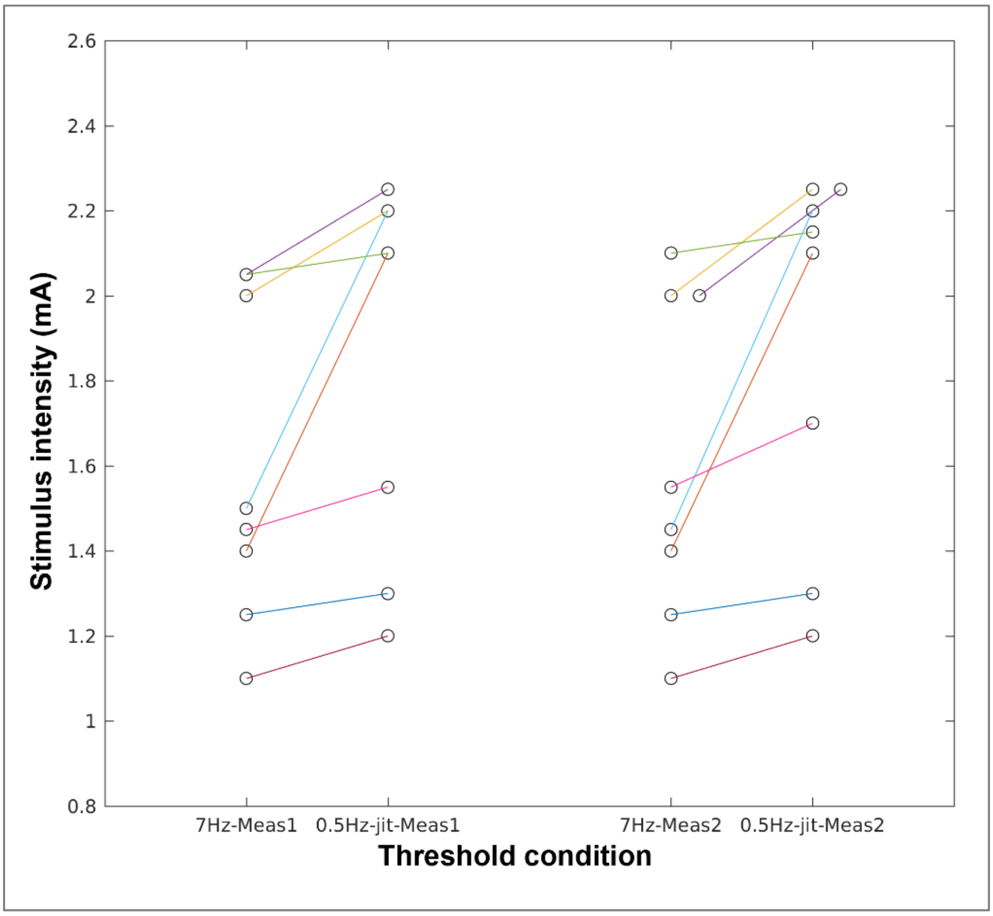

Figure 1. ADTH current values in milliampere for all conditions and all participants (empty circles) showing lower thresholds when stimulated with regular 7Hz compared to jittered 0.5Hz pulses. Consecutive measurements are indicated by the label suffixes "Meas1" for the first and "Meas2" for the second measurement. Lines connect ADTH values from the different stimulation conditions for each participant.

Discussion

This experiment set out to test the influence of stimulation repetition rate on individual ADTH estimates of monophasic electrical currents across time. The results show that the threshold assessment with stimulation trains (7Hz) results in lower ADTH estimates than threshold assessment with short single irregular pulses at 0.5Hz. Furthermore, threshold estimates are relatively stable throughout at least 10 minutes. The interaction between stimulation condition and measurement, together with the post hoc *t*-tests, points toward a possible threshold shift for 0.5Hz stimulation. However, effect size here is tiny, and the average shift is smaller than the resolution of the threshold procedure (current step size was 0.05mA).

The results of peripheral stimulation show a striking concordance with studies in which cortical sensory areas were stimulated directly in order to exert a tactile sensation (Libet et al., 1967; Ray et al., 1999a): the longer the stimulation, the lower the ADTH flooring at stimulation train duration ≥ 1000ms. Thus, extensive neural activation may lead to a higher probability of consciously perceiving sensory stimulation.

The stability 7Hz ADTH estimate over time allows further studies the application of stimulation near ADTH for which variations in stimulus detection probability caused by threshold shifts is unlikely for at least 10 minutes. It has to be noted, however, that the experiment did not test more extended measurement periods. Vigilance drifts may play a role and could lead to ADTH variations earlier than 10 minutes for longer experimental sessions. Furthermore, ADTH assessment with higher stimulation repetition rates than applied during the main experiment should have an advantage when the experimenter strives for chance performance (e.g., during subthreshold stimulation), but false alarm rates of a participant are virtually zero. The criterion of such a participant cannot be estimated reliably and might hide an actual separation of internal signal and noise distribution. Referencing intensities of single irregular subthreshold stimulation to a long duration ADTH (e.g., 7Hz) will put the internal signal distribution of the former closer to the internal noise distribution thereby approaching zero sensitivity for subthreshold stimulation. The latter result warrants one of the central experimental manipulations of the following studies, namely the imperceptibility of subthreshold stimulation.

In sum, manual threshold assessment with 7Hz stimuli of 2–3 seconds is a practical, reliable and relatively fast procedure to estimate the individual ADTH.

2.2.2 Validation of absolute detection threshold assessment by signal detection theory measures and Bayesian Null-Hypothesis testing

> **This section partly originates in Forschack, N., Nierhaus, T., Müller, M. M., & Villringer, A. (2017). Alpha-Band Brain Oscillations Shape the Processing of Perceptible as well as Imperceptible Somatosensory Stimuli during Selective Attention. The Journal of Neuroscience, 37(29), 6983-6994, but addresses the psychophysics experiment and its results in detail.**

While the previous study described a successful setup for measuring the ADTH, chance performance for stimulation intensities below ADTH yet remains to be shown. In this psychophysics study, we, therefore, evaluated the observer's performance in a signal detection theory (SDT) framework allowing the estimation of perceptual sensitivity independent of the observer's response bias (Swets, 1964). Thus, the design included catch trials, i.e., trials without any stimulation. However, as in a classical SDT experiment, observers discriminate only between two situations (trials with or without a stimulus of fixed intensity), this will likely result in significant variations of observers' vigilance in the case of either presenting catch trials or stimuli below ADTH, i.e., subthreshold and putative imperceptible stimulation. We, therefore, applied a variant of the classical design called two-response classification, in which several stimulus intensities are randomly chosen on each trial (Macmillan & Creelman, 2004). Specifically, stimulus magnitudes ranged from subthreshold to consciously perceivable—however not painful—suprathreshold intensities making the task more engaging. As the name "two-response" suggests, the participant responds "yes" if a current pulse can be felt and "no" otherwise. Importantly, we applied the very same procedure for ADTH determination as in the previous experiment and determined perceptual sensitivity (*d'*) for seven stimulation intensities along the individual psychometric function.

The crucial test for rejecting conscious perception is to show zero perceptual sensitivity ($d'=0$) that indicates chance performance by the observers. However, as we have seen previously (section 2.1.3), this is testing the null-hypothesis (NH) and cannot be accomplished with classical test theoretic statistics. Therefore, we used a Bayes-factor approach (Rouder et al., 2009) in order to evaluate evidence for the NH—i.e., subthreshold stimulation exerts zero perceptual performance—against the alternative hypothesis that observers perceive it above chance.

Methods

Participants

We invited 14 volunteers (age range 22–32 yrs, mean 26.7 ± 2.8 yrs S.D.; 7 females) that were all right-handed (mean 90.4 ± 11.7 S.D.) and included in the analysis. The local ethics committee at the medical faculty of the University of Leipzig approved the study.

Experimental Procedures

Somatosensory Stimulation

The same stimulator and electrode setup as in the previous study was used, except that a custom-built interface to the DS7 allowed automatic adjustment of stimulation magnitudes in steps of 0.1mA. Custom scripts running in the stimulation software "Presentation" (Neurobehavioral Systems, San Francisco, U.S.A.) triggered electrical pulses.

Threshold Assessment and Task Design

The experimental session was divided into five blocks (duration ~7-8 minutes per block) each containing 120 trials with or without stimulation. Preceding each block, a trained experimenter manually assessed the individual ADTH with the two-step procedure described in section 2.1.2, i.e., in the same way as in the previous study. A stimulation trial during the experimental session contained a single current pulse scaled with one out of seven different intensities defined relative to the ADTH. There were trials with two different subthreshold intensities (subTH-30%, subTH-15%, i.e., 70% and 85% of ADTH intensity, 100 trials each), the ADTH intensity (60 trials), three near-threshold intensities (NTH25%, NTH50%, NTH75%, 60 trials each), whose current intensities equally divided the distance (in mA) between ADTH and the suprathreshold intensity (STH, 60 trials). The latter was individually adjusted to be the first that the participant perceived throughout all trials during a stimulus detection run preceding each block. This assessment applied five different intensities above ADTH and separated by 0.1mA (five repetitions for each and five catch trials) that remained constant for two minutes (method of constants). If the experimenter could not identify the STH intensity, the participant conducted further stimulus detection runs, with stimulation intensities increased by 0.2mA, until STH criterion was reached.

During an experimental trial, participants performed a forced-choice Yes/No detection (1AFC) task. A trial started with gaze fixation at a centrally presented cross on a monitor screen in front of the participants. In a period of 500ms up to 2500ms after fixation onset, participants either received a pseudo-randomly presented single current pulse scaled by one of the seven individually defined intensities (500 trials) or no stimulation (100 catch trials). Upon switch from fixation cross to question mark, participants indicated detection of a stimulus by pressing the left ("detected") or the right button ("nothing detected") of a response box with the index or middle finger of the right hand, respectively. As soon as participants pressed either button, the question mark disappeared, and a new trial started.

Behavioral Analysis

Hit- and false alarm rates as well as *d*-prime (see section 2.1.3) were calculated across blocks. Individual response tendency, i.e., the criterion, in a two-response classification task is given by:

$$criterion = -z(FAR),$$

where the function z(x) is the inverse-normal transform and converts the false alarm rate to a *z*-score (Macmillan & Creelman, 2004). For any stimulation magnitude for which perceptual sensitivity, i.e., *d'*, is below this *z*–score, participants will have decided to have nothing perceived on more than half of the trials for the specific stimulation magnitude.

D-prime values of all stimulation intensities are tested against zero by one-sample *t*-tests and visualized via boxplots using Matlab. Stimulation conditions that did not show any significant effect were submitted to a Bayes factor analysis incorporating the non-informative JZS-prior (scaling factor $r=\sqrt{2}/2\approx 0.707$) in order to evaluate the evidence for the null hypothesis against the alternative (see section 2.1.3 for details). This approach was implemented in R using the "BayesFactor"-package. Because different JZS prior widths alter the odds ratio of evidence of competing hypotheses, Bayes factor analysis was repeated for different r ranging from 0.1 to 1.5 putting relatively more weight on small to large effect sizes, respectively. The prior scaling effect has been visualized using the statistics software JASP (JASP Team, 2018). Additionally, to test whether observers are still able to classify stimulation below ADTH, d' values for the subthreshold stimulation intensities were compared via a paired Bayes factor test.

Results

Single electrical current pulses were applied in seven different intensities fitted to the individual psychometric function and ranged from intensities below absolute detection threshold to consciously perceivable intensities (*table 1*):

Table 1 shows the average applied electrical current in milliampere (mA) for all stimulation conditions: 1=subTH-30%, 2=subTH-15%, 3=ADTH, 4=NTH25%, 5=NTH50%, 6=NTH75%, 7=STH. 1 and 2 are defined relative to ADTH intensity. 4, 5 and 6 divide the ADTH-STH interval equally. M = mean, SD = standard deviation.

CONDITION	1	2	3	4	5	6	7
***M* (mA)**	1.07	1.29	1.51	1.81	2.12	2.39	2.67
***SD* (mA)**	0.32	0.38	0.45	0.47	0.54	0.62	0.72
Range (mA)	0.64–1.74	0.78–2.08	0.9–2.46	1.18–2.68	1.3–3.12	1.4–3.54	1.5–4.04
Rel. Intensity	0.71	0.85	1	1.22	1.44	1.64	1.85

Participant's sensitivity to single electrical current pulses increased, as expected, with the size of stimulation magnitude from ADTH to STH (ADTH: $d'=0.12$; $t(13)=1.28$; $p=0.11$; NTH25%: $d'=0.37$; $t(13)=2.96$; $p<0.01$; NTH50%: $d'=0.79$; $t(13)=6.06$; $p<0.0001$; NTH75%: $d'=1.62$; $t(13)=6.64$; $p<0.00001$; STH: $d'=2.56$; $t(13)=10.66$; $p<0.0000001$). Subthreshold stimulation trials, however, exerted d' values close to zero (*figure 2*; subTH-30%: $d'=0.04$; subTH-15%: $d'=-0.09$; all $t(13)<0.53$). Observers' response criteria ranged from 0.49 to 2.58 ($M=1.73$; $SD=0.68$) indicating that, in this experiment, observers mainly reported to detect stimuli 5 to 7, but not stimuli 1 to 4.

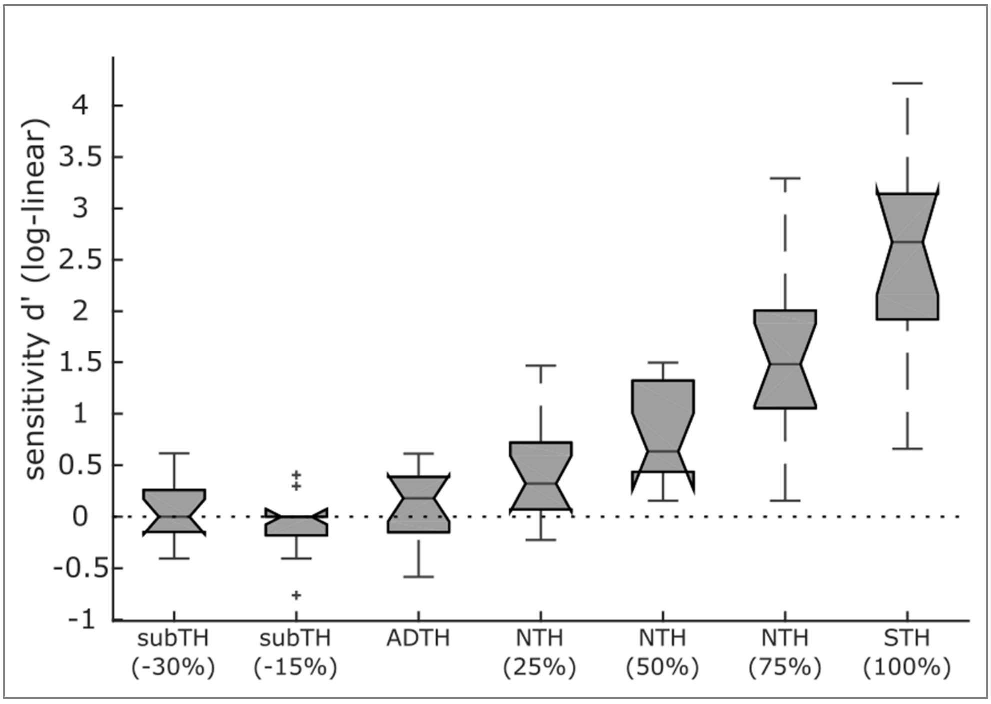

Figure 2. Boxplots depict individually averaged D-prime values across the sample for the seven different stimulation intensity categories showing that participants are zero sensitive to stimulation intensities below the individually adjusted ADTH. Absolute detection threshold served as individual reference for decreasing subTH stimulation intensities by 15% or 30%. NTH intensities were tuned to 25%, 50%, or 75% of the distance between absolute detection threshold and 100% STH. Raw hit and false alarm rates were corrected according to Hautus (1995) to account for extreme values (i.e., no responses to target or catch trials). Notches indicate 95% confidence intervals.

D-prime of ADTH intensities and below are not significantly different from zero and therefore, were submitted to a Bayes factor analysis to test whether the evidence for chance performance outweighs evidence for the alternative hypothesis of above chance performance. Bayes factors of the one-sided test of *d'* values confirm chance performance for both subthreshold stimulation magnitudes with positive to moderate evidence in favor for the NH (BF_{01}: 2.409 (subTH-30%); 6.88 (subTH-15%)). Widely different scaling of the JZS prior revealed that evidence for the null hypothesis, i.e., chance performance after subthreshold stimulation, outweighs evidence for the alternative for virtually all prior widths between 0.1 and 1.5 (*figure 3*). Evidence for the ADTH data is ambiguous, with the posterior odds instead favoring the alternative when the expected effect size is small (i.e., narrow prior) than when the prior weights more prominent effects more strongly (wide prior, *figure 3*).

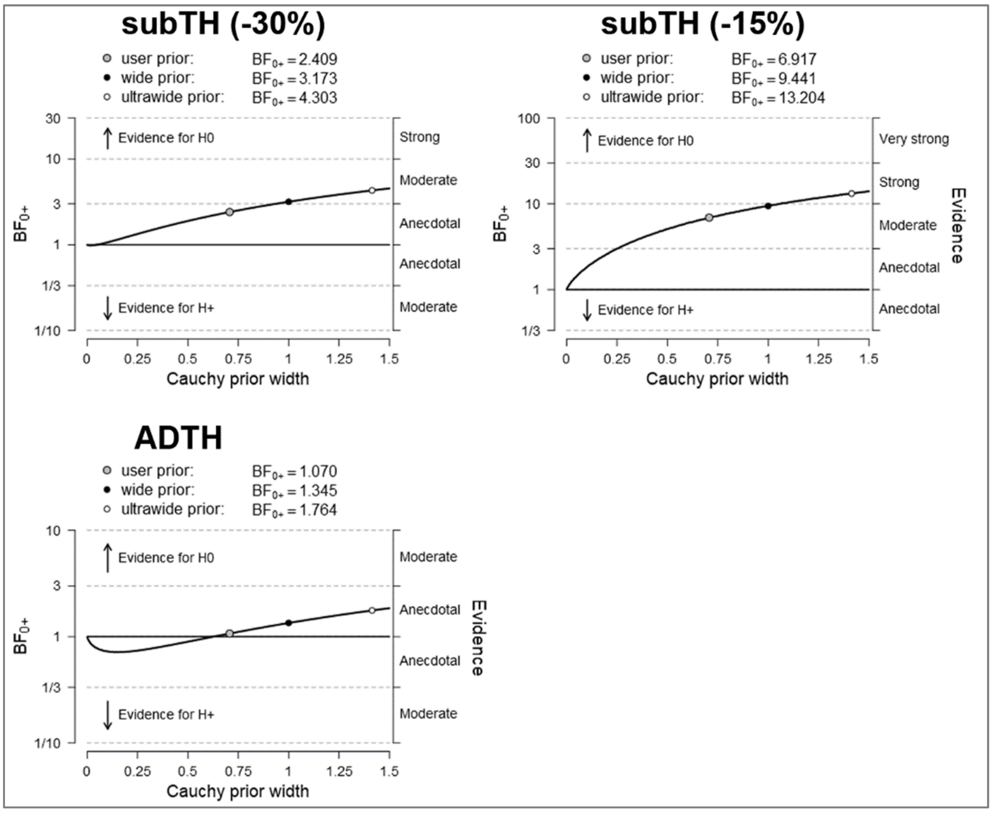

Figure 3. Bayes factor tests of the d-prime values of subTH-30% (top left), subTH-15% (top right) and ADTH (bottom) stimulus intensities. Evidence for the null hypothesis (not different from zero) against the alternative hypothesis (greater than zero) along various Cauchy prior widths is depicted as likelihood values greater than one. The grey filled circle marks the prior width used in the main analysis.

The Bayes factor for *d'* values of stimulation intensities 85% against 70% of ADTH electrical current (JZS prior width $r=\sqrt{2}/2$) revealed that there is 9.16 times more evidence that perceptual sensitivity to both subthreshold intensities (subTH-15% and subTH-30%) is essentially the same.

Discussion

This experiment set out to validate the threshold assessment procedure described in the previous study (section 2.2.1). Specifically, we asked whether the definition of individual subthreshold intensities relative to ADTH results in zero perceptual sensitivity (i.e., *d'*) to these stimulation conditions, i.e., whether these stimuli are reliably undetectable. Indeed, results of the two-response classification task revealed that, contrary to stimulation intensities above the absolute detection threshold, sensitivity exerted by intensities below ADTH did not vary significantly from zero. Model evidence of chance performance for subthreshold stimulation outperforms the model of above chance performance as shown by Bayes factor statistics. Reasonable variations of the prior width did not change the qualitative conclusion of evidence favoring the NH, which indicates that Bayes factor results are robust.

Importantly, the experiment included catch-trials, i.e., trials without any stimulation. Forced responses to catch-trials allowed the calculation of perceptual sensitivity that is independent of individual response bias. Thus, the absence of a behavioral effect for subthreshold stimulation cannot be explained by observers' tendencies to rather respond with "no," i.e., applying a conservative decision criterion. Criterion values per se varied over a range of more than two standard deviations across participants. Even for the most "liberal" measured criteria (about half a standard deviation above zero), perceptual sensitivity to subthreshold stimulation remained largely below decision criterion. In three cases, however, false alarm rates floored to zero. For these observers, the estimate of response bias might not be reliable and could, therefore, "mask" partial conscious processing of applied subthreshold intensities. Three arguments speak against this: (1) Criteria were set to the maximum value according to the log-linear rule (Hautus, 1995). Applying the log-linear rule adds 0.5 to all four cells of the contingency table, thereby increasing the number of stimulus-present trials and catch-trials by one each. Simulations showed that for at least 100 trials of a 1AFC detection task, this method resulted in accurate and unbiased sensitivity values when the true *d'* and false alarm rates were equal or smaller than one and 0.05, respectively (Hautus, 1995). In the current study, hits and false alarm rates were based on 100 trials for each subthreshold intensity and catch trials. (2) For threshold assessment, we used a 7Hz train of 1-second of electrical pulses. As we have seen before, stimulating at a higher rate results in a lower detection threshold estimate. Accordingly, the definition of subthreshold intensities relative to 7Hz detection threshold should converge the signal distribution of stimulation presented at lower rates to the internal noise distribution. (3) The same argument holds for the fact that intensities for subthreshold stimulation were at least 15% lower than ADTH. Therefore, it is unlikely that the three observers showing zero false alarm rates are partially sensitive to subthreshold stimulation.

Despite that a single action potential of an isolated axon innervating the receptive field of mechanoreceptors (Meissner corpuscles) in the glabrous skin might suffice to exert above chance performance (Goodwin & Wheat, 2008; Johansson & Vallbo, 1979; Vallbo & Johansson, 1984), we could present transcutaneous electrical current stimulation that is reliably reported to be absent. This discrepancy might be explained by the convergence of receptive fields in higher-order stages of the somatosensory perceptual system, e.g., in primary somatosensory cortex (SI). There, lateral inhibitory connections may suppress neurons of neighboring receptive fields (Gardner & Kandel, 2000; Kim, Gomez-Ramirez, Thakur, & Hsiao, 2015). Activation of many receptive fields by transcutaneous electrical stimulation might evoke mutual inhibition of the different types of neurons responding to the very receptive fields. The net activation is then smaller as compared to a circumscribed stimulation of a few mechanoreceptors specifically responding to spatially localized skin indentation. The critical question is whether subthreshold stimulation that is defined relative to ADTH still reaches higher order processing stages like SI. If this is the case, cortical activation to subthreshold stimulation may dissociate from cortical processing of suprathreshold stimulation. Thus, event-related potentials and functional magnetic resonance imaging might help to elucidate a putative difference, and that is the central topic of the next section.

2.3 Non-invasive neural markers of unconscious perception

2.3.1 Neural Correlates of Undetectable Somatosensory Stimulation in EEG and fMRI

In the previous section, we saw that transcutaneous electrical current stimulation allows tuning individual detection performance to chance level by adjusting stimulation intensities below ADTH. Here, I will shortly review findings in the literature and own work regarding the neural processing of putatively subthreshold, i.e., undetectable, stimulation for which a rigorous statistical validation was so far missing. Furthermore, I will discuss how quantitative measures of undetectable stimulation differ from detectable stimulation.

In a set of experiments, we recently investigated the neural correlates of subthreshold stimulus processing both with EEG and with fMRI (Nierhaus et al., 2015). For this, stimulation intensities 15% below the ADTH were presented every four seconds on average with a presentation jitter of one second. Importantly, we assessed ADTH in the same way as described in study 2.2.1. Participants had no specific task and did not report any felt stimulation after every 15 minutes block out of three in the EEG or the 6 minutes blocks of the fMRI experiments of subthreshold stimulation. The former included an additional block of suprathreshold stimulation only. The latter consisted of two sessions with a different sample each, in which the first underwent a resting and a subthreshold stimulation block and the second additionally received a suprathreshold stimulation block. In the EEG, somatosensory evoked potentials (SEP) revealed a single positive deflection 60ms after subthreshold stimulus presentation (P1) over somatomotor areas contralateral to the stimulation site.

On the contrary, suprathreshold stimulation caused a bigger P1 that was followed by a negative component around 170ms.

Furthermore, Rolandic alpha amplitudes increased relative to a pre-stimulus baseline contralateral to subthreshold stimulation and decreased for suprathreshold stimulation. A follow-up study with a slightly adjusted design that included infrequently occurring suprathreshold stimuli in addition to the subthreshold stimulation confirmed the increase of Rolandic alpha amplitude after the latter, showing that this effect is robust.

In the first fMRI session, data-driven and spatially assumption-free functional connectivity via eigenvector centrality mapping (ECM, (Lohmann et al., 2001) showed a decoupling of BOLD activity of the somatosensory areas (SI) from whole brain activity during subthreshold stimulation compared to stimulation-free blocks. Suprathreshold stimulation in session two did not varied EC compared to rest, but functional coupling was more substantial than in subthreshold stimulation blocks.

This study showed for the first time non-invasively electroencephalographic components that may indicate processing of putatively unconscious perception, i.e., undetectable stimulation. Previously, this has been observed in small patient samples undergoing brain surgery (Libet et al., 1967; Ray et al., 1999). Interestingly, both observed a stimulus-evoked component 50–60ms following subthreshold stimulation that closely corresponds to the evoked activity measured by Nierhaus et al. (2015). Furthermore, functional connectivity results are in line with previous fMRI studies showing a negative BOLD contrast for subthreshold stimulation in SI (Blankenburg et al., 2003) and a reduced response to suprathreshold stimulation when intermingled with subthreshold stimulation trains to the adjacent finger (Taskin et al., 2008).

Together, these results strongly suggest that perception of stimulation below ADTH dissociates qualitatively from stimulation above ADTH, illustrating neural processes rather dominant in unconscious and conscious perception, respectively (Merikle, Joordens, & Stolz, 1995). In Nierhaus et al. (2015), a single early small positive potential and importantly no detectable later ERP response characterized the processing of subthreshold stimulation. As these later ERP components have been associated with subjective awareness (Auksztulewicz & Blankenburg, 2013; Auksztulewicz et al., 2012), it seems that the subthreshold stimuli do not "proceed" to a pre-conscious or conscious state. Interestingly, in Nierhaus et al. (2015) participants had no task. Therefore, the N170 component that was only present after suprathreshold, i.e., consciously perceivable stimulation, but not following subthreshold stimuli, might indicate a proper marker of the neural correlates of consciousness (Aru et al., 2012; Hillyard et al., 1971). However, different stimulation strengths or the absence of conscious perception might cause this effect. One could speculate that it is both: along with the reduced stimulation strength, there is no neural correlate related to conscious processing (Nierhaus et al., 2015). To investigate this further, an EEG design that contrasts perceived versus unperceived stimuli with the same stimulation strength may reveal neural correlates related to detection rather than stimulation intensity (see next section).

Another qualitative difference is that the commonly found event-related decrease of the alpha band after suprathreshold stimulation turns into an increase when participants are receiving subthreshold stimuli. Post-stimulus decreases in alpha amplitude are usually interpreted as an indicator of local ongoing sensory processing whereas an increase in amplitude indicates inhibition of the respective brain area (Buzsaki, 2011; Jensen & Mazaheri, 2010; Moosmann et al., 2003; Neuper & Klimesch, 2006; Pfurtscheller, 1989; Pfurtscheller & Lopes da Silva, 1999; Ritter et al., 2009; Scheeringa, Petersson, Kleinschmidt, Jensen, & Bastiaansen, 2012). An increase after subthreshold stimulation is remarkable given the fact that undetected near-threshold stimuli, i.e., above ADTH, have been reported to induce a decrease just as suprathreshold stimulation (Palva et al., 2005). It is tempting to speculate that this finding (by Palva et al. 2005) may be an indicator of residual conscious processing despite being classified as undetected (near-threshold) by the subjective response. Alongside the reduced seed-based correlation from SI to frontal-parietal BOLD activity in Nierhaus et al. (2015), the increased alpha amplitude supports the notion that processing of subthreshold stimulation is terminated at an early stage in SI probably due to prevalent local inhibition.

The search for neural correlates of unconsciousness requires stimulus energies as small as possible but sufficient to evoke a measurable signal. In turn, to show compelling unconscious behavioral or neural effects, any study on the topic must provide evidence for qualitative dissociations in the data or chance performance for the alleged below consciousness condition (Merikle et al., 1995). Nierhaus et al. (2015) have shown the former. In the next study, I will show both by concurrently measuring detection performance and the neural correlates of unconsciousness: can we observe qualitative neural differences between supra- and subthreshold stimulation for which we prove observers' perceptual sensitivity being at the chance level?

2.3.2 Prediction of stimulus perception by features of the evoked potential for different stimulation intensities along the psychometric function

Investigating neural processes of perception without awareness may disclose neural phenomena that preclude conscious perception (Baumgarten et al., 2017; Forschack, Nierhaus, Müller, & Villringer, 2017; Merikle & Daneman, 1998; Nierhaus et al., 2015). Additionally, it may reveal markers that are necessary but, apparently, not sufficient for conscious perception and therefore might reflect prerequisites of the neural correlates of consciousness (NCC, Aru et al., 2012). Research dedicated to the identification of electrophysiological predictors of somatosensory detection agrees on the involvement of mid-range event-related components occurring after stimulus presentation, however, differs on the involvement of earlier event-related processes, specifically regarding the strength of the P50 (Auksztulewicz & Blankenburg, 2013; Auksztulewicz et al., 2012; Frey et al., 2016; Palva et al., 2005). These studies typically applied stimulation magnitudes individually tuned to exert detection on 50% of the trials, often called "near-threshold" (NTH) stimulation. Whereas Auksztulewicz and colleagues (2012, 2013) found the most prominent effect of perceptual awareness to occur as a negative potential over contralateral somatosensory areas roughly peaking 140 ms after stimulus presentation, both Frey and colleagues (2016) and Palva et al. (2005) reported global awareness differences even before 60 ms.

A different line of research investigated electrophysiological to stimulation below the absolute detection threshold (ADTH, Forschack et al., 2017; Libet et al., 1967; Nierhaus et al., 2015; Ray et al., 1999). For such imperceptible stimuli, observers exert equal detection probability as compared to catch trials, i.e., trials without any stimulation. Stimulation below ADTH (i.e., subthreshold) evokes a P50 but no further components. While these results agree to the notion that the mere presence of the P50 is not sufficient for stimulus detection, a proper test to the hypothesis that its amplitude or latency might play a role in the detection of stimulation along the individual psychometric function, is hitherto absent. On the contrary, data from a somatosensory extinction patient revealed that attenuation rather than elimination of somatosensory responses in the damaged hemisphere might cause tactile extinction (Eimer, Maravita, Van Velzen, Husain, & Driver, 2002).

Thus, the current study set out to quantify the contribution of somatosensory electrophysiological response strength in stimulus detection by explicitly manipulating stimulation intensities along the individual psychometric function of healthy human volunteers. Specifically, we asked (1) do features (amplitude and latency) of stimulus-evoked potentials in the EEG change gradually for varying stimulation magnitudes and (2), which features predict stimulus detection. Furthermore, as it has been observed previously that pre-stimulus oscillatory amplitude influences tactile perception (Anderson & Ding, 2011; Baumgarten, Schnitzler, & Lange, 2016; Forschack et al., 2017; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004; Schubert, Haufe, et al., 2008; Weisz, Müller, Jatzev, & Bertrand, 2014; Zhang & Ding, 2009), we explored (3) the possible modulation of features of the evoked potential by pre-stimulus somatosensory alpha-band amplitudes.

Methods

Participants

The local ethics committee at the medical faculty of the University of Leipzig approved the study. Before participation, all volunteers underwent a comprehensive neurological examination that screened for a history of neurological or psychiatric diseases or any medication. Forty healthy volunteers participated (age range 20–35 yrs, mean 27.2 ± 3.8 yrs S.D.; 21 females); all were right-handed (laterality score according to the Oldfield questionnaire: mean 92.4 ± 12.8 S.D., over a range of –100 (entirely left-handed) to 100 (entirely right-handed), (Oldfield, 1971). Data of four participants were discarded due to defective (2) or artifactual (2) EEG recordings, and so 36 datasets in total were analyzed.

Experimental Procedures

Somatosensory Stimulation

Hardware, stimulation setup and threshold assessment for ADTH and STH were identical to the previous study. The experimental session comprised ten blocks (duration ~7 minutes per block) each starting with the threshold assessment. Every block contained 134 trials with or without stimulation (i.e., 1340 trial overall). Six different intensities were defined relative to the ADTH. There were trials with two different subthreshold intensities (subTH-30%, subTH-15%, i.e. 70% and 85% of

ADTH intensity, 420 trials each), the ADTH intensity (100 trials), two near-threshold intensities (NTH33%, NTH66%: 100 trials each), whose current intensities equally divided the interval (in mA) between ADTH and the suprathreshold intensity (STH: 100 trials).

Task Design

During an experimental trial, participants performed a forced-choice Yes/No detection (1AFC) task. Trial duration was fixed to 3000 ms and started with gaze fixation at a centrally presented cross on a monitor screen in front of the participants. In a period of 1200 ms up to 2000 ms after fixation onset, a stimulation routine either presented a single current pulse scaled by one of the six individually defined intensities pseudo-randomly (1240 trials), or no stimulation (100 catch trials). Upon switch from fixation cross to question mark (i.e., at 2000 ms after stimulation onset), participants indicated detection of a stimulus by pressing the left ("detected") or the right button ("nothing detected") of a response box with the index or middle finger of the right hand, respectively. The question mark either disappeared after 1000ms or as soon as participants pressed either button; then a new trial started.

EEG acquisition

During 10 stimulation blocks each lasting roughly seven minutes, a BrainAmp actiCap system (Brain Products, Munich, Germany) recorded EEG continuously from 62 scalp channels (61 scalp electrodes plus 1 electrode recording the VEOG below the right eye) attached according to the 10-10 system (Oostenveld & Praamstra, 2001), referenced to midfrontal electrode (FCz) and grounded to an electrode placed at the sternum. Impedances were kept below five kΩ for all channels, sampling frequency 2.5 kHz, analog filter low-cutoff at 0.1 Hz and high cutoff at 1000 Hz, and a low-pass finite impulse response filter (high cut-off: 150 Hz, transition bandwidth: 50 Hz) was applied before downsampling EEG time courses to 500 Hz.

Behavioral Analysis

In most aspects, behavioral data analysis was identical to the previous study. However, because in the current study there were fewer catch trials (by a factor of four) than trials with subthreshold stimulation intensities, the former were expected to show more variance concerning the probability of "yes"-responses. The *z*-transformation used for the calculation of *d*-prime values would artificially amplify differences especially for response rates below 0.1 that might result in *d*-prime values below zero. Therefore, Bayes factor analysis was implemented as paired one-sample tests of hit rates to subthreshold stimulation versus false alarm rates to catch trials. As in the previous study, *d'* values for the subthreshold stimulation intensities were compared via a paired Bayes factor test to check whether observers are still able to classify stimulation below ADTH.

EEG Data Analysis

Preprocessing

As a first step, we ran the standardized early-stage EEG processing pipeline (PREP, Bigdely-Shamlo, Mullen, Kreutz-Delgado, & Makeig, 2013) on the down-sampled data. This algorithm combines 50 Hz line noise removal by a sliding window multi-taper spectral regression approach (Mullen, 2012) and robust average referencing by iteratively detecting and interpolating noisy channels. Next, individual datasets underwent independent component analysis (ICA, adaptive mixture of independent component analyzers (AMICA, Palmer et al., 2011) both to remove sources of ocular and muscle artifacts as well as signals of other non-neural origin (Chaumon, Bishop, & Busch, 2015; Delorme, Palmer, Onton, Oostenveld, & Makeig, 2012; Li, Ma, Lu, & Li, 2006). Before ICA, datasets were prepared by applying the following procedures: training datasets for ICA were high-pass filtered with 1 Hz, all blocks were concatenated, and contiguous epochs of one second were extracted, corrected for the average epoch potential, screened for non-stereotypical artifacts and rejected if contaminated. Then, an initial ICA was performed after which artifactual epochs were identified in ICA space using improbable data estimation on single and across all components and removed semi-automatically (function "pop_jointprob", threshold limit for single channels: 4.5 SD, threshold limit for all channels: 2.5 SD, Delorme et al., 2007). The resulting datasets were submitted to a second ICA (again using AMICA algorithm). We visually inspected the new set of components and identified artifactual components based on various features of IC topographies and time courses calculated by SASICA (Semi-Automated Selection of Independent Components of the electroencephalogram for Artifact correction, Chaumon et al., 2015). Specifically, we regarded components showing correlations with VEOG channel higher than 0.6 or horizontal EOG (bipolarized potential of channel "FT7" and "FT8") higher than 0.4, blink or eye movement typical topographies and IC source activity, abnormal frequency spectrum, i.e., high frequency or line noise, focal topographies as indicative of non-neural origin. Only the unmixing and sphering matrices of artifact-free components were forward-projected to high-pass filtered continuous datasets for the subsequent analysis steps (function "pop_firws" Widmann et al., 2015); low cut-off of 0.1 Hz, maximum pass-band deviation: 0.001 and transition bandwidth: 0.02 Hz with filter order of 9056). On average, 24.6 (4.5 SD) components per participant were rejected (average median component number when sorted from highest to lowest explained variance: 33).

After rejecting artifactual components, data for ERP analysis was downsampled to 250 Hz (high cut-off: 75 Hz, transition bandwidth: 25 Hz) and low-pass filtered by a Kaiser windowed sinc finite impulse response filter with a high cut-off of 41 Hz (high cut-off maximum pass-band deviation: 0.0001 and transition bandwidth: 10.25 Hz with a filter order of 124). Proper epochs were cut from the continuous channel signals ranging from -1200 to 3600 ms relative to stimulus onset (t=0), from which the individual epoch mean was subtracted. Epochs that exceeded the joint logarithmic probability of 4.5 or 2.5 SD within or across independent components, respectively, were discarded after manually reviewing the alleged artifactual epochs (Delorme et al., 2007). Additionally, trials that contained behavioral responses within -800 to 800 ms relative to stimulus onset as well as reaction times smaller than 150 ms or higher than 1100 ms have been excluded. These epoch rejection steps resulted in the following average number of trials per stimulation condition: 374 (21 S.D.) subTH-30%, 371 (22 S.D.) subTH-15%, 90 (5 S.D.) ADTH, 90 (5 S.D.) NTH33%, 88 (6 S.D.) NTH66%, 87 (6 S.D.) STH and 89 (5 S.D.) for catch trials. Linear detrending was applied on the remaining trials over a time range of -0.6–1.2 ms to remove any sustained potential drifts.

Amplitude and latency extraction of SEP components and their statistical analysis concerning stimulation intensity and pulse detection

Analysis of SEP components was based on the average signal of an ad-hoc selection of contralateral central electrode sites ("C2", "C4", "C6", "CP2", "CP4", and "CP6"). A topographical test of the post-stimulus period (0–300 ms) averaged across all stimulation conditions compared to a pre-stimulus baseline ranging from -100 to 0 ms to stimulus onset was conducted to estimate the sensibility of this selection. For multiple comparison correction, we applied threshold-free cluster enhancement (TFCE) with a cluster threshold of $p = 0.05$ (cluster size exponent E = 0.5, statistical intensity exponent H = 2, Mensen & Khatami, 2013; Smith & Nichols, 2009). For this, topographical isocontour voltage maps of P50 and N150 component peaks are represented.

Baseline corrected (-100 to 0 ms) P50 and N150 ERP peak amplitudes and latencies of the stimulation condition averages have been extracted for each participant for the averaged contralateral central electrode cluster signal as neural markers indicative of perceptual changes along the psychometric response function. To this end, we ran a peak and latency detection algorithm within time windows of interest: 32 to 76 ms for the P50 peak latency and 128 to 172 for the N150 peak latency. Average maximal component amplitudes and latency values were plotted together with respective within-subject confidence intervals (Cousineau, Montréal, Paradis, & For, 2005; Loftus & Masson, 1994; Morey, 2008). Pairwise two-tailed t-tests ($p<0.05$) were calculated for each stimulation condition pair and corrected for multiple comparisons using false discovery rate (fdr, $q=0.05$, Benjamini & Hochberg, 1995; Genovese, Lazar, & Nichols, 2002).

We tested the effect of stimulus detection and stimulation intensity on somatosensory electrophysiological response strength by calculating SEPs separately for detected and rejected STH and NTH66% trials. Average potentials were required to consist of, at least, ten trials per condition to assure reasonable noise reduction. Therefore, data of four additional participants were rejected for this specific analysis. P50 and N150 amplitudes of the remaining 32 participants were subjected to a 2 x 2 repeated measures ANOVA with factors "detection" (stimulus detected vs. rejected) and "stimulus intensity" (STH vs. NTH66%). ANOVA statistics and bootstrapped confidence intervals (resampling of subject indices for each condition with 10,000 iterations) were computed with the ez-package developed by Mike Lawrence (2013, version 4.2-2, https://github.com/mike-lawrence/ez). Effect sizes were quantified as generalized eta-squared (η_G^2, Bakeman, 2005).

The six different stimulation intensities were fixed within each block. To test whether detected and rejected trials are comparable concerning stimulation intensities across blocks, we calculated the average stimulation current for each participant and stimulation condition, separately for all trials classified being detected and rejected, respectively. Resulting values were submitted to a paired one-sample *t*-test.

Rolandic Rhythms

To discern Rolandic rhythms from occipital alpha activity, I used the same preselection of the central contralateral electrode cluster as in the ERP analysis above, which is consistent with electrodes found to be predictive for somatosensory masking (Schubert, Haufe, et al., 2008). For this, I convolved every single trial of all stimulation conditions with complex morlet wavelets tuned to include 5.5 cycles of frequencies ranging from 4 to 42 Hz. Frequency bands of interest were defined based on the results by Schubert et al. (2008). However, neighboring alpha and beta bands in Schubert and colleagues (2008) were slightly overlapping. I, therefore, redefined frequency bands of interest to be more distinct. I.e., the alpha band ranged from 9 to 14 Hz and the beta band from 20 to 35 Hz. Wavelet parameters resulted in the following frequency and time smoothing: 3.85 Hz at full-width-half-maximum (FWHM) and 114.5ms (+/- FWHM) at 9 Hz; 5.99 Hz (FWHM) and 73.6 ms (+/- FWHM) at 14 Hz; 8.56 Hz (FWHM) and 51.5 ms at 20 Hz (+/- FWHM); and 14.99 Hz (FWHM) and 29.4 ms (+/- FWHM) at 35 Hz. For the pre-stimulus window that is going to be tested for its predictive value in stimulus detection, I chose it to be as close as possible to stimulus presentation but without smearing into the post-stimulus window; i.e., this window should not include latencies higher than -114.5 ms relative to stimulus onset for the 9 Hz frequency response. This window I defined from -400 to -150 ms relative to stimulus onset, which is following the time window in which Schubert and colleagues (2008) found the frequency band effects. Statistical analysis was performed by testing the pre-stimulus time-frequency-band-of-interest response of the central contralateral electrode cluster for detected versus rejected stimulation (NTH66% and STH only) with cluster-based two-tailed paired t-tests (*p*-level was set to 0.01 and corrected for multiple comparisons by tfce, Mensen & Khatami, 2013).

Prediction of stimulus detection by evoked potentials and Rolandic alpha amplitude

To identify further neural markers predictive for stimulus detection, I calculated SEPs at averaged central contralateral electrode sites separately for detected and rejected finger pulses and averaged these across NTH66% and STH stimulation intensities.

Specifically, we tested whether P50 and N150 latency and amplitude are predictive for behavioral classification. To this end, I applied binomial regularized logistic regression together with six-fold cross-validation (James, Witten, Hastie, & Tibshirani, 2015) to select the essential neural markers for stimulus detection. This procedure selects the best model out of a set of predictors. Regularization was achieved by adding the so-called lasso penalty—or ℓ_1 norm—to the standard maximum-likelihood model coefficient optimization. The influence of this penalty was controlled by the tuning parameter λ ranging from 0 to 100, where zero puts no penalty on the coefficients of the full model and corresponds to standard generalized linear modeling (glm). With increasing λ, predictor coefficients are shrunk towards zero depending on their predictive value for behavioral response classification; thus, the higher λ, the simpler the model. For model selection, I chose the model that shows the smallest cross-validation error (CVE) across all λ.

To assess a probable influence of pre-stimulus Rolandic alpha amplitude on neural markers of stimulus processing and detection, i.e. ERPs, I averaged spectral amplitudes within the alpha band (9 to 14 Hz) for each participant across those time-frames that showed a significant difference between detected and rejected trials for averaged near-threshold stimulation conditions (i.e. NTH66% and STH). After normalizing to the individual condition mean (Cousineau et al., 2005), these alpha band amplitudes were added as an additional factor to the model mentioned above and allowed to interact with the P50 and N150 amplitude. Again, I used 6-fold cross-validation in order to identify the optimal tuning parameter for regularization of the logistic regression model. Regularized logistic regression was implemented with the "glmnet" package in R (Friedman, Hastie, & Tibshirani, 2010).

Results

Behavioral responses

Single electrical current pulses were applied in six different intensities fitted to the individual psychometric function and ranged from magnitudes below absolute detection threshold to consciously perceivable intensities (*table 2*):

Table 2 shows the average applied electrical current in milliampere (mA) for all stimulation conditions: 1=subTH-30%, 2=subTH-15%, 3=ADTH, 4=NTH33%, 5=NTH66%, 6=STH. For

the relative intensities, stimulation magnitudes have been normalized to ADTH. M = mean, SD = standard deviation.

CONDITION	1	2	3	4	5	6
***M* (mA)**	1.12	1.35	1.59	2.01	2.42	2.84
***SD* (mA)**	0.41	0.51	0.59	0.61	0.67	0.75
Range (mA)	0.47–2.03	0.52–2.5	0.66–2.91	0.91–3.39	1.11–3.87	1.24–4.35
Rel. Intensity	0.70	0.85	1	1.3	1.6	1.9

Participant's sensitivity to single electrical current pulses increased, as expected, with the size of stimulation magnitude from ADTH to STH (ADTH: *d'*=0.05; *t*(35)=0.82; *p*=0.21; NTH33%: *d'*=0.48; *t*(35)=5.81; *p*<0.000001; NTH66%: *d'*=1.53; *t*(35)=16.87; *p*<1.0*10^-15; STH: *d'*=3.03; *t*(35)=34.77; *p*<1.0*10^-15). Subthreshold stimulation trials, however, exerted *d'* values close to zero (*Figure 4,* subTH-30%: *d'*=-0.16; subTH-15%: *d'*=-0.19; all *t*(35)<-2.5). Observers' response criteria ranged from 1.1 to 2.58 (*M*=2.16; *SD*=0.41) indicating that, in this experiment, observers mainly reported to detect stimuli 5 to 6, but not stimuli 1 to 4.

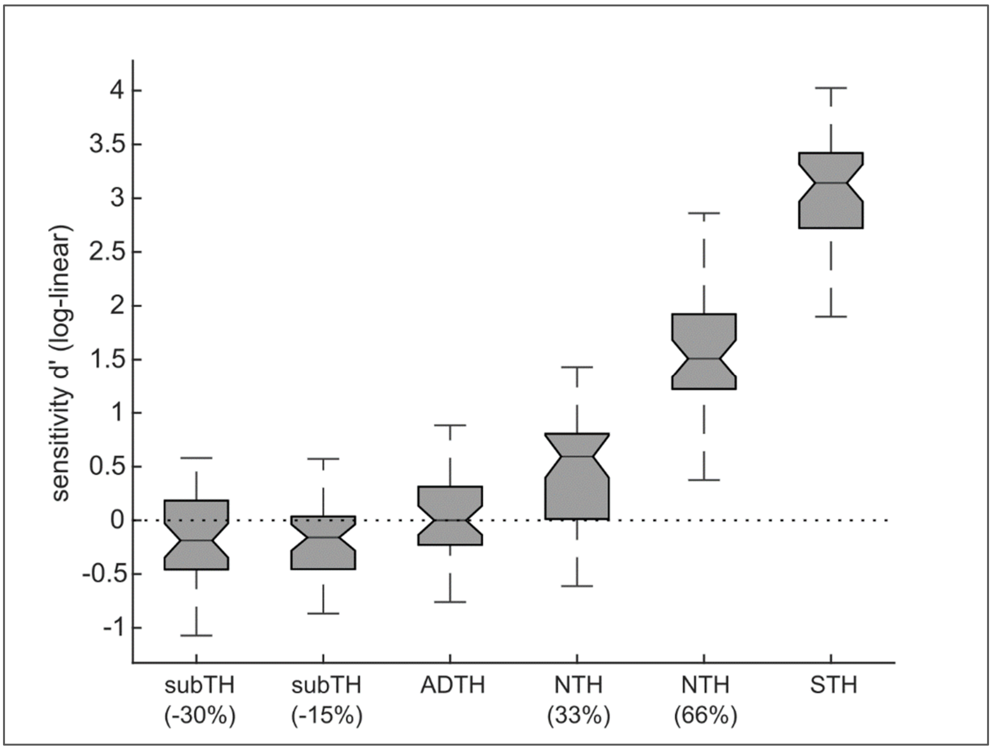

Figure 4. Boxplots depict individually averaged *d*-prime values across the sample for the six different stimulation intensity categories showing that participants are zero sensitive to stimulation intensities below the individually adjusted ADTH. Absolute detection threshold

served as an individual reference for decreasing subTH stimulation intensities by 15% or 30%. NTH intensities were tuned to 33% or 66% of the interval between the absolute detection threshold and 100% STH. Raw hit and false alarm rates were corrected according to Hautus (1995) to account for extreme values (i.e., no responses to target or catch trials). Notches indicate 95% confidence intervals.

D-prime of ADTH intensities and below are not significantly higher than zero. This null-difference is, however, not proof of chance performance (NH) and therefore evidence for the null model was evaluated against evidence for the alternative hypothesis of above chance performance by Bayes factor statistics (Rouder et al., 2009). As subthreshold intensities might suffer from oversampling compared to catch-trials, the *z*-transformation of low "yes"-response rates would artificially amplify any difference between both conditions concerning *d'* values. Thus, Bayes factors are calculated as paired one-sample one-sided test of the hit against false alarm rates and confirmed chance performance with moderate to strong evidence in favor for the NH (FAR=0.018; subTH-30%: HR=0.018, BF_{01}=6.1; subTH-15%: HR=0.016, BF_{01}=10.8). Widely different scaling of the JZS prior revealed that evidence for the null hypothesis, i.e., chance performance after subthreshold stimulation, outweighs evidence for the alternative for virtually all prior widths between 0.1 and 1.5 (*Figure 5 b-c, left*). Evidence for the ADTH data is mixed: the posterior odds favor the alternative when the expected effect size is small (i.e., narrow prior, *r*=0.0757) as compared to when the prior weights bigger effects more strongly (wide prior, *Figure 5 d, left*). Sequential tests show that the Bayes Factor reliably favors the NH across different sample sizes.

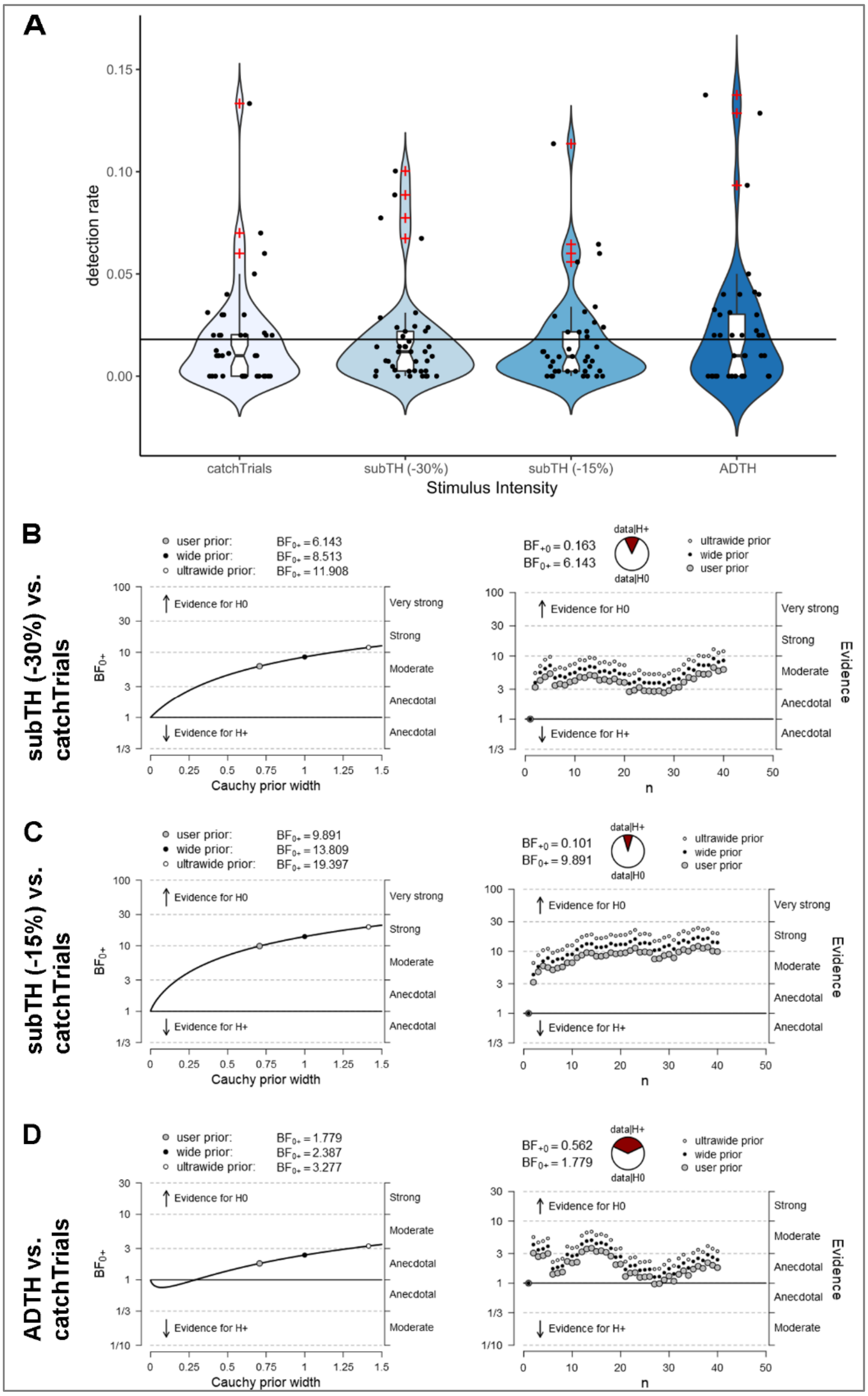

Figure 5. ***A:*** Distributions of "yes"-response rates across all participants (dots) for those stimulation conditions for which d-prime values were not different from zero and the condition without stimulation (catch trials). The horizontal black line indicates the average false alarm rate. ***B-D:*** Bayes factor tests of hit rates of subTH-30% (***B***), subTH-15% (***C***) and ADTH (***D***) stimulus intensities against catch trial condition. Evidence for the null hypothesis (hit rates not different

from false alarm rates) against the alternative hypothesis (hit rates greater than false alarm rates) along various Cauchy prior widths (left) is depicted as likelihood values higher than one. The grey filled circle marks the prior width used in the main analysis. On the right, sequential tests show evidence accumulation when adding single participants until the final sample size for three different prior widths. For subthreshold intensities, there is at least moderate evidence favoring the null hypothesis for all sample sizes.

To further the evidence for the NH, we calculated a Bayes factor meta-analysis (Rouder & Morey, 2011) based on the current detection rates of subthreshold stimulation intensities and the similar psychophysics dataset from section 2.2.2. Accumulated evidence moderately to strongly favors chance performance for subthreshold stimulation intensities ($r=\sqrt{2}/2$, subTH-30%: $BF_{01}=6.73$, subTH-15%: $BF_{01}=12.18$). The Bayes factor for the comparison between *d'* values of stimulation intensities 85% against 70% of ADTH electrical current (JZS prior width $r=\sqrt{2}/2$) revealed 8.14 times more evidence favoring the null hypothesis instead of the alternative that perceptual sensitivity for the higher subthreshold intensity (subTH-15%) is equal to the lower intensity (subTH-30%).

SEP amplitudes and latencies change along the psychometric function

The grand-average SEP across all stimulation conditions over contralateral central electrode sites (*Figure 6)* revealed a positive and negative deflection that peaked around 56 ms (P50) and 148 ms (N150) after stimulus onset, respectively. Statistical comparison of the post-stimulus window (0 to 300 ms) against pre-stimulus baseline (-100 to 0 ms) via TFCE showed C4 and CP5 being significant for the P50 and a cluster of contralateral electrodes (C2, C4, CP2, CP4, P4, FP4, FP6) being significant for the N150. As most of these electrodes correspond to our initially selected electrode cluster, I kept the latter for all further statistical tests (accepting that those might be conservative estimates of the true effects).

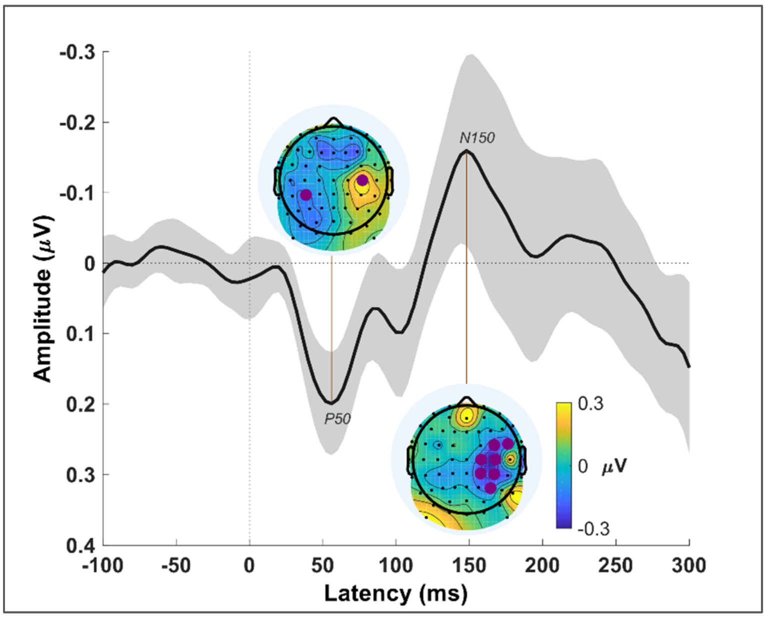

Figure 6 shows the grand-average SEP waveform across all stimulation conditions together with topographic voltage maps at component peaks of interest: P50 and N150. Shaded areas around the curve represent 95% confidence intervals of a running *t*-test for each time point against the averaged baseline. Purple-colored electrodes in the topographic maps mark significant voltage changes compared to baseline at the indicated time point tested with a non-parametric permutation test (10000 iterations) of the time window from 0 to 300 ms post-stimulus. Correction for multiple comparisons for achieved by tfce (Mensen & Khatami, 2013).

Undetectable stimulation (*d*-prime~0, both subTH-30%, and subTH-15%) elicited a P50 after stimulation, but no N150 (*Figure 7*). In contrast, above threshold stimulation evoked both components. Stimulation at ADTH did not result in measurable components, probably due to the small number of averaged trials at this comparably low stimulation magnitude and are therefore not reproduced here.

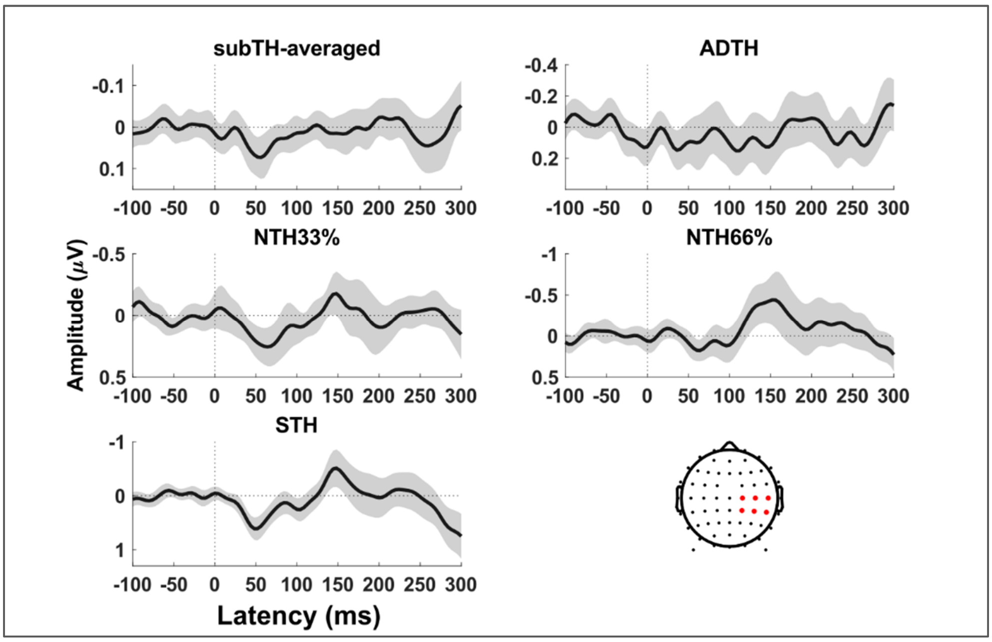

Figure 7. Grand average SEP waveforms for all stimulation conditions extracted from the averaged contralateral electrode cluster indicated by the bottom right plot in red. Shaded areas around the curve represent 95% confidence intervals of a running *t*-test for each time point against the averaged baseline. subTH-averaged: all trials with stimulus intensities below absolute detection threshold (ADTH) averaged. Note the different ordinate scaling, esp. the negative (i.e., upwards) direction when comparing the two near-threshold stimulation conditions (NTH33% and NTH66%).

Generally, both P50 and N150 component peak amplitudes were largest (i.e,. the N150 most negative) for the highest and lowest (N150 highest) for the smallest stimulation intensity, respectively. In *Figure 8,* sample means for each condition are plotted together with within-subject 95%-confidence intervals, so that significant differences are directly observable. Pairwise *t*-tests for all possible stimulation magnitude condition pairs revealed significant P50 amplitude differences (fdr-corrected) from both subthreshold intensities to all above threshold intensities (all $t(35) < -3.08$, $p_{fdr} < 0.01$). NTH33% P50 amplitude was marginally smaller ($t(35) = -2.06$, $p_{fdr} = 0.059$) and P50 amplitude of NTH66% was significantly smaller than P50 amplitude of STH ($t(35) = -4.17$, $p_{fdr} < 0.001$). No statistical difference was observed between the P50 amplitudes of the subthreshold stimulation conditions (subTH-33%-subTH-15%: $t(35) = -0.06$, $p_{fdr} = 0.95$) and the near-threshold conditions (NTH33%-NTH66%: $t(35) = 1.47$, $p_{fdr} = 0.17$).

Estimates of N150 amplitudes of the subthreshold stimulation conditions were not different from zero and significantly smaller than all other N150 amplitudes of the above threshold stimulation conditions (all $t(35) > 2.9$, $p_{fdr} < 0.01$). N150 amplitudes of above threshold stimulation conditions showed no significant difference (NTH33%-NTH66%: $t(35) = 1.94$, $p_{fdr} = 0.087$; NTH33%-STH: $t(35) = 1.8$, $p_{fdr} = 0.1$; NTH66%-STH: $t(35) = 0.09$, $p_{fdr} = 0.93$).

In two previous studies (Forschack et al., 2017; Nierhaus et al., 2015), we noticed a P50 latency shift for subTH-15% to STH stimulation intensities but did not explicitly test this difference. Here, a direct test of the two conditions revealed a small but significant effect of roughly 4 ms ($t(35) = 2.04$, $p = 0.049$, $p_{fdr} = 0.16$). Also, the P50 of the near-threshold stimulation intensities were significantly later than the P50 of the STH intensity. However, no test survived correction for multiple comparisons when all possible condition combinations were tested (NTH33%-STH: $t(35) = 2.56$, $p = 0.015$, $p_{fdr} = 0.075$; NTH66%-STH: $t(35) = 2.56$, $p = 0.015$, $p_{fdr} = 0.075$; all other: $-1.3 < t(35) < 1.4$). N150 latencies were not significantly different (all $-1.4 < t(35) < 1.7$).

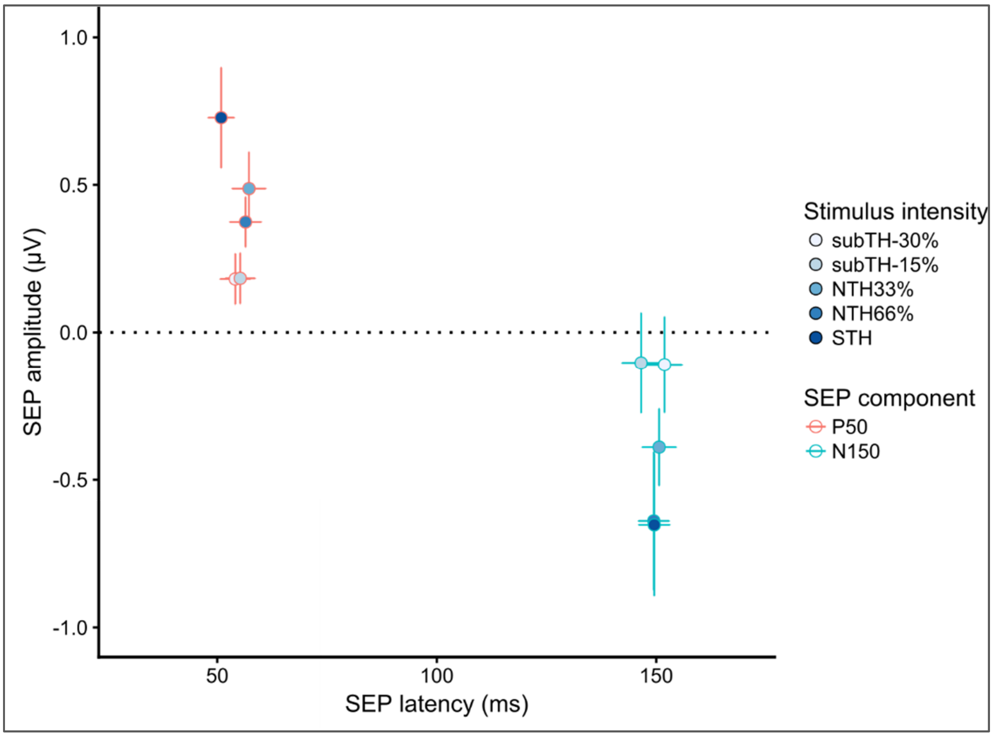

Figure 8. Individual peak SEP amplitudes and latencies have been extracted, and the sample average is produced here as colored circles for each stimulation condition. Circle outlines represent the SEP component of interest; circle fill corresponds to the stimulation condition. Estimates are plotted together with within-subject error bars (i.e., between-subject variance removed, according to Morey, 2008), both for amplitude (vertical bars) and latency (horizontal bars).

P50 amplitude is sensitive to stimulation intensity but not detection

To test the influence of stimulation intensity and detection on the early event-related potential, I modeled the P50 and N150 amplitudes following detected and rejected NTH66% and STH stimulation intensities in a repeated measures design. The ANOVA revealed a significant main effect of stimulation intensity on the P50 amplitude ($F(1,31) = 6.51$, $p = 0.016$, $\eta_G^2 = 0.028$), but interestingly, neither the effect of detecting a successive stimulus ($F(1,31) < 0.6$) nor the interaction of intensity and detection was significant ($F(1,31) < 2.3$). In contrast, both factors showed a pronounced effect on the N150 amplitude (stimulation intensity: $F(1,31) = 9.71$, $p = 0.004$, $\eta_G^2 = 0.028$, detection: $F(1,31) = 15.86$, $p < 0.001$, $\eta_G^2 = 0.15$). ERP average amplitudes and confidence intervals are reproduced in *Figure 9*. All conditions show a measurable P50. Except for undetected suprathreshold intensities, this is also true for the presence of the N150 as indicated by the bootstrapped confidence intervals.

Average stimulation currents across blocks differed significantly between detected and rejected trials for STH stimulation condition ($M_{detected} = 2.84$ mA, $M_{rejected} = 2.79$ mA, $t(31) = 3.53$, $p = 0.0013$, maximum difference: 0.23 mA, i.e., two step sizes of the constant current stimulator, median difference: 0.04 mA), but not for NTH66% ($M_{detected} = 2.43$ mA, $M_{rejected} = 2.42$ mA, $t(31) = 1.26$, $p = 0.22$, maximum difference: 0.17 mA, median difference: 0.01 mA).

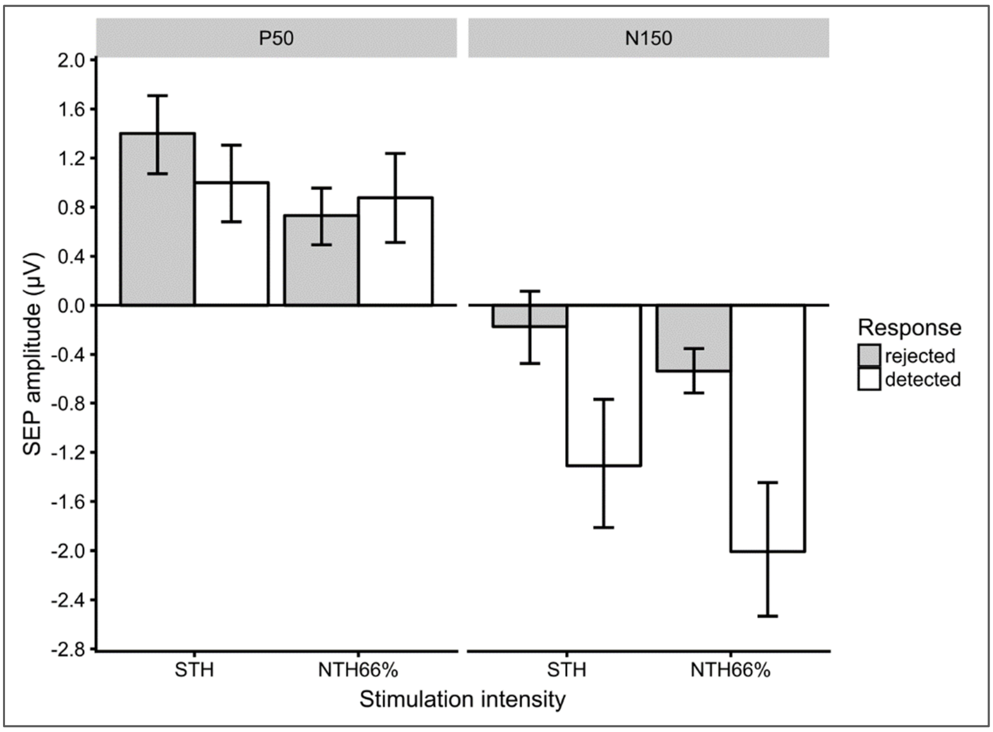

Figure 9. Average P50 and N150 amplitudes for the strongest stimulation intensities (NTH66% and STH) plotted for the factors stimulation intensity and behavioral response. Bootstrapped 95% confidence intervals, obtained by shuffling condition labels across participants 10000 times, indicate the presence of the component within the specific condition if not overlapping with the zero lines (i.e., the amplitude is significant from zero).

Pre-stimulus Rolandic alpha amplitude predicts stimulus detection

I assessed the overall effect of pre-stimulus frequency band amplitude (alpha band: 9–14 Hz, beta band: 20–35 Hz) on near-threshold stimulus detection by comparing the averaged STH and NTH66% stimulation conditions between detected and rejected stimuli at the contralateral central electrode cluster. As indicated in *Figure 10,* there was no significant difference in the beta band as in Schuber and colleagues (2008).

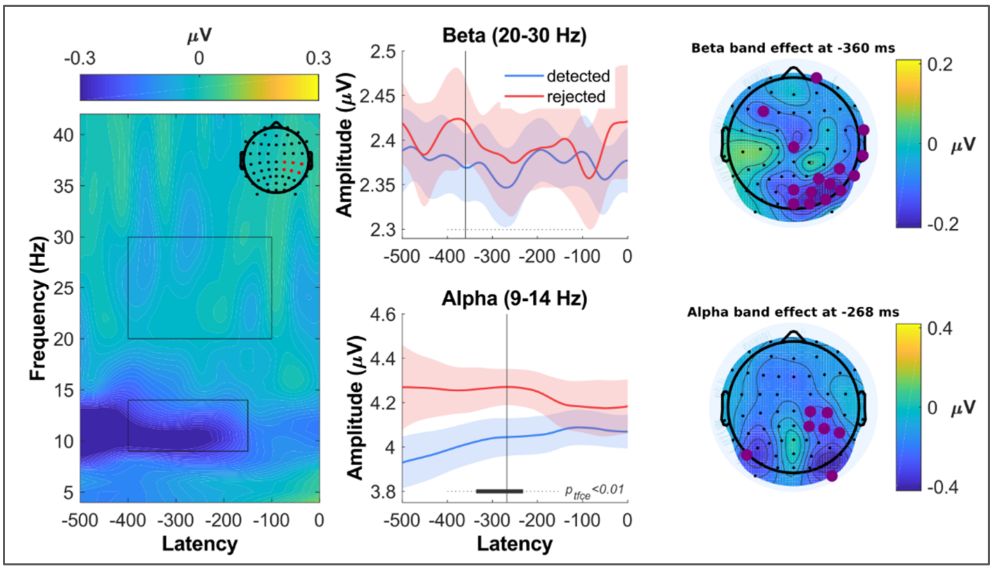

Figure 10. Pre-stimulus oscillatory amplitudes effects on subsequent stimulus detection for a contralateral central electrode cluster and a time window of interest according to Schubert et al. (2008). *Left*: Pre-stimulus time-frequency amplitude difference of averaged NTH66% and STH stimulation conditions at the averaged central contralateral electrode cluster highlighted as red dots in the topographic map inset. The black boxes mark the time-windows for subsequent statistical analysis of alpha- and beta band responses, respectively. Middle: Alpha- and beta band pre-stimulus time courses for detected and undetected upcoming near-threshold stimulation. Average values are plotted together with within-subject confidence intervals of detection-by-time repeated measures ANOVA according to Cousineau et al. (2005) and Morey (2008). The horizontal dotted line indicates a paired cluster based *t*-test, which is thresholded at $p = 0.01$ and corrected for multiple comparisons with tfce (Mensen & Khatami, 2013). The bold line depicts the period with amplitude differences exceeding this threshold. Vertical lines indicate the amplitude difference showing the smallest *p*-value, subsequently used for representing the topographic changes across all electrodes. Right: Topographic amplitude difference at the most prominent time frame for both alpha- and beta band. None of the electrode tests survived multiple comparison correction.

However, there is a definite alpha band amplitude difference with alpha being lower for successively detected stimuli as compared to undetected stimuli that survive multiple comparison correction at $p < 0.01$ for a time range that extended from -336 to -232 ms relative to stimulus onset (middle part of *Figure 10*).

Pre-stimulus alpha and N150 amplitude best explain stimulus detection

To assess whether further neural features despite amplitude are relevant for stimulus detection and rejection, I conducted regularized binomial logistic regression modeling including both P50, N150 amplitude and latency for various λ. *Figure 11* shows the predicted detection probabilities of the model with a lasso penalty having the smallest cross-validation error. This model only contains N150 amplitude as a predictor for stimulus detection and is accurate in 72.2% of the tested cases (*p* = 0.0001). Shrinking non-predictive coefficients excluded N150 latency and P50 amplitude and latency to zero.

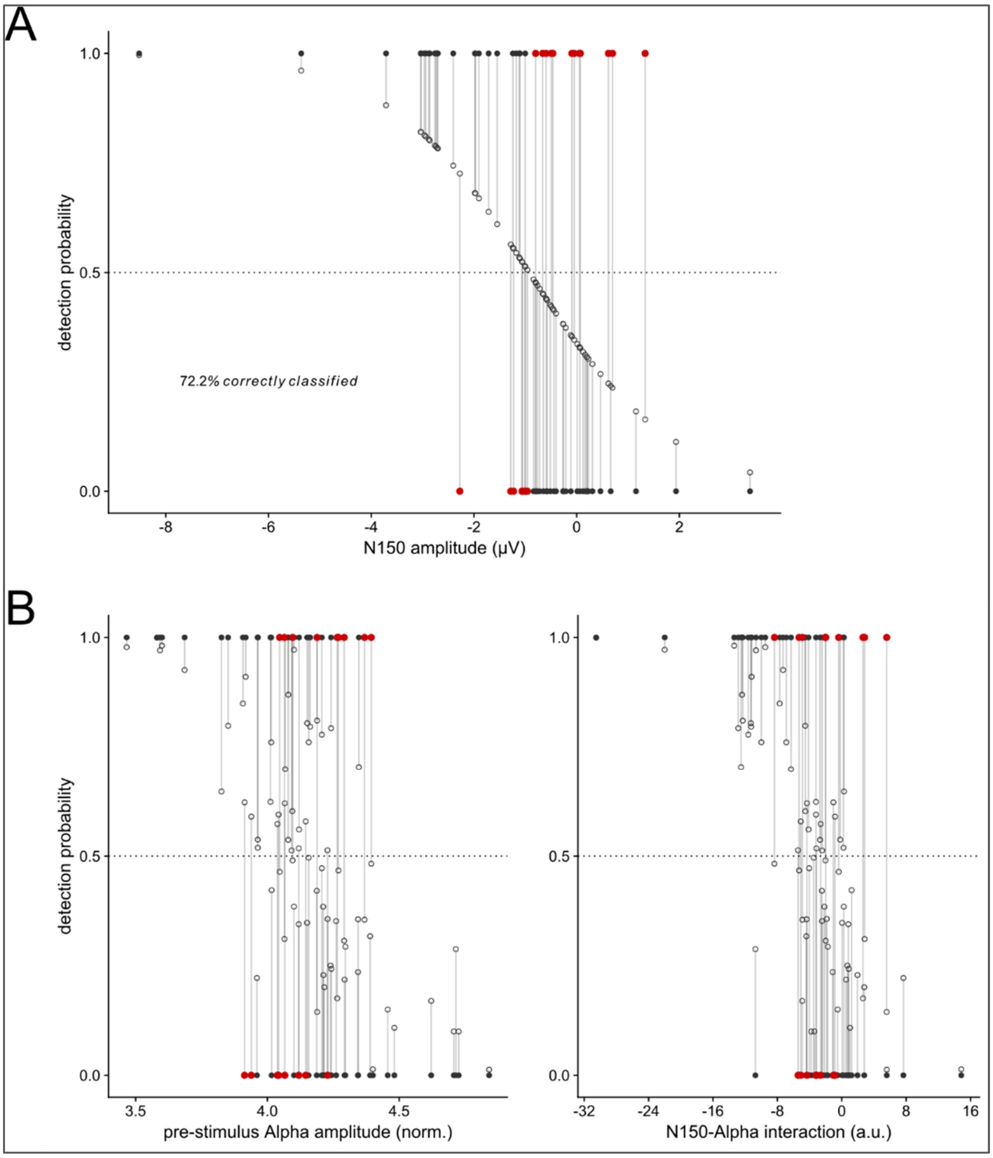

Figure 11. Detection probability predicted by the lasso regularized binomial logistic model showing the smallest cross-validation error (empty circles) together with the actual subject-level response data (filled circles) for averaged NTH66% and STH stimulus conditions. *A*: This model only contains N150 amplitude as a predictor for behavioral responses. Grey lines represent the model error, the shorter, the better. Black circles correspond to correctly and red circles to incorrectly classified responses. *B*: Winning model when including pre-stimulus contralateral alpha amplitudes averaged at 268 ms preceding detected and rejected stimuli. This model correctly classifies 76.4% of the cases. The between-subject variance was removed for alpha band amplitude values in order to center them along the behavioral response differences.

Because in the previous analysis, the pre-stimulus alpha amplitude is higher during rejected stimulation than during detected stimulation, I included alpha as a factor in the binomial regression model and allowed it to interact with P50 and N150 amplitude. Interestingly, the model with the smallest CVE was accurate in 76.4% of the cases and only contained alpha amplitude as a main predictor and alpha and N150 amplitude as interaction predictor. Alpha and N150 amplitude were significantly correlated by $r = 0.35$ ($p = 0.003$) thereby sharing 12.2% of the variance in the data.

Discussion

Using a two-response classification task for various stimulation intensities along the individual psychometric response function while recording EEG, I investigated, which early electrophysiological neural features are related to the encoding of stimulation intensity and decoding of stimulus detectability. Importantly, including stimulation intensities below absolute detection threshold (ADTH), allowed to ask the question how measures of undetectable stimulation (subthreshold) might dissociate from stimulation above ADTH that may or may not be detected. For the subthreshold stimuli, there was only a P50 component, but no further event-related potentials, thereby replicating previous research (Libet et al., 1967; Ray et al., 1999b; Nierhaus et al., 2015; Forschack et al., 2017). P50 amplitude scaled with increasing stimulation intensities but was not predictive for stimulus detection for each of the two highest stimulation intensities. A more negative potential 150 ms after stimulus onset (N150) together with pre-stimulus somatosensory alpha amplitude best explained perceptual awareness of somatosensory stimulation.

Stimulation intensity and awareness are highly collinear, i.e., higher stimulus intensities lead to enhanced perceptual evidence of having felt something. In the current experiment, participants received various stimulation intensities that were tuned to provide zero to high perceptual evidence (indicated by the detection rates and *d'* values). In the framework of classical test theoretic statistics, it is only possible to prove the latter but not the former, as this would require testing the NH (null-hypothesis Rouder et al., 2009). Therefore, I used a Bayesian statistical framework to test for zero perceptual sensitivity (ibid.) Bayes Factors supported that the probability of reporting to feel stimulation below ADTH is identical to make a false positive response upon null stimulation.

In contrast, for stimulation above ADTH, observers showed increasing perceptual sensitivity, the higher the stimulation intensity. Thus, the presence of the P50 does not provide sufficient evidence for perceptual awareness (Forschack et al., 2017; Nierhaus et al., 2015) but, together with the absence of the N150 component, appears to be a neural dissociation of perceptual processing for stimulation below ADTH from stimulation above it. For the latter, we still measured the N150 even for undetected NTH stimuli, again suggesting that its mere presence does provide sufficient evidence for perceptual awareness.

However, the N150 was not present for undetected stimulation at the highest intensity. On the one hand, this might be a result of the post hoc condition split into detected and rejected stimulation, for which the highest stimulation intensity is based on the smallest number of rejected trials, thereby reducing the likelihood of capturing a small potential. On the other hand, this could also mean that there is less chance of making a negative report (“rejected”) despite having perceived the stimulation, which could be related to individual response criteria.

Furthermore, we observed a roughly 10 ms earlier P50 peak latency from the largest to the second largest stimulation intensity. This shift cannot be explained by SNR differences, which could influence the smoothness of the potential curve and thereby affecting latency estimation, because this latency shift was most pronounced from the largest (STH) to the second largest stimulation intensity. At the physiological level, this latency shift might indicate a shifted excitation-inhibition balance toward a dominant rapid activation of principal excitatory neurons (Isaacson & Scanziani, 2011; Nierhaus et al., 2015). On a cognitive level, one might argue that the strongest stimulation condition may trigger exogenous attention more reliably than weaker stimulation intensities. Thus, ERPs evoked by attended stimuli show a shorter latency than ERPs evoked by unattended stimuli, which is known as Titchener’s law of prior entry (see Spence & Parise, 2010 for an overview).

So far, we discussed the effect of perceptual sensitivity and awareness on the presence or absence of the P50 and N150. However, sensitivity and awareness might be reflected within the component’s amplitude. Despite being positively dependent, our results suggest two independent mechanisms for encoding perceptual sensitivity and perceptual awareness within the event-related potential. First, P50 component amplitudes are sensitive to stimulus intensity but, second, only the N150 amplitude appeared to be distinctive for detecting a given stimulus. This finding seems highly relevant for studies investigating perceptual awareness when comparing detected versus rejected stimuli at intensities close to the 50% detection threshold. Some studies (Weisz, Wühle, et al., 2014; Wühle, Mertiens, Rüter, Ostwald, & Braun, 2010) used an ongoing staircase procedure throughout the experimental protocol to control detectability. Although this might be (probably) the best method when aiming at almost equal trial numbers for the detection contrast, it produces different stimulation intensities for trials in which stimulation was detected versus those trials in which stimulation was missed. By increasing stimulation strength in the successive trial after the participant reports not having felt the stimulus and decreasing it after a positive report, the ongoing staircase results in stimulation intensities higher for detected and lower for undetected stimulation, thereby conflating effects of stimulation intensity and perceptual report concerning ERP amplitudes. To control for stimulation intensity within a specific stimulation condition in the current study, I kept stimulation intensities constant for a given block; however, adjusted these between blocks to account for threshold shifts. Although electrical stimulation currents differed slightly for the STH condition between detected and rejected trials (ranging from less than one current step size of the DS7 to two current step sizes), there was no significant difference regarding the P50 amplitude, which is sensitive for stimulation intensity (see above). Furthermore, stimulation currents did not differ for the NTH66% condition, but the N150 nevertheless decreased for detected trials. Taken together these results strengthen the assumption that the STH electrical current differences were minor and unlikely to affect ERP amplitudes concerning the detectability of the stimuli.

Some previous research, however, found the P50 amplitude to be sensitive for stimulus detectability. Eimer and colleagues (2002) studied a patient who had a right-hemispheric stroke leading to a neurological disorder called extinction. The patient was able to recognize left unilateral stimuli to the index finger; however, such contralesional stimuli were missed—i.e., extinguished—on 75% of the trials when concurrently presented together with a stimulus at the right index finger. Contralateral ERP responses to these extinguished left stimulations contained a P50 and N110, which were not present at the same sites during unilateral right stimulation but were numerically smaller—however not statistically—as compared to (felt) unilateral left stimulation. Furthermore, unilateral contralesional left stimulation resulted in smaller components over the damaged hemisphere as compared to left hemisphere responses found after unilateral right stimulation. These results led to the hypothesis that extinction may arise from attenuation rather than the absence of early event-related components. Interestingly, components over the damaged hemisphere on bilateral extinguished trials were not different from felt unilateral left stimulation, suggesting that concurrent right tactile events might trigger competitive mechanisms that influence initial tactile processing. Modulations of P50 amplitude affecting perceptual awareness, therefore, could be less pronounced when stimuli are presented in isolation (Eimer et al., 2002), as it is the case for the current study.

Regarding the role of the N150 as a marker of stimulus detection, the current results are well in line with previous research (Auksztulewicz et al., 2012; Cauller & Kulics, 1991; Schubert et al., 2006; Zhang & Ding, 2009). However, none of these studies, including the current one, provide evidence for a proper neural correlate of consciousness (NCC, Aru et al., 2012), because all task paradigms will necessarily conflate perceptual awareness with decisional processes. It has been pointed out that a proper candidate component for NCC must not cease when participants passively perceive suprathreshold stimuli in the absence of a task (Hillyard et al., 1971; Squires, Hillyard, & Lindsay, 1973; Verleger, 2010). In our previous study (Nierhaus et al., 2015), we did find the N150 during electrical finger stimulation well above ADTH while participants had no task, which provides initial suggestive evidence for the N150 resembling an NCC proper (Aru et al., 2012). Future studies, however, should ideally include a passive and an active condition within one experiment while sampling intensities close to NTH50% threshold. To re-evaluate the effect of the P50 amplitude on perceptual awareness, these studies additionally might present concurrent contralateral tactile stimuli that trigger competitive early-stage processes and hence could increase the influence of P50 amplitude on the perceptual fate of near-threshold stimuli (Eimer et al., 2002).

Finally, the current study replicates a large body of previous research showing that pre-stimulus alpha amplitude is predictive for the detectability of an upcoming event (Chaumon & Busch, 2014; Iemi et al., 2017; Limbach & Corballis, 2016; Linkenkaer-Hansen et al., 2004; Ruhnau et al., 2014; Schubert, Haufe, et al., 2008; Weisz et al., 2014;

Zhang & Ding, 2009). Like these studies, I found that increased pre-stimulus alpha is related to negative behavioral responses regarding the presence of a stimulus. Specifically, there is a positive correlation between alpha amplitude and successive N150 amplitude. I.e., the larger the alpha, the closer the N150 to zero. This result is in line with the results by Zhang and Ding (2009) who reported an inverse u-shape relationship between pre-stimulus alpha amplitude and both N150 amplitude and detection rate. Here, I tested in a single model whether there are further electrophysiological markers despite pre-stimulus alpha and N150 amplitude predicting stimulus detection, as, e.g., ERP peak latencies and P50 amplitude and failed to see an effect. Future studies might prove whether these features become relevant when attention and stimulus competition are experimentally manipulated.

In conclusion, using Bayesian statistical inference, I fostered results from our previous studies that reliably undetectable stimulation, for which observers do not provide any sign of perceptual awareness, generates an early event-related potential, the P50. This component does not sufficiently predict upcoming stimulus detection but is driven by stimulation intensity. The successive N150 best explains behavioral responses and interacts with pre-stimulus oscillatory amplitude dynamics in the alpha band. Thus, alpha band amplitudes may describe a brain state that renders upcoming stimulation being reportable or not (Weisz et al., 2014). A thrilling question is whether the latter indicates the amount of attentional deployment to the sensory modality where a stimulus arrives and whether this still shapes the neural fate of undetectable and supposedly irrelevant stimulation. These questions are the central topic of the next and final study.

2.4 The role of Rolandic Alpha Activity in Somatosensation and its Relation to Attention

Based on
Forschack, N., Nierhaus, T., Müller, M. M., & Villringer, A. (2017). Alpha-Band Brain Oscillations Shape the Processing of Perceptible as well as Imperceptible Somatosensory Stimuli during Selective Attention

As discussed in section 1.4, selective attention is "a mechanism by which information relevant to a perceptual decision is filtered or weighted, in the service providing the observer with the most efficient and accurate interpretation of the local sensory environment" (Summerfield & Egner, 2014). Attention facilitates conscious perception across sensory domains (Schröger, Marzecová, & SanMiguel, 2015; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006), as indexed by its well-documented influence on evoked potentials, evoked fMRI/PET signals or oscillatory activity (somatosensory evoked potentials, SEP: Desmedt and Robertson, 1977; Zopf et al., 2004; Schubert et al., 2008b; visually evoked potentials, VEP: Eason et al., 1969; auditory evoked potentials, AEP: Hillyard et al., 1973; somatosensory fMRI: Johansen-Berg et al., 2000; Goltz et al., 2013, 2015; visual fMRI: Gandhi et al., 1999; auditory fMRI: Alho et al., 1999; PET: Wu et al., 2007; brain rhythms: Clayton et al., 2015).

However, attention processes do not necessarily depend on conscious percepts (Graziano, 2013; Kentridge, Nijboer, & Heywood, 2008; Koch & Tsuchiya, 2007). Attention effects on subliminal processing have been shown in the visual modality (Boxtel, Tsuchiya, & Koch, 2010; de Haan, Stoll, & Karnath, 2015; Watanabe et al., 2011), but based on paradigms involving masking or extinction. However, subliminal brain responses to masked stimuli have been shown to be interrupted by the brain responses of the mask (Fahrenfort et al., 2007; Victor A. F. Lamme et al., 2002), which may preclude observations unique to genuine processes below consciousness elicited by unmasked subliminal stimulation. Neural markers for cerebral processing of somatosensory stimuli below absolute detection threshold (i.e., stimulation is never reported: subthreshold) have been described previously. However, these were only based on invasive studies using subdural electrodes under clinical conditions (Libet et al., 1967; Ray et al., 1999a) limiting potential investigations. Recently, Nierhaus et al.

(2015) have identified an event-related potential in response to subthreshold stimulation (a positive deflection occurring about 60 ms after stimulation: P1). First, these findings allowed us to address the question whether attention also modulates neural processing of subthreshold, that is, undetectable, somatosensory stimuli as it has been suggested previously (Dehaene et al., 2006). Second, we examined the role of alpha-band brain oscillations activity to the effect of attention. While several studies conclude that attention decreases the amplitude of baseline (pre-stimulus) alpha rhythm (Anderson & Ding, 2011; Haegens, Händel, et al., 2011; Haegens, Nácher, Luna, Romo, & Jensen, 2011; Jensen, Bonnefond, & VanRullen, 2012; S. R. Jones et al., 2010; Palva & Palva, 2007), evidence for the relationship of pre-stimulus alpha power on the amplitudes of evoked potentials is ambiguous. Both linear (Nikouline, Wikström, et al., 2000; Reinacher, Becker, Villringer, & Ritter, 2009; Roberts, Fedota, Buzzell, Parasuraman, & McDonald, 2014) and non-linear relationships (Anderson & Ding, 2011; Zhang & Ding, 2009) have been reported. While the latter findings challenge the view of alpha activity directly reflecting cortical excitation (Foxe & Snyder, 2011; Jensen & Mazaheri, 2010), one might still argue that the variation of pre-stimulus alpha activity in spatial attention leads to a modulation of evoked activity (Haegens, Händel, et al., 2011; Haegens, Luther, et al., 2011; Jensen et al., 2012; S. R. Jones et al., 2010). Consequently, with attention, the highest P1 amplitudes should be accompanied by low pre-stimulus alpha power in the case of a linear relationship, or by intermediate power ranges in the non-linear case (Anderson & Ding, 2011).

This study investigated the role of pre-stimulus peri-Rolandic alpha, that is, sensorimotor alpha or simply mu, amplitude and its (modulatory) impact on central stimulus processing using EEG recordings and event-related potentials in humans. We presented subthreshold and—at a lesser number—irregularly intermingled suprathreshold single electrical current pulses to the index fingers of both hands during variation of spatial attention. Thus, we tested whether attention and alpha activity operate analogously both for subthreshold and suprathreshold stimuli. *Figure 12* illustrates potential functional relationships between attention, mu rhythm activity, and evoked brain activity.

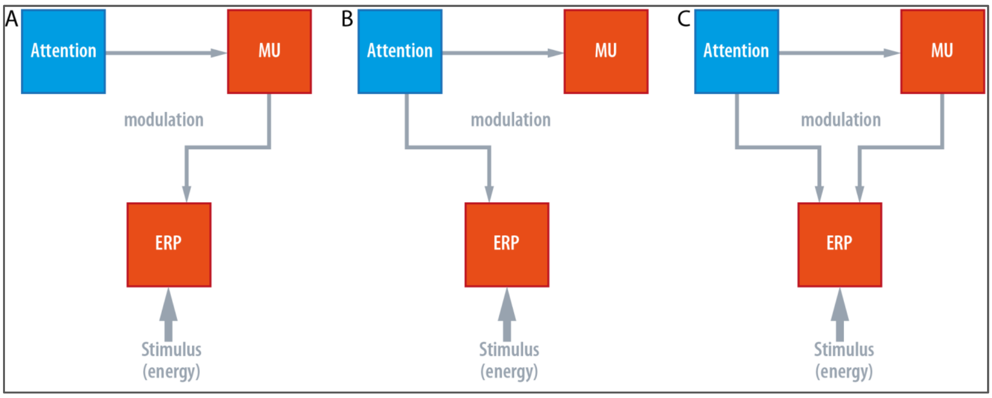

Figure 12. Three different models of possible relationships between attention, pre-stimulus somatosensory alpha (mu), and ERP/SEP amplitude. *A:* The mediator model: pre-stimulus mu mediates the effect of attention. *B:* Attention influences both pre-stimulus mu and SEP amplitude, but SEP modulation is independent of pre-stimulus mu amplitude (independence model). C, The interaction model: the relationship between pre-stimulus mu and SEP amplitude depends on the attentional state.

Methods

Participants

The local ethics committee at the medical faculty of the University of Leipzig approved the study. Before participation, all volunteers underwent a comprehensive neurological examination. They had no history of neurological or psychiatric diseases and were not on any medication. Forty healthy volunteers participated (age range 20–32 yrs, mean 25.1 ± 2.9 yrs S.D.; 20 females); all were right-handed (laterality score according to the Oldfield questionnaire: mean 91.6 ± 10.2 S.D., over a range of –100 (entirely left-handed) to 100 (entirely right-handed), (Oldfield, 1971). Data of three subjects were discarded due to defective or artifactual EEG recordings, so in total 37 datasets were analyzed.

Experimental Procedures

Somatosensory Stimulation and Task Design

A pair of steel wire ring electrodes was attached to the left and right index finger and delivered stimulation as described in section 2.1.1. A trained experimenter manually assessed ADTH, which—again—was defined as the lowest current intensity (for continuous 7 Hz electrical stimulation) at which participants just reported a sensation. A rough estimate of this detection threshold was derived by applying one trial of the method of limits with ascending intensities separately for the left and right index finger (just before the first block). In order to control for threshold stability and to readjust stimulus intensities in case of a threshold shift, we precisely determined (0.05 mA precision) absolute detection thresholds before each EEG acquisition block using a yes/no detection procedure (one-alternative forced-choice, 1AFC, Kingdom and Prins, 2009, not included in the EEG recording of ~8 min duration per block). Thus, the experimenter presented current intensities (at 7 Hz for one second each) around the previously estimated rough detection threshold (or the previous precise threshold for block numbers > 1) as well as catch/ blank trials (20% of all 1AFC trials) to control for potential response bias. From our experience, false alarm rates are mainly zero for this specific procedure, and this was also true for the current threshold assessments. Participants responded with "yes" if they felt a stimulus and "no" if otherwise. Intensities were selected adaptively, according to the participant's responses; for example, if an observer perceived a given stimulus, the intensity for the following trial was usually (but not necessarily) decreased and vice versa. However, occasionally a stimulus at a high intensity was presented reminding the observer what to "look" for. The range of applied intensities was also decreased successively until an intensity was identified which satisfied the above definition of an absolute detection threshold, that is, an intensity that enables a stimulus to be just discriminated from its null (Kingdom and Prins, 2009). For instance, if an observer reliably responded with "No" to a given intensity "x" but reported to perceive the next higher intensity "x + 0.05 mA" on a fraction of the trials, the latter intensity value served as detection threshold (30–60 trials which took maximally 5 minutes). To ensure imperceptibility of subthreshold stimuli during the entire experiment, subthreshold stimulation intensity (left finger) was set to 15% below absolute detection threshold and tested to be reliably imperceptible when presented as single pulses. The intensity of suprathreshold stimulation was adjusted within a range of 25 to 200% above detection threshold (*Table 3*) depending on the participants' subjective report of experiencing a clear (i.e., conscious) isointense but innocuous percept on both fingers. During experimental blocks, sub- and suprathreshold stimulation intensities were kept constant and subthreshold stimulation was applied to the left hand only (*Figure 13*). Participants were instructed to respond to perceived stimuli only to the cued hand (left or right) via button press with their right foot.

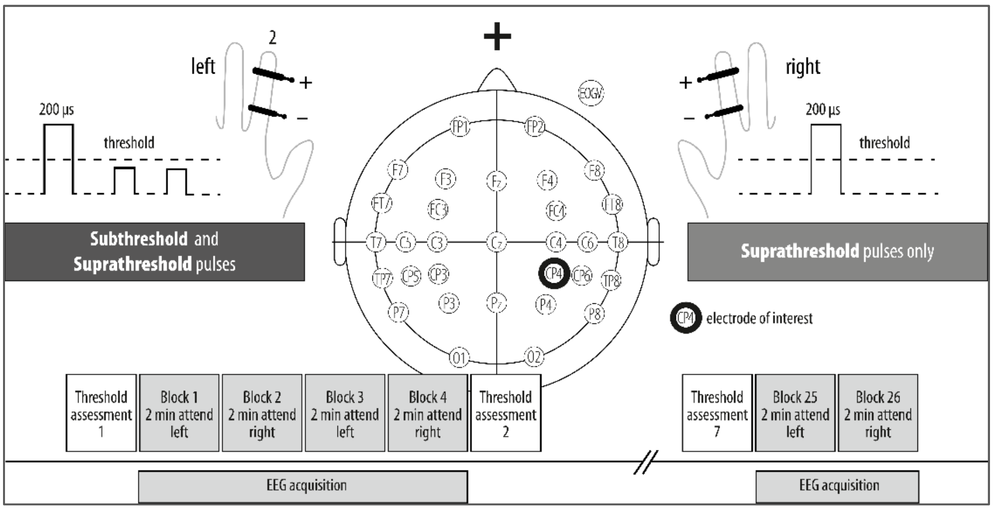

Figure 13. Experimental setup and stimulation paradigm. Forty subjects received 936 imperceptible electrical pulses to the left index finger via the DS7A (Digitimer) over 26 two-minute blocks. In each block, up to four perceptible stimuli were randomly presented to the left or right hand (in total 104). Absolute detection thresholds were determined initially using the method of limits (one ascending trial) and a subsequent yes/no adaptive detection task consisting of 30–60 trials (maximally 5 min, including blank/ catch trials) and subsequently every four measurement blocks.

Accordingly, the following stimulation conditions were presented during the experiment: subthreshold stimulation to the left hand that was either attended (“subthreshold left attended” condition) or unattended (“subthreshold left unattended” condition) and four conditions, in which suprathreshold stimulation to the left or the right hand was attended or unattended, respectively (“suprathreshold left attended”, “suprathreshold left unattended”, “suprathreshold right attended”, “suprathreshold right unattended” conditions). In the offline analysis, we only focused on left-hand stimulation (data on right-hand stimulation was not considered, *Table 3*).

Table 3. Stimulation conditions and parameters. The intensity of stimuli is given in milliampere (mA). ADTH, absolute detection threshold; M, Mean; SD, Standard Deviation.

	Stimulation left	**Stimulation right**
subthreshold	ISI 3.2 s, ±1.0 s jitter 936 stimuli, 36 per block 1.48 mA (M), 0.45 mA (SD) 15% below ADTH	-
suprathreshold	pseudo-randomized 52 stimuli, up to 4 per block 2.94 mA, 0.65 SD	pseudo-randomized 52 stimuli, up to 4 per block 3.05 mA, 0.66 SD

	28–200% above detection threshold: 79% (M), 41% (SD)	24–192% above perception threshold: 83% (M), 37% (SD)

EEG acquisition

During stimulation blocks, EEG was recorded continuously from 32 scalp channels (international 10-20 system; actiCap, BrainAmp, Brain Products, Munich, Germany): midfrontal electrode (FCz) as reference and a sternum electrode as ground with impedances ≤5 kΩ for all channels, sampling frequency 1 kHz, a low-pass finite impulse response filter (250 Hz) was applied before downsampling EEG time courses to 500 Hz.

To allow for reliable detection of SEPs and Rolandic rhythms, stimuli were presented at comparatively long interstimulus intervals, that is, subthreshold stimuli at a mean interstimulus interval of 3.2 s (jitter of ±1000ms during a block of ~2 min, in total 26 blocks, i.e., 936 trials per subject). Moreover, in each block no or up to four suprathreshold stimuli were presented pseudo-randomly to the left or the right hand (total 52 suprathreshold stimuli on either hand). Subjects were instructed to report the perception of stimuli only when presented to the cued side and to “ignore” stimuli to the non-cued hand. Finally, two additional blocks were appended comprising only suprathreshold stimulation of the left and right index finger without attention task (stimulation frequency every 1.6 ± 0.3 s, resulting in 360 trials, ~5 min block duration), so we obtained a sufficient number of trials with suprathreshold stimulation (for a criterion-guided independent component selection in later steps of the analysis procedure, see below).

EEG Data Analysis

Preprocessing

EEG data analysis was performed offline using custom-built Matlab scripts (Mathworks, Natick, MA, USA, RRID: SCR_001622) and toolbox algorithms from EEGLAB (Delorme and Makeig, 2004, RRID: SCR_007292). Individual datasets underwent an independent component analysis (ICA, infomax extended) both to remove sources of ocular and muscle artifacts (Delorme et al., 2012; Li et al., 2006) and to select components resembling mu activity sources. Before ICA, datasets were prepared by applying the following procedures: training datasets for ICA were high-pass filtered with 1 Hz, all blocks were concatenated, contiguous epochs of 1 s were extracted, screened for non-stereotypical artifacts and rejected if contaminated. Then, an initial ICA was performed that removed artifactual epochs semi-automatically using improbable data estimation on single and across all components (function "pop_jointprob," Delorme et al., 2007). The resulting datasets were submitted to a second ICA: The new set of components was visually inspected, artifactual components were identified (i.e., correlation with EOG channel higher than 0.8, blink or eye movement typical topographies and IC source activity, abnormal frequency spectrum, i.e., high frequency or line noise, focal topographies). Only the unmixing and sphering matrices of artifact-free components were forward-projected to the unfiltered datasets for the subsequent analysis steps.

SEPs

Epochs were defined ranging from -1200 to 2200 ms relative to stimulus onset (t=0), from which the individual epoch mean was subtracted. Those epochs, which exceeded the joint logarithmic probability of 4.5 or 2.5 SD within or across independent components, respectively, were discarded after manually reviewing the alleged artifactual epochs (Delorme et al., 2007). This resulted in an average number of 420 trials (+/-14 S.D.) for attending left subthreshold stimulation and 420 trials (+/-13 S.D.) for "ignoring" left subthreshold stimulation (i.e., attending right); 23 trials (+/-3 S.D.) for attending left suprathreshold stimulation and 24 trials (+/-2 S.D.) for ignoring left suprathreshold stimulation. In a next step, data was low-pass filtered applying the standard EEGLAB Hamming windowed sinc finite impulse response filter (zero-phase FIR, passband edge: 41 Hz, high cut-off (-6 dB): 46.125 Hz, filter order 162, Widmann et al., 2015). Trials with behavioral responses following or preceding subthreshold stimulation were very rare and excluded from further analysis (only eight participants responded to subthreshold stimulation once or twice out of 960 trials).

Topographical analysis via isocontour voltage maps 50 to 60 ms post-stimulation revealed that contralateral somatosensory areas were most sensitive to somatosensory stimulation in comparison to pre-stimulus baseline (paired t-tests, fdr-corrected). Therefore, statistical analysis of SEP amplitude was performed on electrode CP4 (i.e., in close vicinity to somatosensory cortex contralateral to stimulation site that has been also previously found to exert maximum SEP amplitudes, Nierhaus et al., 2015), by averaging the amplitude of time points 50 to 60 ms post-subthreshold stimulation (P60) and performing a paired two-tailed t-test ($p<0.05$) against baseline (-100 to -20 ms relative to stimulus onset, Zhang and Ding, 2009). The definition of a time range of interest was hypothesis-driven because previously we only found the P60 and no additional components to be indicative of subthreshold somatosensory processing (Nierhaus et al., 2015). A known marker for early attention modulation of suprathreshold stimulation, the P50–N80 complex (Michie, Bearparic, Crawford, & Glue, 1987), was extracted by subtracting averaged amplitudes around 80 to 100 ms (N80) from averaged amplitudes around 50 to 60 ms (P50) post-stimulus. As for the P60, the amplitude of the P50N80 complex was tested between attention conditions using a paired t-test against the baseline. In order to test for the presence of further evoked potentials, each sample point of a 400 ms post-stimulus epoch was successively compared with the mean pre-stimulus baseline value (paired t-tests ($p<0.05$), multiple comparisons correction with fdr, not shown).

Rolandic Rhythms

In order to discern Rolandic rhythms from dominating occipital alpha activity, a preselection of "central" ICA components was performed before trial segmentation. For this purpose, all blocks (including the pure suprathreshold stimulation blocks) were concatenated to run a subject wise ICA. As in Nierhaus et al. (2015), we selected Rolandic background rhythms according to three criteria for each subject: (1) a central localization, (2) two peaks in the power spectrum, at alpha (8–15 Hz) and beta (16–30 Hz) frequency bands, respectively, and (3) a pronounced power reduction of these bands after suprathreshold stimulation. Using this procedure, 1–4 (mean 2 ± 1 S.D.) ICs per subject were selected (all 37 participants showed at least one right hemispheric lateralized mu component, 24 showed a left-lateralized mu component additionally). Only these components were forward projected and included in the further analysis of somatosensory oscillatory activity. After forward projection of the "central" ICs and segmentation of sub- and suprathreshold epochs as defined above (-1200 to 2200 ms), wavelet analysis was performed for frequencies from 6–30 Hz in 1 Hz increments to allow for time-resolved frequency analysis of event-related power modulation. The wavelet transformation was performed on every single trial using wavelet cycle lengths from 4 to 7 cycles increasing with frequency in linear steps. Subsequently, the resulting time-frequency response was averaged over trials.

Statistical analysis was performed on electrode CP4 (located over SI contralateral to the stimulation site on the left hand and also showing maximal weights in independent component maps) by means of two-tailed paired t-tests of post-stimulus time points against frequency specific baseline average (p-level was fdr-corrected with q=0.05, Genovese et al., 2002, with a pre-stimulus baseline of -700 to -200 ms). In order to test the condition contrast across post-stimulus values, we compared baseline-normalized alpha band values (8–15 Hz) for attended and unattended sub- and suprathreshold stimulation conditions (fdr-corrected).

Regression of SEPs and behavior on pre-stimulus mu amplitude

In order to test the relationship between oscillatory brain state (mu amplitude) and stimulus processing (SEP amplitude and hit rates), we pooled trials across attention conditions on subject level and calculated the average mu amplitude (estimated by a 10 Hz wavelet kernel with 4.9 cycles) for each trial 300 to 200 ms prior to stimulus onset. These values were reordered from smallest to largest amplitude and assembled into five consecutive bins (indexed by 1 to 5) with 50% overlap of trials for successive bins. Afterward, we separated the trials in each bin according to the attention condition. This binning procedure serves as normalization and compensates for inter-individual differences in absolute mu amplitude. Importantly, this also yields comparable mu amplitudes between attention conditions for any of these bins (tested via two-way repeated measures ANOVA with factors power bin (5 levels) and attention (2 levels) and mu amplitude as the dependent variable). Effect sizes were quantified as generalized eta squared (Bakeman, 2005). It has to be noted, however, that the number of trials within each bin may differ between attention conditions, which was tested by paired t-tests (average number and SEM of trials per bin 1–5 for subthreshold attended: 143 (9), 143(9), 140 (8), 139 (8), 137 (10); subthreshold unattended: 138 (10), 137 (9), 140 (7), 141 (7), 144 (9); suprathreshold attended: 8 (2), 8 (1), 8 (2), 8 (2), 7 (2); suprathreshold unattended: 8 (1), 8 (2), 8 (2), 8 (2), 8 (2); significant between attention condition trial number differences: subthreshold bin 2 ($t(36)=2.05$, $p=0.048$); subthreshold bin 5 ($t(36)=-2.3$, $p=0.027$); remaining tests yield absolute t-scores < 1.8). We then calculated the sub- and suprathreshold SEP for each bin and attention condition, and extracted the amplitude of the key component (P1) as described above in the section *SEPs*. Bin-wise hit rates (HR) were calculated for the suprathreshold left attended condition.

To assess the grand-average relationship between SEP amplitude and pre-stimulus mu amplitude for each attention condition, we calculated a standard linear regression with mu amplitude bins serving as predictor (quadratic and linear, including an intercept, i.e., the ordinate (SEP amplitude) offset) and bin SEP amplitude (and HR) serving as regressor (in fact, there are five values that the predictor can attain). However, this approach has some substantial drawbacks as it obscures inter-subject variability. Factors like vigilance regulation patterns (Bekhtereva et al., 2014), individual behavior adjustments, threshold variations, which are deemed to be random across the sample, may influence the relationship between experimentally relevant factors. With linear mixed effects modeling (LMM), we acknowledge between- and within-subject variations in the data from the model's fixed effects estimates (i.e., the grand average effect). We conducted the LMM analysis in R (R Core Team, 2014), RRID: SCR_001905) within the lme4 framework proposed by Bates et al. (2014). For our LMM fixed effects, we estimated intercept and weights for a quadratic and linear mu amplitude predictor just as for the standard regression in the fixed effects part (i.e., the grand average relationship, inter-subject variation ignored).

Additionally, the same predictor structure was used for the random effects part of the model with "participant" as the grouping variable. This has the advantage of (1) being the maximal random effect structure required for hypothesis testing as claimed by Barr et al. (2013), and (2) it yields subject-specific deviation predictions from the fixed effects within a single model estimation instead of multiple by-participant ordinary regressions (Baayen, Davidson, & Bates, 2008; Zhang & Ding, 2009). LMMs are defined in the following form: outcome ~ predictor(s) + (predictor(s) | subject), which will fit predictors of the fixed effect part (next to the "~") and predictors of the random effects part (in brackets) grouped by a factor for which the predictors vary randomly, in our case, subject.

All in all, we computed four LMMs which regressed SEP amplitude on pre-stimulus mu amplitude bin separately for each attention (attended, unattended) and stimulation condition (P1 amplitude for subthreshold and suprathreshold stimulation) and one LMM in which hit rate was the dependent variable. To check the significance of each of the five models and the relevance of specific predictors, maximum-likelihood ratio test statistics (which account for model complexity) between the complete (all predictors) and reduced models (one model assuming no relationship—i.e., only the intercept serves as predictor—and one model assuming a linear relationship, see *Table 4* for detailed model definitions) were parametrically bootstrapped with 10000 simulations (pbkrtest-package by Halekoh and Højsgaard, 2014). All these models describe the relationship between mu amplitude and SEP amplitudes (and HR) but do not consider the subjective attentional state (see next paragraph), because fitting was done separately for each attention condition.

Assessment of the relationship between pre-stimulus mu amplitude, somatosensory evoked potential, and attention

How does attention affect pre-stimulus mu amplitude and SEP amplitudes? Is a putative attention effect on SEP amplitude mediated (or indexed) by pre-stimulus mu? Does attention affect both pre-stimulus mu and SEP amplitudes independently? Alternatively, do responses of these variables depend on each other, or, in other words, do they interact? In order to evaluate these questions, we tested three different types of possible relationships depicted in *Figure 12*. For this purpose, following LMMs were fitted to data including both attention conditions, not separately as in the previous paragraph.

If the influence of attention is solely mediated by pre-stimulus mu amplitude (*Figure 12a*, “mediator model”), any form of relation between pre-stimulus mu amplitude and SEP amplitude will not be differentiable between the two attention conditions. Therefore, we fitted two LMMs to sub- and suprathreshold SEP amplitudes (dependent variable) with intercept, linear, and quadratic predictor of pre-stimulus mu amplitude both for fixed and random effects grouped by subject (in fact the same model definition as for single attention condition fits above), neither of which including attention as predictor in the fixed nor random effects part. In other words, it is assumed that the attention effect on SEP amplitude is completely reflected in the variation of pre-stimulus mu amplitude.

However, if the effect of attention on SEP amplitudes is independent of an attention effect on pre-stimulus mu amplitude (*Figure 12b*, “independence model”), a significant relationship between pre-stimulus mu amplitude and SEP amplitudes will not be observable. Here, the two LMMs fitted sub- and suprathreshold SEP amplitudes with the factors intercept and attention in the fixed effects part and intercept grouped by subject and attention as a within-subject factor in the random effects part (see *Table 4* for detailed model definitions). In short, the relationship between pre-stimulus mu amplitude and SEP amplitudes would appear to be flat, but SEP amplitudes between attention conditions would differ. (Note that an absence of significant relationships of any sort for the single attention conditions (see the previous section) would support the independence model).

Finally, if the type of relationship between pre-stimulus mu amplitude and SEP amplitudes essentially depends on the subjective state of attention (*Figure 12c*, "interaction model"), we will observe different relationships for each attention condition. The LMM definitions to fit sub- and suprathreshold SEP amplitudes, therefore, include the factors intercept, attention, the linear and quadratic mu amplitude predictor, as well as the interaction of the latter and attention in the fixed effect part. The random effects part contains intercept, the linear and quadratic mu amplitude predictor grouped by subject, as well as attention as a within-subject factor (see model definitions in *Table 4*).

Models were evaluated by their ability to explain the data, here maximum-likelihood, and significance was assessed via parametric bootstrapped likelihood ratio tests (10000 simulations).

Results

We stimulated the left and right index finger with electrical pulses (*Table 3*) while participants responded to perceived sensations only on the cued side and ignored sensations on the other side (*Figure 13*), thus characterizing the effects of attention on central somatosensory stimulus processing.

Behavioral responses

The resulting average hit and false alarm rates for suprathreshold stimulation of attended left (hit rates: 71.06 +/-17.88% S.D, false alarm rates: 0.82 +/-0.17% S.D.) and right index finger (hit rates: 73.76 +/-17.59% S.D., false alarm rates: 0.66 +/-0.11% S.D.) did not differ significantly ($-1<t(36)<1$ in all cases). The average number of responses to subthreshold stimulation for both attention conditions was negligible (two subjects responded twice, six subjects responded once out of 480 subthreshold trials).

Responses to sub- and suprathreshold stimulation evolves differentially over time for SEP and sensorimotor alpha and beta band power

SEPs in response to left-hand somatosensory stimulation were lateralized to the right hemisphere. As in our previous study (Nierhaus et al., 2015), we restricted our analysis to the contralateral hemisphere because only the left index finger received both sub- and suprathreshold stimulation. Depending on stimulation intensity (i.e., either above or below detection threshold), we observed different evoked components: for suprathreshold stimulation, a P50 was followed by an N80 and at least one following component (P150). For subthreshold stimuli, we observed a single early positivity around 60 ms, roughly 10 ms later than the first component for suprathreshold stimuli (*Figure 14*).

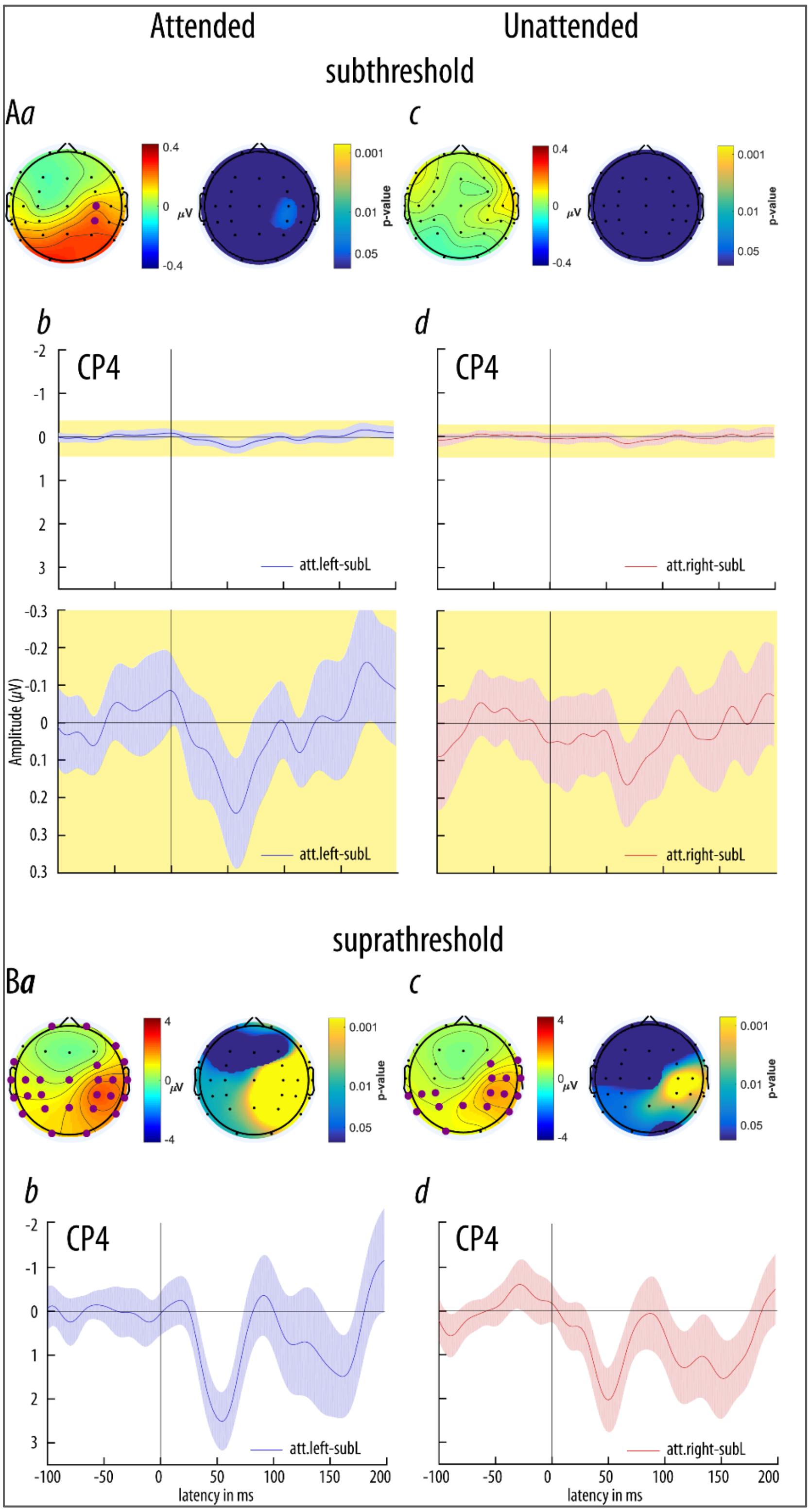

Figure 14. **Subthreshold (*A*) and suprathreshold (*B*) isocontour voltage maps and SEPs. *Aa*, Average voltage topographies for a window of 50–60 ms poststimulus (grand average, GAVG, n=37 participants) for the subthreshold left attended condition on the left and topographical *p*-value**

distribution on the right side (*t*-tests against a baseline -100 to -20 ms pre-stimulus, fdr-corrected). Nonsignificant electrodes (*p*>0.05) are masked in dark blue, significant electrodes are emphasized by large purple discs in the voltage plot. *Ab*, Grand average SEPs at channel CP4 for the subthreshold left attended condition. The bottom plot shows the SEPs on a zoomed scale for the yellow shaded area of the top plot. Time is expressed relative to stimulus onset (0 ms). Lightly shaded background areas indicate 95% confidence intervals derived from paired *t*-tests of each data point against average baseline activity. *Ac*, *Ba*, and *Bc* are the same as *Aa,* but for the subthreshold left unattended, suprathreshold left attended and suprathreshold left unattended conditions, respectively. Note the different scaling of the ordinate for suprathreshold stimulation. *Ad* is the same as *Ab* but for the subthreshold left unattended condition. *Bb* and *Bd* are the same as *Ab* and *Ad* but for the suprathreshold left attended and suprathreshold left unattended conditions, respectively. Note the different scaling of the ordinate.

Regarding mu amplitude, we found opposing effects: a decrease—as compared to baseline—after suprathreshold stimulation and an increase after subthreshold stimulation, which confirms our previous findings (Nierhaus et al., 2015). It is noteworthy that in the condition where the left index finger was *unattended* (attention directed to the right hand), an early increase of mu amplitude (13–15 Hz) and a decrease of beta amplitude (20–23 Hz, around 150–200 ms) following subthreshold left index finger stimulation was prevalent (t-test, fdr-corrected with $p<0.05$). When the left index finger was *attended*, an increase in mu amplitude (9–10 Hz) and a concomitant decrease in beta amplitude (20–24 Hz) occurred—approximately 200 to 300 ms later (fdr-corrected, $p<0.05$; *Figure 15*). When directly comparing the stimulation effect of the averaged somatosensory alpha band (8–15 Hz) between attention conditions, this temporal dissociation was not significant (fdr-corrected).

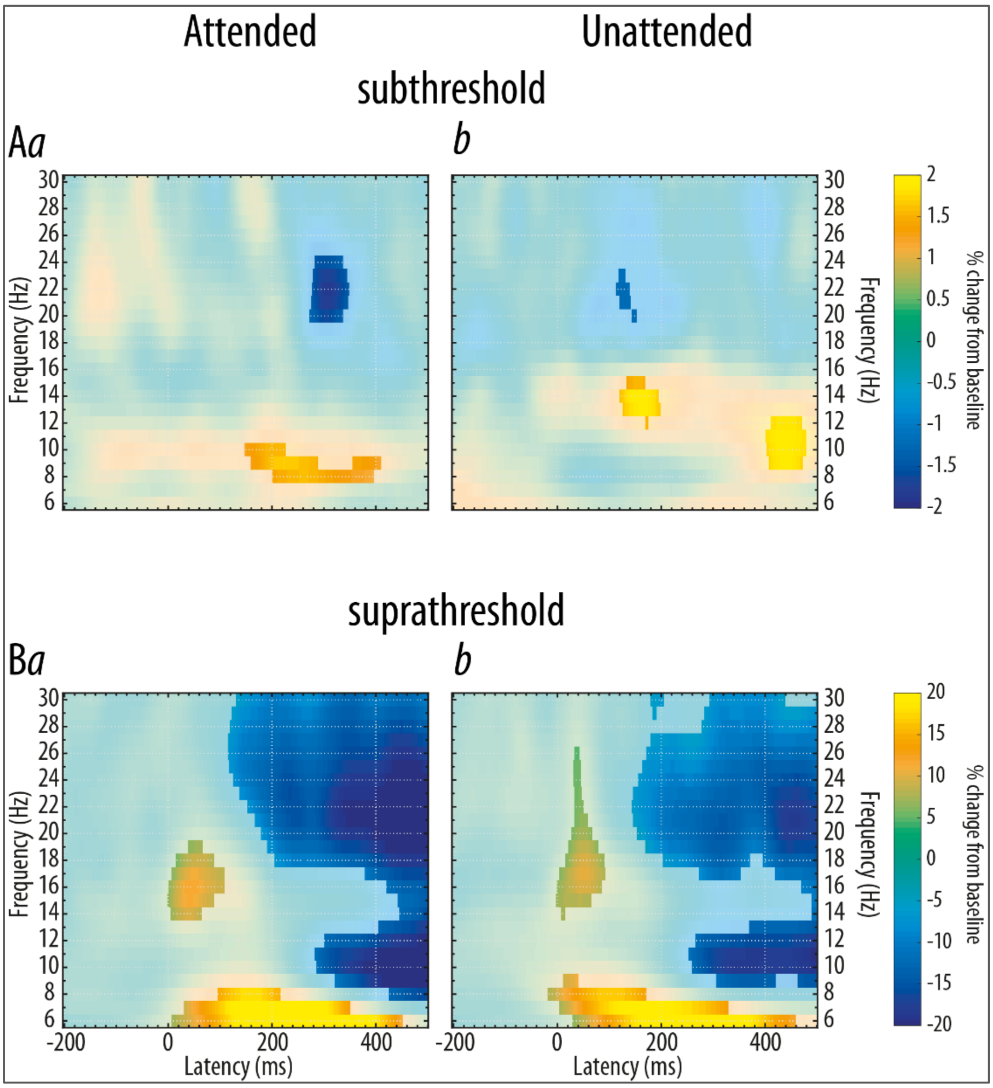

Figure 15. Subthreshold stimulation increases, suprathreshold stimulation decreases Rolandic rhythms. Grand average time-frequency plots (contralateral to stimulation side at CP4) for subthreshold (*Aa* and *Ab*) and suprathreshold (*Ba* and *Bb*) stimulation after selection and forward projection of pericentral independent mu components. Time is expressed relative to stimulation onset; oscillatory activity is expressed relative to baseline amplitude (baseline: -700 to -200 ms pre-stimulus). Light colored areas did not survive fdr-correction for multiple comparisons at *q*=0.05 (Genovese et al., 2002).

Sub- and suprathreshold SEPs and pre-stimulus mu amplitude are modulated by selective spatial attention

We tested the main effect of attention on SEPs for averaged amplitudes 50–60 ms post-stimulus. Subthreshold stimulation evoked a P1 at posterior peri-central electrode sites (CP4) that was significantly enhanced when the finger was attended compared to when it was unattended (*Figure 16a*, $t(36) = 2.21$, $p < .04$). This confirms our first hypothesis that attention modulates neural processing of subthreshold, that is, unconsciously “perceived,” somatosensory stimuli.

For suprathreshold stimulation, we subtracted averaged amplitudes around 80 to 100 ms (N80) from averaged amplitudes around 50 to 60 ms (P50) post-stimulus onset. The P50–N80 complex (i.e., the peak between P1 and N1) was significantly increased during the attended as compared to the unattended condition (*Figure 16a*, $t(36) = 2.22$, $p < .04$).

As expected, attention modulated overall mu amplitude preceding stimulation, with higher amplitudes contralateral to the unattended side (*Figure 16b*, $t(36) = -2.34$, $p < .025$).

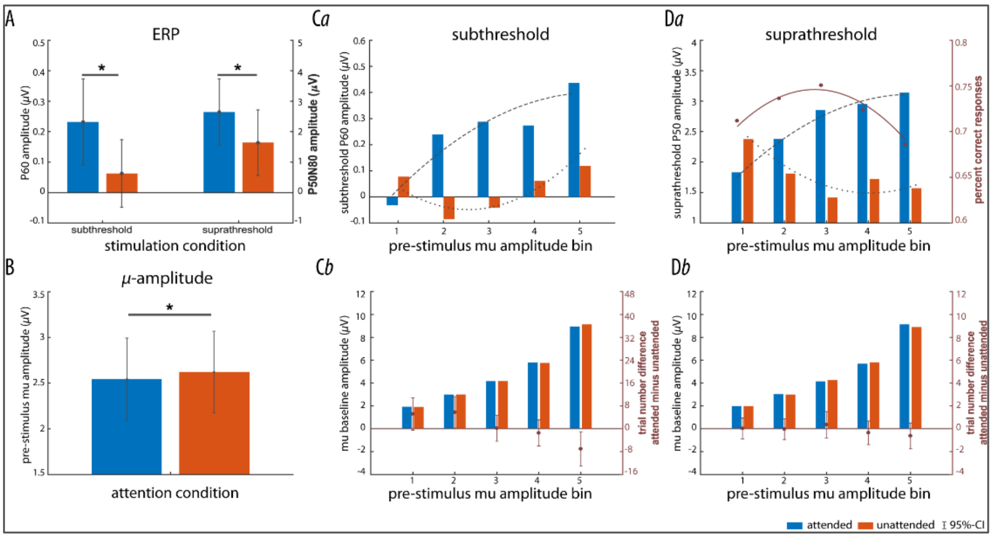

Figure 16. For all subplots, blue and red bars depict the attended and unattended conditions, respectively. *A*: Subthreshold (left) and suprathreshold (right) SEPs and (*B*) grand-average attention effect for pre-stimulus mu amplitude (-1000 to -200 ms). Error bars indicate 95% confidence intervals of the mean. Asterisks indicate significance at $p<0.05$. *C*, Subthreshold stimulation: relationship between pre-stimulus mu and SEP amplitudes (*Ca*) and pre-stimulus mu amplitude values averaged across trials within each bin (-300 to -200 ms; *Cb*). *D*, Suprathreshold stimulation: same as *C* but for the suprathreshold left attended condition. *Da*, Additionally, red dots show the average hit rates for each mu amplitude bin and the solid red line depicts the fit of the LMM for the suprathreshold left attended condition. Overlaid dashed and dotted lines in *Ca* and *Da* are fits of the LMM for respective SEP amplitudes. Red dots (with 95% confidence intervals) in *Cb* and *Db* depict the difference in an absolute number of trials of each mu amplitude bin between attention conditions.

The relationship between pre-stimulus mu and SEP amplitude depends on attention

To investigate the relationship between pre-stimulus mu amplitude (pre-mu) and SEPs and hit rates (HR), we aggregated trials for each attention and stimulation condition (attended or unattended and sub- or suprathreshold) separately over five bins of increasing mu amplitude. The procedure resulted in mu amplitude bins with comparable (almost equal) mu amplitude between attention conditions within a given bin (*Figure 16cb+db*, see methods section for details). The repeated measures ANOVA for binned mu amplitude preceding subthreshold stimulation reveals a significant main effect of both amplitude bin and attention ($F(4,144)=1489.6$, $p[GG]<0.0001$, $\eta^2_G=0.44$ and $F(1,36)=6.7$, $p<0.014$, $\eta^2_G=0.00003$, respectively). Post-hoc comparisons via paired t-tests identified the bin with the highest mu amplitude as the driver of the attention main effect ($t(36)=-2.86$, $p<0.01$). A similar ANOVA, testing binned mu amplitude preceding suprathreshold stimulation, only showed the expected main effect of amplitude bin ($F(4,144)=1264.5$, $p[GG]<0.0001$, $\eta^2_G=0.44$). Average bin amplitude values are therefore comparable between attention conditions (except for bin 5 preceding subthreshold stimulation).

In order to test the relationship between pre-stimulus mu amplitude and SEP amplitude, we calculated a linear mixed effects model (LMM) regression fits with both linear and quadratic predictors for each stimulus and attention condition. For suprathreshold stimulation, regressions both for attended and unattended stimulation turned out to be highly significant compared to an intercept-only model (i.e., a model with no relationship assumed, attended: $\chi^2=26.01$, $p=0.0001$; unattended: $\chi^2=46.04$, $p=0.0001$, see models 9 and 12 in *Table 4*). As can be seen in *Figure 16da*, the relationship for the attention conditions is reversed: We find a negative quadratic relationship when the stimulated finger is attended and a regular (positive) quadratic relationship when it is unattended. For subthreshold stimulation, we again observe a significant negative quadratic relationship when the stimulated side is attended ($\chi^2=22.25$, $p=0.0013$, see model 3 in *Table 4*), and a positive quadratic relationship when the stimulated side is unattended ($\chi^2=30.03$, $p=0.0002$, see model 6 in *Table 4*).

Table 4. LMM testing the relationship between pre-stimulus mu amplitude bin and SEP amplitude for each attention condition separately (model no. 1–12). The likelihood depicts the models' log transformed likelihood; bigger is better, i.e., the model is more likely. LRT is the likelihood ratio test comparing two models for the same dataset [Bigger models (more parameters) are compared with respective smaller ones]. This returns a χ^2 value. However, *p* values are based on parametric bootstrapping (10,000 simulations; Halekoh and Højsgaard, 2014): *<0.05– 0.01, **<0.01– 0.001, *<0.001– 0.**

Condition	Model No.	Lmer syntax	Likeli-hood	LRT
Subthreshold attended	(1) (2) (3)	P60~1+(1|Subject) P60~1+Bin+(1+Bin|Subject) P60~1+Bin+I(Bin^2)+ (1+Bin+I(Bin^2)|Subject)	-177.49 -170.52 -166.37	 χ^2=13.94** χ^2=8.31*
Subthreshold unattended	(4) (5) (6)	As (1), (2), (3), respectively	-176.32 -170.67 -161.3	 χ^2=11.29** χ^2=18.73***
Suprathreshol attended	(7) (8) (9)	P50~1+(1|Subject) P50~1+Bin+(1+Bin|Subject) P50~1+Bin+I(Bin^2)+ (1+Bin+I(Bin^2)|Subject)	-439.65 -434.98 -426.65	 χ^2=9.34* χ^2=16.7**
Suprathreshold unattended	(10) (11) (12)	As (7), (8), (9), respectively	-458.01 -452.7 -435	 χ^2=10.7** χ^2=35.34***

We also evaluated the relationship between pre-stimulus mu amplitude and hit rates for the suprathreshold attended condition, as this is the one condition in which subjects responded to perceived stimuli via a button press. As for the SEPs in the previous section, we found a significant quadratic relationship compared to the no-relationship (intercept-only) model (χ^2=42.44, *p*=0.001, see *Table 5* also including the test against a pure linear model).

Table 5. LMM testing the relationship between pre-stimulus mu amplitude bin and HR for the suprathreshold left attended condition (model no. 13–15). Models are evaluated as in *Table 4* (bootstrapped p values are based on 10,000 simulations): *<0.05–0.01, **<0.01–0.001, *<0.001–0.**

Condition	Model No.	Lmer syntax	Likeli-hood	LRT
Suprathreshold attended	(13) (14) (15)	HR~1+(1|Subject) HR~1+Bin+(1+Bin|Subject) HR~1+Bin+I(Bin^2)+ (1+Bin+I(Bin^2)|Subject)	73.02 82.8 94.23	 χ^2=19.57*** χ^2=22.87***

In order to test whether the variation of pre-mu solely reflects tactile attention, we fitted the data combining both attention conditions (*Figure 12a*, the mediator model, see paragraph ”Assessment of the relationship between pre-stimulus mu amplitude, somatosensory evoked potential and attention” for details) with the very same model definition as above. For the case where the effect of attention on SEP amplitudes is independent of the effect on pre-mu activity (*Figure 12b*, independence model), we only included “attention” as fixed effect factor and within-subject factor in the random effects part in order to model SEP amplitudes across attention condition. Alternatively, if the relationship between pre-stimulus mu amplitude and SEP amplitude essentially depends on the actual attention state (*Figure 12c*, interaction model), a model with attention included as an interacting factor should better fit the very same dataset. Indeed, a bootstrapped likelihood ratio test revealed the attention interaction model to be significantly more likely than both the mediator and the independence model for both sub- and suprathreshold stimulation (*Table 6*; subthreshold: χ^2=50.22, p=0.0016 and χ^2=45.41, p=0.0001; suprathreshold: χ^2=56.94, p=0.024 and χ^2=51.4, p=0.0006, respectively).

Table 6. LMM testing the relationship between pre-stimulus mu amplitude bin and SEP amplitude for datasets that combine both attention conditions (model no. 16 –21; *Figure 12 A–C*). The interaction model is compared with the two smaller models (mediator model and independence model, indicated by the model number given in the LRT column). Parametric bootstrapping was based on 10,000 simulations: *<0.05–0.01, **<0.01–0.001, *<0.001–0. [a] For this test, we doubled the number of simulations, because the *p*-value based on 10,000 simulations marginally missed significance (*p*=0.058).**

Condition	Model No.	Lmer syntax	Likelihood	LRT
Subthreshold, both attention conditions	(16)	As (3), but across conditions, mediator model, *Figure 12a*	-355.71	(17) χ^2=-4.8
	(17)	P60~1+Att+(1+Att|Subject), independence model, *Figure 12b*	-353.3	
	(18)	P60~1+Bin+I(Bin^2)+Bin*Att+ I(Bin^2)*Att+ (1+Bin+I(Bin^2)|Subject:Att), interaction model, *Figure 12c*	-330.6	(16) χ^2=50.22** (17) χ^2=45.41***
Suprathreshold, both attention conditions	(19)	As (9), but across conditions, mediator model, *Figure 12a*	-894.7	(20) χ^2=-5.5
	(20)	P50~1+Att+(1+Att|Subject) , independence model, *Figure 12b*	-891.93	
	(21)	P50~1+Bin+I(Bin^2)+Bin*Att+ I(Bin^2)*Att+ (1+Bin+I(Bin^2)|Subject:Att), interaction model, *Figure 12c*	-866.23	(19) χ^2=56.94*[a] (20) χ^2=51.4***

Discussion

In the present study, we investigated (1) whether spatial attention modulates the amplitude of early SEP components in response to electrical left finger nerve stimulation both for supra- and subthreshold intensities, and (2) the role of pre-stimulus mu activity on this attentional modulation. Taken together, we found that attention increases the amplitude for the P1 component for both kinds of stimulation. Furthermore, pre-stimulus mu amplitude (pre-mu) interacts with stimulus-related responses. Interestingly, pre-mu activity affects both behavioral responses and evoked brain activity, the latter differentially depending on the attentional state: With spatial attention, there is a negative quadratic relationship between pre-mu and evoked amplitudes whereas without spatial attention the relationship is positive quadratic. Intermediate and higher mu amplitudes go along with large evoked activity during spatial attention and with small evoked activity without attention.

Sustained attention is widely known to improve perception in a variety of tasks and virtually all modalities (Carrasco, 2011; Kastner, Pinsk, De Weerd, Desimone, &

Ungerleider, 1999; Marks & Wheeler, 1998; Sathian & Burton, 1991; C. J. Spence & Driver, 1994; C. Spence, Kettenmann, Kobal, & McGlone, 2001; C. Spence, Pavani, & Driver, 2000). The deployment of attentional resources should facilitate perception to any task-relevant sensory input as long as it proceeds along the same bottom-up somatosensory pathway (Dehaene et al., 2006; Kiefer, 2012; Schröger et al., 2015). Whether this also holds for subthreshold stimuli, however, is not known, since non-invasive recordings of evoked activity to unmasked subthreshold stimulation have been obtained in only a few studies (somatosensation: Nierhaus et al., 2015; vision: Bareither et al., 2014; Sperdin et al., 2014) and did not investigate attentional modulation. Our results clearly support this postulate by showing an increase in the P1 amplitude with spatial attention, 60ms after stimulation. This effect coincides with an attention effect in the same time range (P50–N80) for suprathreshold stimulation as it has been shown previously (Michie et al. (1987). However, evidence regarding the effect of attention on P1 is ambiguous, because Schubert et al. (2008b) found the attention effect on P1 only on one side (left but not right) and Zopf et al. (2004) did not find it at all. Interestingly, in our study, the attentional modulation of P1 was most clearly evident in the interaction between attention, pre-mu activity, and SEP, and the observed non-linear relationship between mu and P1 might explain why the effect of attention on P1 has not been seen in some previous studies. Future studies need to show whether this is also true for right index finger stimulation, for which perceptual differences have been reported (Meador et al., 1998).

As we reported previously (Nierhaus et al., 2015), upon subthreshold stimulation, we did not observe any further ERP component beyond P1. However, a transient increase of mu amplitude has been observed after subthreshold stimulation (*Figure 15*), which contrasts the post-stimulus decrease typically seen after externally triggered near- and suprathreshold stimulation (Pfurtscheller, 1989; Nikouline, Linkenkaer-Hansen, et al., 2000; Palva et al., 2005; Nierhaus et al., 2015). Generally speaking, increases in mu amplitude may be induced by the feed-forward inhibition associated with subthreshold stimulation as we have discussed previously (Blankenburg et al., 2003; Nierhaus et al., 2015; Taskin et al., 2008).

With respect to the attention effect on pre-mu activity, our results are in line with several studies reporting that attention leads to a decrease of alpha power contralateral to where spatial attention is directed compared to ipsilateral sites (somatosensory: Pfurtscheller and Lopes da Silva, 1999; Jones et al., 2010; Anderson and Ding, 2011; Haegens et al., 2011a, 2011b; visually: Thut et al., 2006; auditory: Weisz et al., 2014a; Wöstmann et al., 2016). This strongly supports the assumption of selective attention relying on intrinsic oscillatory activity in the somatosensory cortex already *prior to* the incoming stimulus (Thut et al., 2006).

Regarding the relationship between pre-mu activity and perceptual performance, we show detection rates to be largest for intermediate pre-mu and lowest for either minimal or maximal pre-mu, which is in line with previous research reporting inverse U-shaped relationships (Linkenkaer-Hansen et al., 2004; Zhang & Ding, 2009). Consistent with this, some studies reported a co-modulation of pre-stimulus mu activity and early SEP components in response to near- and suprathreshold electrical stimuli (Zhang and Ding 2009; Anderson and Ding 2011), both cases exhibiting an inverted U-shaped relationship between pre-stimulus mu power and the respective N1.

Contrasting two alpha power ranges (e.g., “high” and “low”) can allow only for describing linear effects as done in other studies. Here, we extracted five bins of pre-mu that resulted in comparable mu amplitudes between attention conditions for each bin (*Figure 16cb, db*). We observe a non-linear influence of pre-mu activity on P1 amplitudes for both attention conditions, which is in line with the findings of Zhang and Ding (2009) and Anderson and Ding (2011). Moreover, we find that the very same alpha amplitudes (intermediate to highest) are related to the highest SEP amplitudes under attention but also to the lowest SEP amplitudes during inattention. Thus, attention might alter the functional relationship between pre-mu activity and stimulus-related processing (SEP components) according to the task requirements. Rather than serving the deployment of attention alone, mu activity may maximize evoked activity related to the “to-be-attended” stimulus (facilitation), but at the same time minimizes evoked neural processing related to the “to-be-unattended” stimulus (suppression).

At first glance, this interpretation seems to contradict the initial hypothesis that alpha mediates the effect of attention: The very same pre-mu activity would convey the same attentional influence, and the relation between pre-mu activity and SEP amplitude would not be differentiable between the two attention conditions. Indeed, a different role for alpha has been suggested in recent studies which indicate that it might reflect the expectation of upcoming events (Bauer, Stenner, Friston, & Dolan, 2014; Sedley et al., 2016) rather than attention (Anderson & Ding, 2011; Foxe & Snyder, 2011; Zhang & Ding, 2009). However, in our study, neither frequency nor timing of an upcoming perceivable event differed between attention conditions, so it is improbable that the differential influence of mu activity on SEP amplitudes concerning attention reflects differences in expectation. Admittedly, individual variations in the ability to predict an upcoming stimulation within a specific attentional state, which, then, might be related to different pre-mu activity, cannot be excluded. Whether this also holds for subthreshold stimulation is an interesting question, which we address by experimentally manipulating both attention and expectation in the future.

Second, the underlying local spatial pattern of alpha distribution across the cortex might differ between the two conditions, which is possibly smeared given the limited spatial resolution of EEG (Lopes da Silva, van Rotterdam, Barts, van Heusden, & Burr, 1976; Palva & Palva, 2007; Suffczynski, Kalitzin, Pfurtscheller, & Lopes da Silva, 2001). For the visual cortex, it is well-established that selective attention to a particular location or stimulus feature enhances the response of the coding receptive field while suppressing the immediate surrounding and leaving the further surrounding unaffected (Harvey et al., 2013). This is known as the "Mexican hat" distribution of selective attention (N. G. Müller & Kleinschmidt, 2004; N. G. Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005; Treue, 2014). Such a distribution improves the internal signal-to-noise ratio and could explain why the attention–mu relationship is not linear in our case: The mu rhythm (based on ICA) that was measured over an electrode (CP4) contralateral to the stimulation site is most probably a compound of rhythmic activities in adjacent brain areas. Thus, the intermediate overall mu amplitude may reflect a balance between decreased mu in the brain regions representing the receptive field of the attended finger (facilitation) and increased mu in adjacent topological fields (surround suppression, Suffczynski et al., 2001).

Interestingly, this framework predicts smallest SEP amplitudes for intermediate mu activity as a consequence of compound rhythmic activities originating from adjacent brain areas: The response of the to-be-ignored receptive field is suppressed, thereby exhibiting higher mu activity while at the same time adjacent fields might be less suppressed. Following this concept, the effect of attention is mediated by mu activity, albeit on a more local spatial scale than can be resolved with the common EEG approach. In future studies, simultaneous EEG-fMRI (in which the fMRI correlate of mu rhythm is expected to differ between the different attention conditions) or invasive electrocorticography may help to elucidate this question.

In conclusion, our results show that although access to conscious perception is prevented, attention nevertheless affects neural processing of subthreshold stimuli in a top-down manner as it does for suprathreshold stimuli. Furthermore, pre-stimulus mu activity differentially influences neural processing to enable optimal performance in a given task and we suggest this to be a general neural signature for attentional deployment as it encompasses both conscious and unconscious perception.

3 General Discussion and Conclusions

3.1 Summary of empirical results

In the course of four empirical studies, I tested (1) the feasibility of investigating undetectable stimulation by unmasked electrical finger nerve pulses, (2) how its neural correlates dissociate from detectable stimulation and (3) whether and how selective somatosensory attention nevertheless affects the neural representation of stimuli destined to go by unnoticed.

Study 1 showed that the intensity of just detectable stimulation (i.e., at ADTH) is lower for short repetitive pulse trains compared to single pulses. Defining subthreshold intensities relative to the ADTH of pulse trains lowers the sensory evidence for the same stimulation intensities of single electrical pulses and thereby minimizes possible effects of partial consciousness. Therefore, stimulus intensities in all subsequent experiments were derived from threshold assessments applying a higher repetition rate (here 7 Hz) of electrical pulses than in the actual experiments.

Study 2 provided definitive proof that observers are zero sensitive to electrical finger stimulation intensities below ADTH. I showed that there is a physical range of electrical stimulation intensities that cannot be detected. Processing of subthreshold stimulation has been reported previously (Baumgarten et al., 2017; Blankenburg et al., 2003; Ferrè et al., 2016; Iliopoulos et al., 2014; Klostermann et al., 2009; Libet et al., 1967; Ray et al., 1999a; Taskin et al., 2008), however, a rigorous statistical evaluation of its un-detectability has not been shown yet. By the assessment of the bias-free measure of perceptual sensitivity, Bayes factor statistical inference indicated that the evidence of chance performance after subthreshold stimulation reliably outweighed evidence of above-chance performance.

Study 3 set out to investigate how the neural correlates of subthreshold stimulation differ from neural processing above ADTH all the way up to clearly detectable stimuli with respect to electrophysiological recordings in humans. This study was designed to comply with signal detection theoretical analyses and could, therefore, like study 2, control for perceptual sensitivity at each stimulus intensity independent of subjective response tendencies. Together with own previous work applying similar subthreshold stimulation during resting-state functional magnetic resonance imaging, these data revealed qualitative differences between detectable and undetectable stimulus processing evident in altered event-related potentials, induced oscillatory activity, blood-oxygen-level-dependent responses, and functional connectivity.

Finally, study 4 investigated how the deployment of attentional resources might shape the neural processing of undetectable somatosensory stimulation and contrasted this to the processing of detectable stimuli. Attention modulated early SEP amplitudes to both detectable and undetectable stimulation fostering the view of attention and awareness being two separate and mostly independent mechanisms. Furthermore, this study tested the effect of pre-stimulus Rolandic alpha amplitude on early somatosensory evoked potentials and its putative relationship to the guidance of selective spatial attention. The results clearly show that pre-stimulus Rolandic alpha was predictive for the upcoming SEP amplitude. However, the relationship of pre-stimulus alpha and SEP amplitude depended on the current attentional state indicating that both processes are interacting but not functionally matching.

3.2 Neural processing of undetectable stimulation

This work strongly supports the view that neural effects to undetectable somatosensory stimulation are a valid source of information to understand the underpinnings of functional brain activity. This view is not self-evident and has been debated controversially in the past. In a set of physiological studies, Johansson and Vallbo (1979) recorded peripheral nerve impulses from single fibers in the median nerve while perturbing single mechanosensitive afferent units in the glabrous skin of human participants. They found that in the most sensitive areas (the volar aspect of the fingers and peripheral parts of the palm) psychophysiological thresholds were identical to the physiological thresholds of the afferent. Moreover, participants' false alarm rates in the 1AFC task were close to zero. The correspondence of psychophysiological and physiological threshold together with low false alarm rates to catch trials generally speak for a low noise afferent signal transmission to the brain and leaves no space for neural processing of undetectable stimulation.

It is conceivable that different stimulation types—mechanical or electrical—might play a role and could explain why minimal neurographic responses to mechanical touch lead to above chance performance whereas the current thesis showed brain physiological responses to electrical finger stimulation for which behavioral performance is indeed at the chance level. Whereas little mechanical indentation mainly recruits afferent fibers innervating confined receptive fields containing rather few receptors (Goodwin & Wheat, 2008; Johansson & Vallbo, 1983), the flow of a small electrical current would depolarize all afferent fibers between the two terminals of a voltage source irrespective of their innervated receptor types. Intuitively, one should think that the more innervated afferents, the better the detection. Textbook knowledge, however, suggests the parallel processing of different stimulus attributes through converging and diverging afferent fibers (Gardner & Martin, 2000; Pei, Denchev, Hsiao, Craig, & Bensmaia, 2009) onto higher order relay (projection) neurons and its feature selective mapping in different areas of the cortex (Gardner & Kandel, 2000; Kim et al., 2015). This spread of neural activity might dampen the overall response to concurrently activated, adjacent receptive fields by local phenomena of surround or lateral inhibition (ibid.; Goldstein, 2009) in the case of transcutaneous electrical stimulation and thereby allowing a divergence of psychophysical and sensory receptor threshold.

Undetectable somatosensory stimulation applied here was tuned to intensities 30–15% below ADTH and reliably produced sensitivity values of zero. Nevertheless, these subthreshold stimuli lead to a positive potential change about 50 milliseconds after their onset, the P50. Despite this early component, no further significant deflection has been observed. The absence of later components is remarkable in the light of earlier work on unconscious word processing in the visual domain (see Shevrin, 2001, for an overview). In 1968, Shevrin and Fritzler reported that the ERPs of detected and undetected stimuli appear to have a similar structure, however, ERP amplitudes of unconscious stimuli being at least four times smaller than conscious stimuli (see also Bernat, Bunce, & Shevrin, 2001 for similar results on unconscious valence recognition). In a set of other studies the same group (Bernat, Shevrin, & Snodgrass, 2001; Silverstein et al., 2015a; Snodgrass, Bernat, & Shevrin, 2004; Snodgrass & Shevrin, 2006) suggested that conscious and unconscious perception are functionally exclusive and should qualitatively dissociate from each other, which is at odds with the finding of similar ERP structure but weaker component amplitudes for unconscious stimuli. Effects that are just a weaker version of conscious perception effects do not strongly indicate unconscious perception and could point to residual conscious perception and therefore obey the so-called single process conscious perception model (ibid.). Data in the current thesis and previous work suggests qualitative different processing of undetectable compared to detectable somatosensory stimulation in several aspects: (1) the absence of late components (study 3, 4 and Nierhaus et al., 2015, esp. the N150 that is indicative of stimulus detection (study 3), (2) increased instead of decreased event-related somatosensory alpha amplitude (study 4), (3) reduced instead of elevated BOLD activity (Blankenburg et al., 2003) as well as (4) reduced functional connectivity of primary somatosensory cortex to areas associated with conscious and higher somatosensory processing (Nierhaus et al., 2015). Despite the apparent difference of stimulus presentation modality in the studies by the Shevrin group and the current thesis, a couple of potentially relevant factors may have led to the diverging ERP findings. First, the visual studies (Bernat, Shevrin, et al., 2001; Silverstein et al., 2015) applied stimulus material that conveyed rather complex semantic information as compared to the small electrical pulses in the current studies. Such stimulation differences may have triggered effects in components beyond the initial processing stages, which is indicated by their frontal spatial origin. Second, it might be the case that subthreshold electrical somatosensory stimuli recruit more divergent fibers than the short flashing of words do (see the similar argumentation at the beginning of the section). This could cause relatively more mutual inhibition to occur in the neighboring neurons of primary sensory cortices coding adjacent receptive fields, which impede further processing. Likewise, subthreshold somatosensory stimulation might shift the excitation-inhibition-balance (Isaacson & Scanziani, 2011) toward inhibition indicated by high stimulus-related alpha amplitude and decreased functional connectivity as Nierhaus et al. (2015) have argued and thereby preventing perceptual awareness at later stages.

3.3 Attention, awareness and neural oscillatory activity

Study three (section 2.3.2) showed contralateral N150 to be the earliest component indicative of stimulus detection, which mirrors previous research (Auksztulewicz & Blankenburg, 2013; Auksztulewicz et al., 2012; Schubert et al., 2006). Auksztulewicz and colleagues (2012) stimulated the median nerve with a single near-threshold intensity. Besides an elevated N150 amplitude for detected compared to rejected stimulation, source connectivity modeling indicated that this component might reflect increased recurrent (both feedforward and feedback) processing between primary and secondary somatosensory cortex (ibid.). Absence of N150, as I reported (study 3 and 4), for subthreshold, i.e., undetectable, stimulation then could point to an unmodulated connection between primary sensory cortices relative to baseline activity or even to reduced connectivity of S1 to the frontal-parietal network (Nierhaus et al., 2015). As I discussed earlier (section 2.3.1), the presence of N150 seems to be independent of the experimental context as Nierhaus and colleagues (2015) did not require participants to engage in a detection task but rather let them passively observe suprathreshold, i.e., detectable, stimulation. Its presence during passively observed detectable stimulation makes the N150 a candidate for a proper neural correlate of consciousness (Aru et al., 2012; Verleger, 2010). In a visual backward masking study, a mid-latency negativity (VAN) indicated visual awareness of stimuli that were not task-relevant, but it was absent when participants did not perceived the stimuli (Pitts et al., 2014). Similarly, the posterior-contralateral negativity with a latency of roughly 200 ms (N2pc) only appeared after a valid compared to an invalid spatial attention cue was consciously perceived but was missing when the cue was masked (Giattino, Alam, & Woldorff, 2018). Although the latter findings could not rule out task-relevance as confounding factor, both studies corroborate the present results that perceptual awareness might emerge within 200 ms upon stimulus presentation but not as early as 60 ms.

For this early time range, however, I reported an attentional modulation of the P50 and that this modulation was independent of stimulus awareness (study 4). Together with the results by Giattino and colleagues (2018), who reported enhanced P1 amplitude upon validly relative to invalidly cued targets both for consciously perceived and non-perceived cues, early attentional modulation of sensory input speaks for a general signal gain mechanism. In this sense, the results of the current thesis reject theories that envision attention as a gating mechanism putting unconscious perception and selective attention at the endpoints of a continuum (Brigard & Prinz, 2010; Dixon, 1971). I.e., attention does not shield the brain from faint but principally task-relevant information as long as this information proceeds along the same feedforward processing pathway where the focus of attention currently rests. Furthermore, this also foils theoretical accounts viewing attention to be sufficient for consciousness (Brigard & Prinz, 2010). Dividing attention in (1) attention to space and (2) attention to perceptual representations, Brigard and Prinz (2010) regard attention necessary and sufficient for consciousness “when and only when a perceptual representation of something (a color, shape, object, movement and so on) is modulated by attention" but importantly not when attention is spatially focused. Instead, although attention is not a uniform phenomenon, and the current results shed some light on one, but arguably central aspect of it, namely focused selective attention (W. James, 1890), I think that the early P50 modulation under no sign of stimulus awareness triggered by top-down selective attention strongly speaks for an independence of attention from consciousness. It is not conclusive but seems arbitrary to claim that attention is sufficient for consciousness while only referring to one aspect of attention but not the other.

Furthermore one may question whether "attention selection of perceptual representations to be passed onto working memory" (Brigard & Prinz, 2010) is different from "items that are in mind and have reportability," which is taken from the definition of consciousness in the introduction put forward by Gilchrist and Cowan (2010). That is, passing perceptual representation to working memory might already reflect emerging consciousness. In that sense, attentional selection does not gate information but rather tries to increase the signal to noise ratio and thereby to boost the chance for stimulus reportability. However, that does not mean attention does not gate *ignored* stimuli. There are many studies of inattentional or change blindness showing that quite salient stimuli might be overseen (e.g., Rensink, O'Regan, & Clark, 1997; Simons & Chabris, 1999). If the stimulation site is attended, gating for perceptual awareness happens at later processing stages, starting roughly from 80 ms as previous research (Auksztulewicz & Blankenburg, 2013; Auksztulewicz et al., 2012; Cauller & Kulics, 1991; Schubert et al., 2006; Zhang & Ding, 2009) and the current data indicate (study 3) but does not seem to be a function of early selective attention. The referenced research and the current data are better explained by two alternative but complementary accounts that describe attention selection and awareness as two independent, however, interrelated concepts (Dehaene et al., 2006; Kiefer, 2012; Kiefer & Martens, 2010). In the model by Dehaene, the extent to which a stimulus is processed and eventually becomes detected depends on its bottom-up stimulus strength and the amount of available attentional resources deployed to it. In that scheme, weak stimuli go unnoticed regardless how much attentional resources are available, which is consistent with the attentional modulation of subthreshold stimulus ERPs in study 4. If stimuli are principally strong enough, observers still might be unaware of them as long as attention is occupied elsewhere (see change blindness above). The attentional sensitization model of Markus Kiefer builds on Dehaene's taxonomy and extends it, especially concerning how the attentional modulation of undetectable stimulation is implemented. Regardless of whether the stimulus is consciously perceived or not, the mechanism for attentional control is the same: "processing of task-relevant pathways is enhanced by increasing the gain of neurons in the corresponding areas, whereas the processing of task-irrelevant pathways is attenuated by a decrease of the gain" (Kiefer, 2012; Kiefer & Martens, 2010).

Although beyond the scope of the current thesis, it might be worth to reconcile the view of facilitation or signal enhancement by tactile attention along the awareness spectrum to elaborated models of visual attention that are able to integrate a whole lot of different empirical results in vision (Buschman & Kastner, 2015; Carrasco, 2011; Reynolds & Heeger, 2009). For a moment putting awareness aside, the increased P50 amplitude for both undetectable and detectable somatosensory stimuli during attention may reflect a contrast gain in the stimulus coding neural population. I.e., neural population activity in primary cortices as a function of stimulus intensity increases across the whole stimulus intensity range. This neural gain decreases the stimulus intensity required for the neural population to respond and is equivalent to the neural response following increased stimulus intensity without attention (Carrasco, 2011). Computationally, this can be implemented by multiplying the "stimulus drive" (i.e., the neural response to the stimulus per se without modulation) with the "attentional field" (i.e., the actual gain for each neuron in the population depending on its spatial extent, Reynolds & Heeger, 2009). The result is divided by a normalization factor, the "suppressive drive," to scale the neural population response. This suppressive drive reflects the amount of suppression due to the activity of other neurons responding to the surrounding context (Reynolds & Heeger, 2009) and therefore compete for neural representation (Buschman & Kastner, 2015; Desimone & Duncan, 1995). Attention then is a mechanism that alters activity across neural populations by shifting the balance between excitation and suppression. According to the normalization model of attention (Reynolds & Heeger, 2009), the bigger P50 contralateral to the attended finger in study 4 is due to the multiplicative gain of the attention field and the stimulus drive. Thus, the smaller P50 contralateral to the unattended finger is governed by the suppressive drive probably resulting from local competitive interactions (Buschman & Kastner, 2015; Reynolds & Heeger, 2009) that are not resolved by attention (Desimone & Duncan, 1995). Unfortunately, it is not possible to prove suppression based on the relatively reduced P50 amplitude alone because study 4 is lacking a neutral baseline. However, increased sensory suppression has been argued to correlate with heightened alpha band amplitudes (Haegens, Nácher, et al., 2011; Jensen & Mazaheri, 2010; Kelly, Lalor, Reilly, & Foxe, 2006; Klimesch, 2012; Pfurtscheller, 1989; Thut et al., 2006) and to reflect the neural mechanism for the deployment of attention (Foxe & Snyder, 2011).

Surprisingly in study 4, there was no statistically reliable difference in event-related alpha-band suppression when a suprathreshold stimulus was attended compared to when it was ignored. Supporting this finding, van Ede and colleagues (2014) did not observe any post-stimulus attention differences after tactile stimulation, too. Thus, post-stimulus alpha-band amplitude does not seem to indicate attentional deployment. As discussed above, suppression is likely due to local competitive interactions that are increased the more stimuli compete for processing resources (Desimone & Duncan, 1995). Thus, if alpha reflects sensory suppression the presence of an amplitude difference when comparing attended versus unattended stimuli might depend on the number of stimuli that are ignored. This hypothesis gets some support by research from visual-spatial and feature-based attention, which did not analyze alpha amplitudes, though, but the steady-state-visual evoked potential (SSVEP). For measuring an SSVEP, one or more stimuli are tagged with specific presentation frequencies, which amplitudes can be analyzed in M/EEG. In a study by Fuchs, Andersen, Gruber, and Müller (2008) the SSVEP signal of an unattended flickering bar only became suppressed when a second bar was presented close to it. Likewise, work in feature-based attention showed that the signal of the unattended feature was reduced compared to a neutral baseline when a local competitor was presented (Forschack, Andersen, & Müller, 2016; Müller, Gundlach, Forschack, & Brummerloh, 2018). Importantly, these studies could not analyze alpha, because SSVEP frequencies were covering the alpha-band range. Future studies should center flicker frequencies well above the alpha band to measure putative sensory suppression indicated by alpha amplitude increases concurrently with SSVEP amplitude reduction.

Contrary to stimulus-induced alpha amplitude modulation, pre-stimulus alpha amplitudes might be relevant for the allocation of attentional resources. This link has been shown by relatively larger pre-stimulus alpha-band amplitudes when the finger was unattended compared to when it was attended in both van Ede and colleagues' (2014) study and here in study 4. The relationship of alpha and attention regarding early sensory stimulus processing, though, does not seem to be straight forward because the size of the P50 is either maximal or minimal for the same alpha amplitude depending on the attentional state (Forschack et al., 2017). Indeed, alpha-band modulations have been shown to correlate with attentional performance increases, especially for designs employing anticipatory attention. Thus, one conclusion is that alpha does not reflect attention in general but rather specific aspects of it (Klimesch, 2012), or might be indicative of the respective task context (van Ede et al., 2014).

3.4 Limits of the current studies and future perspectives

In the final section, I want to step back a bit and reflect on the scope of my thesis, which questions are arising and may trigger new research avenues. For this, I will first discuss the investigation of (un-) consciousness in tactile perception and finish with some consideration for selective spatial attention in touch.

Although this thesis provides direct evidence for the effectiveness of unconscious content on neural processes and thereby rejects single-process models where only conscious processing appears effective (Schmidt & Vorberg, 2006), the current experiments have not investigated unconscious effects on obvious behavior as classic experimental approaches in the field of unconscious perception do (Merikle, Smilek, & Eastwood, 2001). Instead, by concurrently measuring the activity of neural populations with EEG, I hope to have demonstrated qualitative differences in the processing of consciously perceivable all the way down to non-perceivable stimuli. This approach has the potential to reveal effects about unconscious processing that go beyond a dichotomous view of perception either regarded as conscious or unconscious (Jacoby, 1991). It allows investigating the depth of neural processing (Haynes, 2013) and opens the perspective on unconscious processing maybe happening mostly in parallel to or even independent of conscious processing (Dixon, 1971; Haynes & Rees, 2005). Nonetheless, for the effect of subthreshold stimulation on conscious perception, the current results provide a precise prediction. A subthreshold stimulus-induced event-related increase in the alpha band amplitude, as shown in study 4 (section 2.4) should result in a decreased detection probability of a subsequent target stimulus under the assumption that high alpha band amplitudes correlate with functional inhibition.

Empirical support for the latter comes from a repetitive transcranial magnetic stimulation study (rTMS) that found decreased sensitivity to a vibrotactile stimulus after frequency specific entrainment in the alpha band over contralateral primary somatosensory cortex and intraparietal sulcus (Ruzzoli & Soto-Faraco, 2014).

In the first part of the discussion, I speculated that the divergence of psychophysical and sensory receptor threshold for electrical in contrast to mechanical stimulation could be explained by an overall dampened cortical response due to mutual inhibition of concurrently activated afferent fibers. Of course, my thesis cannot decide on this hypothesis because it lacks measurements of the finger receptor afferents. Therefore, it would be interesting to compare mechanical and electrical finger nerve stimulation concerning the microneurographic activity of the median nerve in combination with a signal detection theoretic analysis of the behavioral responses. The prediction would be that small mechanical skin indentations only activate fast adaptive afferents of the receptive field leading to above chance performance (Vallbo & Johansson, 1984), whereas electrical perturbation of the skin at absolute detection threshold results in the parallel activation of multiple afferent types.

The definition of consciousness as referring to stimuli either having objective reportability or not is a rather operational constriction. It cannot be concluded, though, that the early P50 amplitude after subthreshold stimulation does not relate to subjective reports like ratings. However, recent studies that employed peri-threshold median nerve stimulation (Auksztulewicz & Blankenburg, 2013) and continuous flash suppression in vision (Hesselmann et al., 2011) while asking the participants to rate the stimulus intensity/ visibility, provide evidence against this argument. These studies showed that only later electrophysiological response, the P300 (Auksztulewicz & Blankenburg, 2013), and high-order visual areas (Hesselmann et al., 2011) distinguished variations in the subjective report but not the early ERP or activity of the lower visual hierarchy, respectively. Nevertheless, experimental designs combining both objective and subjective reports are a promising account to disentangle further the neural underpinnings of the emergence of conscious perception and the participant's current subjective experience (Haynes, 2009).

The focus on spatially localized signals in the EEG, i.e., ERPs and oscillatory activity based on one or a cluster of electrodes, is a further limitation given that perceptual awareness has been argued to arise from the interaction between more or less distributed brain areas (e.g., Baars, 1997; Crick & Koch, 2003; Dehaene & Changeux, 2011; Lamme, 2004; Lau & Rosenthal, 2011; Tononi & Koch, 2015). This is not to say that there is no regional interaction underlying e.g., the N150. In fact, Auksztulewicz and Blankenburg, (2013) have shown that the N150 might reflect reverberating activity between primary and secondary somatosensory cortex. The study by Nierhaus and colleagues (2015, see section 2.3.1) could dissociate subthreshold from suprathreshold stimulation during resting-state fMRI where the former evoked a functional decoupling of primary somatosensory cortex from fronto-parietal areas. Additionally, recent fMRI graph theoretic results by (Grund, Forschack, Nierhaus, & Villringer, submitted) reveal a tight relationship of a sparse task-relevant network supporting perceptual awareness. Thus, future EEG research may benefit from investigating global scale activity and connectivity measures (as already has been done by a few groups: Hirvonen & Palva, 2016; Weisz, Wühle, et al., 2014) but, importantly, should relate and benchmark it to the accumulated wisdom of past decades of ERP experimental designs (Haynes, 2009; King & Dehaene, 2014).

Contrarily, a much more fine-grained spatial resolution might be needed when it comes to interpreting oscillatory data. Invasive research in macaque monkeys found functionally dissociable alpha band activity even between different cortical layers (Bollimunta, Mo, Schroeder, & Ding, 2011). As discussed in section 2.4, it is possible that EEG level oscillations reflect a compound signal from nearby local oscillators and thereby obscuring their true functional role about cognitive factors like selective attention that arguably act at the scope of receptive field coding single cells (Carrasco, 2011). Thus, in human research, invasive electroencephalography (iEEG) carefully designed to study selective attention would be a reasonable step toward proving the functional role of alpha and its relation to attention.

Regarding the nature of the effect of attention in the somatosensory system, research relating it to signal enhancement or external/ internal noise suppression (Carrasco, 2011) or computational models of attention (Reynolds & Heeger, 2009) is very scarce (see the review by Gomez-Ramirez et al., 2016). The facility to precisely adjust parameters makes electrical stimulation a valuable tool to approach these questions in psychometric designs. Furthermore, as the concurrent presentation of targets and external noise has been shown previously (Iliopoulos et al., 2014), the manipulation of external noise levels in combination with attention would leverage this field of research and shed light on the generalizability of attention mechanisms from other sensory modalities.

Indeed, many questions remain to be studied. With the results of the present thesis, I hope to have provided new insights into the domain of somatosensation, which is central to the way everyone perceives and acts as an individual within a complex and continually changing environment.

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Summary

Introduction

Humans are in touch with themselves (Metzinger, 2004). With touch, we explore our surrounding environment and distinguish us from it. For this, the sense of touch provides a unique heterogeneous structure comprised of a variety of mechano-, chemo-, thermoreceptors as well as noci- and proprioceptors. Continuously exposed to sensory input, we may miss tactile stimuli, no matter how much attention we pay to them. Under optimal conditions, however, humans may consciously perceive skin indentations of the fingertip as small as 11 μm (Johansson & Vallbo, 1979). This thesis examines the possibility of sensory events escaping conscious access and the puzzling question whether there are correlates of such unconscious sensations in the brain. What do these neural markers—or the absence of those that are present during conscious perception—tell us about the mechanisms precluding awareness and what is the role of cognitive factors, foremost attention, in modulating such perceptual processes. The present dissertation comprises four empirical studies investigating behavioral responses and neural activity using electroencephalography (EEG) in humans that receive somatosensory stimulation. First of all, it is investigated in which range electrical impulses on the finger nerves can no longer be detected consciously. Secondly, this thesis demonstrates how neuronal correlates of undetectable stimulation dissociate from neuronal correlates of detectable stimulation.; and thirdly, it shows that selective attention affects the neuronal representation of somatosensory stimuli independently of their detectability, which supports the assumption of a general and consciousness-independent neuronal signature for the distribution of attention (Koch & Tsuchiya, 2007).

There are two common ways to render stimuli undetectable. One is backward masking, in which a shortly presented target stimulus turns invisible when another non-target stimulus follows within tens of a seconds (Enns & Lollo, 2000). However, masking may preclude observations unique to early neural processes that are unique for processing unmasked but undetectable stimulation. Thus, the present studies employ another method that limits stimulation energy as a function of stimulus intensity and duration to control the detectability of stimuli (Iliopoulos et al., 2014; Shevrin, 2001). Two studies (n = 22) in this thesis, therefore, carefully validate the threshold assessment procedure, which sets the stimulation parameters for each observer individually. A particular challenge is to show that a specific stimulus intensity cannot be detected, i.e., more precisely, that the detection rate for that stimulus is no different from chance. Testing this null hypothesis (NH) cannot be carried out with classical test theoretical methods, which were constructed to reject the NH, but not to confirm it.. Instead, in the present thesis, Bayes factor statistics evaluate the empirical support for the chance level performance (i.e., the NH) of putative undetectable stimuli against above chance performance (i.e., the alternative hypothesis, AH).

In two subsequent studies (n = 80), this thesis investigates the neural responses of the processing of undetectable stimulation, what the difference is to the processing of detectable stimulation, and whether and how selective spatial attention modulates the neural signal of stimuli that are adjusted to escape conscious perception. The high temporal resolution of the EEG allows studying temporally distinct neural mechanisms of stimulus processing and attention: single successive stimulus-locked somatosensory evoked potentials (SEP) in the EEG can change along different stimulation intensities, with stimulus detection and by different attention states. In addition, brain oscillations both before and shortly after a stimulus may mediate the top-down deployment of selective spatial attention. In general, this thesis asks to what extent the neural responses to different stimulation intensities distinguish from neural responses that correlate with stimulus awareness and selective attention.

Experiments and results

Study I establishes a fast and reliable, manual threshold assessment procedure to estimate observers' absolute detection thresholds (ADTH) below which they provide random detection rates. It shows that the intensity of just noticable stimulation (i.e., at ADTH) is lower with short repetitive pulse trains than with single pulses. Defining subthreshold stimulus intensities relative to the ADTH of pulse trains lowers the sensory evidence for the same stimulation intensities of single electrical pulses and thus minimizes possible effects of partial consciousness. Therefore, stimulus intensities in all subsequent experiments were derived from threshold assessments applying a higher repetition rate (here 7 Hz) of electrical pulses than in the actual experiments.

Study II validates this threshold assessment procedure by applying a One-Alternative-Forced-Choice-(1AFC, i.e., yes-no detection) task for stimuli ranging from intensities below absolute detection threshold to intensities clearly above but still below the pain threshold. Importantly, the design includes trials without any stimulation (catch trials) to allow for the estimation of perceptual sensitivity (*d*-prime) and response bias (criterion) according to signal detection theory, and validates the chance performance for stimulation intensities below ADTH (i.e., subthreshold) statistically by Bayes factor null-hypothesis testing. The results indicate that there is a physical range of electrical stimulation intensities that cannot be detected because the statistical evidence for detection rates at random level after sub-threshold stimulation indicated by the Bayes factor reliably outweighs the statistical evidence for detection rates above random level.

Study III asks whether there are measurable neural correlates of subthreshold stimulation intensities. If so, are there qualitative differences between stimulation below and above ADTH concerning the stimulus-evoked response and oscillatory activity that could prevent access to conscious experience in the case of subthreshold stimulation? Furthermore, this study tests, which features of the earliest neural responses (amplitude and latency of the SEP) after somatosensory stimulation are predictive of its detection and how these post-stimulus features interact with pre-stimulus intrinsic oscillatory activity in the alpha-band that has been surmised to regulate the excitability of sensory cortices awaiting stimulus input? Study III was therefore designed as an EEG adaptation of study II and investigates these neural stimulus-related responses for various stimulation intensities. For the subthreshold stimuli, there was only one P50 component 50 ms after stimulation, but no further event-related potentials, thereby replicating previous research (Libet et al., 1967; Ray et al., 1999; Nierhaus et al., 2015; Forschack et al., 2017). The P50 amplitude scaled with increasing stimulation intensities but was not predictive for stimulus detection for the two highest stimulation intensities. A stronger negative potential 150 ms after stimulus onset (N150) together with the pre-stimulus somatosensory alpha (i.e., mu) amplitude best explains perceptual awareness of somatosensory stimulation.

Selective attention plays a crucial role in stimulus detection by amplifying the task-relevant neural responses and suppressing task-irrelevant noise (Desimone & Duncan, 1995; Hillyard et al., 1973). In addition, attention affects both SEPs and alpha-band activity. Therefore, study IV examines the modulatory role of selective spatial attention in somatosensory stimulus processing across awareness conditions by its relation to early SEPs and oscillatory mu-alpha activity. The results reveal that attention increases the amplitude for the P50 component to both detectable and undetectable stimulation and foster the view of attention and awareness being two separate and mostly independent mechanisms. In addition, pre-stimulus mu amplitudes (pre-mu) interact with stimulus-evoked responses.

Interestingly, pre-mu activity affects both behavioral responses and SEP amplitudes, the latter differentially depending on the attentional state: With spatial attention there is a negative quadratic relationship between pre-mu and evoked amplitudes whereas without spatial attention the relationship is positive quadratic. I.e., Intermediate and higher pre-mu amplitudes go along with large evoked activity during spatial attention and small evoked activity without attention. This result pattern suggests that pre-mu amplitude and attention are interrelated but are not functionally matching.

Discussion

This work strongly supports the view that neural responses to undetectable somatosensory stimulation are a valid source of information to understand the underpinnings of functional brain activity. Undetectable somatosensory stimulation applied here was tuned to intensities 30–15% below ADTH and reliably produced sensitivity values of zero. Nevertheless, these subthreshold stimuli led to a positive potential change about 50 milliseconds after their onset, the P50. Apart from this early component, no further significant deflection was observed. The data in the present thesis and in earlier collaborative work indicate a qualitative different processing of undetectable compared to detectable somatosensory stimulation in several aspects: (1) the absence of late components (study 3, 4 and Nierhaus et al., 2015), especially the N150 that is indicative of stimulus detection (study 3), (2) increased but not decreased stimulus-related somatosensory alpha amplitudes (study 4), (3) decreased instead of increased BOLD activity (Blankenburg et al., 2003) and (4) reduced functional connectivity of primary somatosensory cortex with areas associated with conscious and higher somatosensory processing (Nierhaus et al., 2015). In summary, one can speculate that this result pattern indicates a shift in the balance between neural excitation and inhibition (Isaacson, Scanziani, 2011) in favor of inhibition, which prevents stimulus detection in later processing phases, as Nierhaus et al. (2015) have argued.

The absence of the N150 for subthreshold, i.e., undetectable, stimulation then could point to an unmodulated connection between primary sensory cortices relative to baseline activity or even to reduced connectivity of S1 with the frontal-parietal network (Nierhaus et al., 2015) compared to detectable stimulation (Auksztulewicz et al., 2012). Furthermore, the presence of the N150 seems to be independent of the experimental context since Nierhaus and colleagues (2015) did not require participants to engage in a detection task but instead let them passively observe suprathreshold, i.e., detectable, stimulation. The presence of the N150 after passively perceived detectable stimulation makes this EEG component a candidate for a proper neural correlate of consciousness (Aru et al., 2012; Verleger, 2010).

For an earlier time range, however, this thesis reports an attention modulation of the P50, and this modulation is independent of stimulus detection (study 4). In this sense, the results reject theories that envisage attention as a gating mechanism that places unconscious perception and selective attention on the endpoints of a continuum (Brigard & Prinz, 2010; Dixon, 1971). This means that attention does not shield the brain from faint but potentially task-relevant information as long as this information proceeds along the same feedforward processing pathway on which attention is currently focused (Forschack et al., 2017). In addition, this also foils theoretical accounts viewing attention sufficient for consciousness (Brigard & Prinz, 2010). Instead, although attention is not a uniform phenomenon and the current results shed some light on one, but arguably central, aspect of it, namely focused selective attention (James, 1890), early P50 modulation by attention under no sign of stimulus detection strongly speaks for an independence of attention and consciousness.

The current data is best explained by two alternative but complementary accounts that describe attention and consciousness as two independent but interrelated concepts (Dehaene et al., 2006; Kiefer, 2012; Kiefer & Martens, 2010). In the Dehaene model, the extent to which a stimulus is processed and eventually detected depends on its bottom-up stimulus strength and the amount of attention resources available. In this scheme, weak stimuli remain unnoticed regardless how much attention resources are available, which is consistent with the attentional modulation of subthreshold stimulus ERPs in study 4. If stimuli are strong enough in principal, observers may not be aware of them yet, as long as attention is occupied elsewhere. Markus Kiefer‘s attentional sensitization model builds on Dehaene's taxonomy and expands on it, especially concerning the question of how attention modulation is implemented in the processing of undetectable stimulation. Regardless of whether the stimulus is consciously perceived or not, the mechanism of attention control is the same: "processing of task-relevant pathways is enhanced by increasing the gain of neurons in the corresponding areas, whereas the processing of task-irrelevant pathways is attenuated by a decrease of the gain" (Kiefer, 2012; Kiefer & Martens, 2010).

In contrast to the absence of stimulus-induced mu amplitude modulations by attention, pre-stimulus mu amplitudes may be relevant for the allocation of attention resources. This link was shown in both the study by Ede, Lange and Maris (2014) and here in study 4 as relatively larger pre-Mu amplitudes with unattended compared to attended fingers. However, the relationship of alpha and attention regarding early sensory stimulus processing does not appear to be proportional, since the size of the P50 at the same alpha amplitude is either at maximum or minimum, depending on the attentional state (Forschack et al., 2017). In fact, alpha-band modulations have been shown to correlate with attentional performance increases, especially for designs employing anticipatory attention. Thus, one conclusion is that alpha does not reflect attention in general, but can refer to specific aspects of it (Klimesch, 2012), or to the the respective task context (van Ede et al., 2014).

Zusammenfassung

Einleitung

Der Tastsinn erlaubt es dem Menschen, die nahe Umgebung zu „begreifen“ und sich selbst von dieser zu unterscheiden. Dafür bietet der Tastsinn eine einzigartige heterogene Struktur, die aus einer Vielzahl von Mechano-, Chemo-, Thermorezeptoren sowie Nozi- und Propriozeptoren besteht. Unablässig dem Strom sensorischer Reize ausgesetzt, können diese uns unbemerkt beeinflussen, egal wie viel Aufmerksamkeit wir ihnen schenken. Unter optimalen Bedingungen hingegen kann der Mensch eine Verformung der Fingerspitze von nicht mehr als 11 μm bewusst wahrnehmen (Johansson & Vallbo, 1979). Diese Arbeit untersucht den Bereich der *nicht* bewusstseinsfähigen sensorischen Reize und geht der Frage nach, ob es Korrelate solcher unbewussten Empfindungen im Gehirn gibt. Welche Rückschlüsse erlauben diese neuronalen Indikatoren—oder das Fehlen derer, die während bewusster Wahrnehmung vorhanden sind—auf Mechanismen, welche die bewusste Wahrnehmung taktiler Reize verhindern; und welche Rolle spielen kognitive Faktoren, vor allem Aufmerksamkeit, bei der Modulation solcher Wahrnehmungsprozesse? Die vorliegende Dissertation umfasst vier empirische Studien, die sowohl Verhaltensreaktionen als auch neuronale Aktivität—gemessen mittels Elektroenzephalographie (EEG)—beim Menschen unter somatosensorischer Stimulation untersuchen. Zunächst wird untersucht, in welchem Bereich elektrische Impulse an den Fingernerven nicht mehr bewusst detektiert werden können. Zweitens zeigt diese Arbeit, wie sich neuronale Korrelate nicht detektierbarer Stimulation von neuronalen Korrelaten detektierbarer Stimulation dissoziieren; und drittens, dass selektive Aufmerksamkeit die neuronale Repräsentation von somatosensorischen Reizen unabhängig ihrer Detektierbarkeit beeinflusst und dies die Annahme einer allgemeinen und bewusstseinsunabhängigen neuronalen Signatur für die Verteilung von Aufmerksamkeit unterstützt (Koch & Tsuchiya, 2007).

Es gibt zwei gängige Methoden, Reize so zu präsentieren, dass diese bewusst nicht wahrgenommen werden. Eine davon ist die sog. rückwärtsgerichtete Maskierung, bei der ein kurz dargestellter Zielreiz unsichtbar wird, wenn innerhalb von Zehntelsekunden ein weiterer Reiz folgt (Enns & Lollo, 2000). Dadurch kann die

Maskierung jedoch frühe neuronale Prozesse verdecken, die für die Verarbeitung unmaskierter aber nicht detektierbarer Stimulation einzigartig sind. Daher wenden die vorliegenden Studien eine andere Methode an, welche die Stimulationsenergie als Funktion der Stimulusintensität und -dauer einschränkt, um die Detektierbarkeit von Reizen zu kontrollieren (Iliopoulos et al., 2014; Shevrin, 2001). Zwei Studien (n = 22) dieser Arbeit validieren sorgfältig das Verfahren zur Schwellenwertbestimmung, mit dem die Stimulationsparameter für jeden Beobachter individuell eingestellt werden. Eine besondere Herausforderung besteht darin, zu zeigen, dass eine bestimmte Reizstärke nicht erfasst werden kann, d. h. genauer gesagt, dass sich die Detektionsrate auf diesen Reiz nicht vom Zufall unterscheidet. Die Überprüfung dieser Nullhypothese (NH) kann nicht mit klassischen testtheoretischen Verfahren durchgeführt werden, welche daraufhin konstruiert wurden die NH zurückzuweisen, jedoch nicht zu bestätigen. Stattdessen setzen die Bayes-Faktor-Statistiken in der vorliegenden Arbeit die Wahrscheinlichkeit, dass die Detektionsraten für eine vermeintlich nicht bewusst wahrnehmbare Reizintensität auf Zufallsniveau liegen (d. h. die NH) ins Verhältnis zur Wahrscheinlichkeit, dass diese über dem Zufall liegen (d. h. die Alternativhypothese, AH).

In zwei weiteren Studien (n = 80) untersucht diese Arbeit die neuronalen Korrelate der Verarbeitung nicht detektierbarer Stimulation, was der Unterschied zur Verarbeitung detektierbarer Stimulation ist, und ob und wie selektive räumliche Aufmerksamkeit das neuronale Signal von Reizen moduliert, die der bewussten Wahrnehmung stets entgehen. Die hohe zeitliche Auflösung des EEG ermöglicht die Untersuchung zeitlich unterschiedlicher neuronaler Mechanismen der Reizverarbeitung und der Aufmerksamkeit: Einzelne somatosensorisch evozierte Potentiale (SEP) im EEG können sich entlang verschiedener Stimulationsintensitäten, mit der Stimulusdetektion und durch verschiedene Aufmerksamkeitszustände verändern. Darüber hinaus könnten Oszillationen des Gehirns sowohl vor, als auch kurz nach einem Stimulus den Top-down-Einsatz selektiver räumlicher Aufmerksamkeit vermitteln. Im Allgemeinen fragt diese Arbeit, inwieweit sich die neuronalen Reaktionen auf verschiedene Stimulationsintensitäten von neuronalen Reaktionen unterscheiden, die mit Reizbewusstsein und selektiver Aufmerksamkeit korrelieren.

Experimente und Ergebnisse

Studie I etabliert ein schnelles und zuverlässiges, manuelles Verfahren zur Schwellenwertbestimmung, um die absoluten Detektionsschwellen (ADTH) der Beobachter abzuschätzen, unterhalb derer sie Detektionsraten auf Zufallsniveau erbringen. Sie zeigt, dass die Intensität der eben merklichen Stimulation (d. h. ADTH) bei kurzen repetitiven Impulsfolgen geringer ist als bei Einzelpulsen. Die Definition von unterschwelligen Reizintensitäten relativ zur ADTH von repetitiven Impulsen senkt die sensorische Evidenz für die gleichen Stimulationsintensitäten einzelner elektrischer Impulse und minimiert dadurch mögliche Auswirkungen von residualer bewusster Wahrnehmung. Daher wurden die Reizintensitäten in allen nachfolgenden Experimenten aus Schwellwertbestimmungen mit einer höheren Wiederholrate (hier 7 Hz) der elektrischen Impulse abgeleitet als in den eigentlichen Experimenten.

Studie II validiert dieses Schwellenwertbestimmungsverfahren durch die Anwendung einer One-Alternative-Forced-Choice-(1AFC, d.h. Ja-Nein-Detektions-) Aufgabe für Stimuli, die von Intensitäten unterhalb der absoluten Detektionsschwelle bis hin zu Intensitäten deutlich darüber, aber immer noch unterhalb der Schmerzgrenze reichen. Wichtig ist, dass das Design Versuchsdurchgänge ohne Stimulation („catch-trials“) vorsieht, um die Bestimmung der Sensitivität (*d*-prime) und des Antwort-Bias (Kriteriums) gemäß der Signal-Entdeckungs-Theorie zu ermöglichen, und dass Detektionsraten auf Zufallsniveau für Stimulationsintensitäten unterhalb von ADTH (d. h. unterschwellig) statistisch durch den Bayes-Faktor Null-Hypothesentest abgesichert werden. Die Ergebnisse zeigen, dass es eine physikalische Bandbreite von elektrischen Stimulationsintensitäten gibt, die nicht erkannt werden können, da die statistische Evidenz für Detektionsraten auf Zufallsniveau nach unterschwelliger Stimulation—angezeigt durch den Bayes-Faktors—zuverlässig die statistische Evidenz für Detektionsraten über Zufallsniveau überwiegt.

Studie III fragt, ob es messbare neuronale Korrelate der unterschwelligen Stimulationsintensitäten gibt. Wenn ja, gibt es qualitative Unterschiede zwischen Stimulation unterhalb und oberhalb der ADTH in Bezug auf das Stimulus-evozierte Potential und die oszillatorische Aktivität, die den Zugang zu bewusster Erfahrung im Falle der unterschwelligen Stimulation unterbinden könnte? Darüber hinaus testet diese Studie, welche Merkmale der frühesten neuronalen Reaktionen (Amplitude und Latenz des SEP) *nach* somatosensorischer Stimulation für deren Detektion prädiktiv sind und wie diese Stimulus-evozierten Merkmale mit der intrinsischen oszillatorischen Aktivität unmittelbar *vor* Stimulation im Alpha-Band interagieren, von dem angenommen wird, dass es die Erregbarkeit der sensorischen Kortizes und damit deren Empfänglichkeit für die Verarbeitung externer Reize anzeigt. Studie III wurde daher als EEG-Anpassung der Studie II konzipiert und untersucht diese neuronalen Stimulus-bezogenen Reaktionen für verschiedene Stimulationsintensitäten. Für unterschwellige Reize gab es nur eine P50-Komponente 50 ms nach Stimulation, aber keine weiteren evozierten Potentiale, wodurch frühere Studien repliziert wurden (Libet et al., 1967; Ray et al., 1999; Nierhaus et al., 2015; Forschack et al. 2017). Die P50-Amplitude vergrößerte sich mit zunehmender Stimulationsintensität, war jedoch für die Stimulusdetektion der beiden höchsten Stimulationsintensitäten nicht prädiktiv. Ein stärkeres negatives Potential 150 ms nach Beginn des Stimulus (N150) zusammen mit der somatosensorischen Alpha-Amplitude (d. h. Mu) vor dem Stimulus erklärt am besten die Detektion der somatosensorischen Stimulation.

Die selektive Aufmerksamkeit spielt eine entscheidende Rolle bei der Stimulusdetektion, indem sie die aufgabenrelevanten neuronalen Reaktionen verstärkt und aufgabenunabhängiges Rauschen unterdrückt (Desimone & Duncan, 1995; Hillyard et al., 1973). Darüber hinaus wirkt sich Aufmerksamkeit sowohl auf SEPs als auch auf die Alpha-Band-Aktivität aus. Daher untersucht Studie IV den modulatorischen Einfluss der selektiven räumlichen Aufmerksamkeit bei der Verarbeitung bewusster und unbewusster somatosensorischer Stimuli anhand ihrer Beziehung zu frühen SEPs und der oszillatorischen Mu-Aktivität. Die Ergebnisse zeigen, dass die Aufmerksamkeit die Amplitude der P50-Komponente auf detektierbare und nicht detektierbare Stimulation erhöht und festigen die Vorstellung von zwei getrennten und größtenteils unabhängigen Mechanismen für Aufmerksamkeit und Bewusstsein. Darüber hinaus interagiert die Prä-Stimulus-Mu-(Prä-Mu) Amplitude mit den Stimulus-evozierten Reaktionen.

Interessanterweise beeinflusst die Prä-Mu-Aktivität sowohl Verhaltensreaktionen als auch SEP-Amplituden, wobei letztere je nach Aufmerksamkeitszustand differenziert sind: Mit räumlicher Aufmerksamkeit besteht eine negative quadratische Beziehung zwischen Prä-Mu und evozierten Amplituden, während ohne räumliche Aufmerksamkeit die Beziehung positiv quadratisch ist. D. h., mittlere und höhere Prä-Mu-Amplituden gehen mit großer evozierter Aktivität während räumlicher

Aufmerksamkeit einher und mit geringer evozierter Aktivität ohne Aufmerksamkeit. Dieses Ergebnismuster deutet darauf hin, dass Prä-Mu-Amplitude und Aufmerksamkeit interagieren, jedoch funktional nicht identisch sind.

Diskussion

Diese Arbeit unterstützt nachdrücklich die Ansicht, dass neuronale Reaktionen auf nicht detektierbare somatosensorische Stimulationen eine valide Informationsquelle sind, um die Grundlagen funktioneller Gehirnaktivität zu verstehen. Die unterschwellige somatosensorische Stimulation in dieser Arbeit wurde auf Intensitäten von 30–15% unter ADTH eingestellt und erzeugte zuverlässig Sensitivitätsswerte von Null. Nichtsdestotrotz führen diese nicht detektierbaren Reize etwa 50 Millisekunden nach ihrem Auftreten, zu einer positiven Potentialänderung, der P50. Neben dieser frühen Komponente wurde keine weitere signifikante Potentialveränderung beobachtet. Die Daten in der vorliegenden Dissertation und in früheren kooperativen Arbeiten deuten auf eine qualitativ unterschiedliche Verarbeitung nicht detektierbarer im Vergleich zu detektierbarer somatosensorischer Stimulation in mehreren Aspekten hin: (1) das Fehlen späterer Komponenten (Studie 3, 4 und Nierhaus et al., 2015), insbesondere der N150, welche die Stimulusdetektion anzeigt (Studie 3), (2) erhöhte, nicht aber verringerte Stimulus-bezogene somatosensorische Alpha-Amplituden (Studie 4), (3) verringerte statt erhöhter BOLD-Aktivität (Blankenburg et al., 2003) sowie (4) verringerte funktionelle Konnektivität des primären somatosensorischen Kortex mit Bereichen, die mit bewusster und höherer somatosensorischer Verarbeitung verbunden sind (Nierhaus et al., 2015). Zusammenfassend kann man spekulieren, dass dieses Ergebnismuster eine Verschiebung des Gleichgewichtes zwischen neuronaler Erregung und Hemmung (Isaacson, Scanziani, 2011) zu Gunsten neuronaler Hemmung anzeigt, was die Stimulusdetektion in späteren Verarbeitungsphasen verhindert, wie Nierhaus et al. (2015) argumentiert haben.

Das Fehlen der N150 für unterschwellige, d. h. nicht detektierbare Stimulation, könnte dann auf eine unmodulierte Verbindung zwischen primären sensorischen Kortizes relativ zur Basisaktivität oder sogar auf eine verringerte Konnektivität von S1 mit dem frontal-parietalen Netzwerk (Nierhaus et al., 2015) im Vergleich zu detektierbarer Stimulation hinweisen (Auksztulewicz et al., 2012). Darüber hinaus scheint die Anwesenheit der N150 unabhängig vom experimentellen Kontext zu sein, da Nierhaus und Kollegen (2015) die Teilnehmer ihrer Studie keine Detektionsaufgabe durchführen ließen, sondern diese passiv die überschwellige, d. h. detektierbare Stimulation wahrnahmen. Die Anwesenheit der N150 nach passiv wahrgenommener detektierbarer Stimulation macht diese EEG Komponente zu einem Kandidaten für ein reines neuronales Korrelat des Bewusstseins (Aru et al., 2012; Verleger, 2010).

Für eine frühere Phase der neuronalen Verarbeitung berichtet diese Arbeit jedoch eine Aufmerksamkeitsmodulation der P50, und diese Modulation ist unabhängig von der Stimulusdetektion (Studie 4). In diesem Sinne weisen die Ergebnisse Theorien zurück, die sich Aufmerksamkeit als einen „Gate"-Mechanismus vorstellen, der unbewusste Wahrnehmung und selektive Aufmerksamkeit auf die Endpunkte eines Kontinuums platziert (Brigard & Prinz, 2010; Dixon, 1971). Das heißt, die Aufmerksamkeit schirmt das Gehirn nicht vor schwachen, aber potentiell aufgabenrelevanten Informationen ab, solange diese Informationen denselben Verarbeitungspfad beanspruchen, auf dem der Fokus der Aufmerksamkeit derzeit liegt (Forschack et al., 2017). Darüber hinaus werden auch theoretische Darstellungen, die Aufmerksamkeit als ausreichend für das Bewusstsein betrachten, verworfen (Brigard & Prinz, 2010). Obwohl Aufmerksamkeit kein einheitliches Phänomen ist und die aktuellen Ergebnisse etwas Licht auf einen, wohl aber zentralen Aspekt davon werfen, nämlich fokussierter selektiver Aufmerksamkeit (James, 1890), spricht die frühe P50-Modulation durch Aufmerksamkeit in Abwesenheit von Stimulusdetektion stark für eine Unabhängigkeit von Aufmerksamkeit und Bewusstsein.

Die aktuellen Daten lassen sich am besten durch zwei alternative, aber komplementäre Modelle erklären, die Aufmerksamkeit und Bewusstsein als zwei unabhängige, jedoch miteinander verbundene Konzepte beschreiben (Dehaene et al., 2006; Kiefer, 2012; Kiefer & Martens, 2010). In dem Modell von Dehaene hängt das Ausmaß, in dem ein Stimulus verarbeitet und schließlich detektiert wird, von seiner Stimulusintensität und der Menge verfügbarer Aufmerksamkeitsressourcen ab. In diesem Schema bleiben schwache Reize unbemerkt, unabhängig davon, wie viele Aufmerksamkeitsressourcen verfügbar sind, was mit der Aufmerksamkeitsmodulation der ERPs nach unterschwelligen Reizen in Studie 4 übereinstimmt. Wenn Stimuli prinzipiell stark genug sind, sind sie den Beobachtern möglicherweise noch nicht bewusst, solange die Aufmerksamkeit an anderer Stelle liegt. Das Aufmerksamkeits-Bewusstseinsbildungs-Modell von Markus Kiefer baut auf der Taxonomie von Dehaene auf und erweitert diese insbesondere hinsichtlich der Frage, wie die Aufmerksamkeitsmodulation bei der Verarbeitung nicht detektierbarer Stimulation umgesetzt wird. Unabhängig davon, ob der Reiz bewusst wahrgenommen wird oder nicht, ist der Mechanismus der Aufmerksamkeitskontrolle derselbe: „aufgabenrelevante Verarbeitungspfade werden, durch die Erhöhung der neuronalen Reaktion entsprechender Bereiche im Gehirn, verstärkt, wohingegen aufgabenirrelevante Verarbeitungspfade, durch eine Verringerung der neuronalen Reaktion, abgeschwächt werden“ (übersetzt aus Kiefer, 2012; Kiefer & Martens, 2010).

Im Gegensatz zum Ausbleiben Stimulus-induzierter Mu-Amplitudenmodulationen durch Aufmerksamkeit können die Mu-Amplituden vor dem Stimulus für die Zuweisung von Aufmerksamkeitsressourcen relevant sein. Dieser Zusammenhang wurde sowohl in der Studie von Ede, Lange und Maris (2014) als auch hier in Studie 4 als relativ größere Prä-Mu-Amplituden bei unbeachtetem im Vergleich zu beachtetem Finger gezeigt. Die Beziehung zwischen Alpha und Aufmerksamkeit bei der frühen sensorischen Stimulusverarbeitung scheint jedoch nicht proportional zu sein, da die Größe der P50 bei gleicher Alpha-Amplitude je nach Aufmerksamkeitszustand entweder maximal oder minimal ist (Forschack et al., 2017). Tatsächlich wurde gezeigt, dass Alpha-Band-Modulationen mit der Verbesserung von Verhaltensleistungen durch Aufmerksamkeit korrelieren, insbesondere bei Experimenten zur zeitlichen Aufmerksamkeitssteuerung. Eine Schlussfolgerung lautet daher, dass Alpha nicht die Aufmerksamkeit im Allgemeinen widerspiegelt, sondern spezifische Aspekte davon (Klimesch, 2012), oder auf den jeweiligen Aufgabenkontext hinweisen kann (van Ede et al., 2014).

Curriculum Vitae

Personal Data

Name:	Norman Forschack
Date of birth	11th August, 1985
Children	2
Nationality	German

Education

01/2012–12/2015	**PhD candidate**, DFG funded Graduate School ‘Function of Attention in Cognition, Leipzig
2011	**Diplom (MSc equivalent)**, Psychology, University of Leipzig, Germany Thesis title: *Neuronale Korrelate merkmalsbasierter Aufmerksamkeit in einem Multistimulusdisplay*
2004	**Sophiengymnasium Colditz, Germany,** **Abitur** (A-Level equivalent)

Research and professional experience

Since 03/2018	**Research Associate**, Department of Experimental Psychology and Methods, University of Leipzig, Germany DFG funded project: *The role of alpha rhythm in sensory input control during selective attention*
Since 03/2018	**Guest Scientist**, Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
01/2016–02/2018	**Research Associate**, Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

10/2011–12/2011	**Research Associate**, Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
05/2011–07/2011	**Research Associate**, Department of Experimental Psychology and Methods, University of Leipzig, Germany
09/2008–12/2008	**Research Internship**, Department of Developmental Psychology, University of Leipzig, Germany
03/2007–03/2011	**Undergraduate Research Assistant**, Department of Experimental Psychology and Methods, University of Leipzig, Germany

Teaching

Forschack, N.; Mueller, M. M. (2019). Declarative memory. Seminar: Allgemeine Psychologie II [Basic psychology II], University of Leipzig, Januar 30, 2019

Forschack, N.; Mueller, M. M. (2019). Procedural memory. Seminar: Allgemeine Psychologie II [Basic psychology II], University of Leipzig, January 23, 2019

Forschack, N.; Mueller, M. M. (2018). Procedural memory. Procedural learning. Seminar: Allgemeine Psychologie II [Basic psychology II], University of Leipzig, January 24, 2018

Forschack, N.; Mueller, M. M. (2016). Object-based attention. Seminar: Allgemeine Psychologie I [Basic psychology I], University of Leipzig, November 09, 2016

Forschack, N.; Mueller, M. M. (2015). Object-based attention. Seminar: Allgemeine Psychologie I [Basic psychology I], University of Leipzig, November 11, 2016

Forschack, N.; Kumar, S.; Mehnert, J. (2015) Introduction to scientific research approaches: Brain Computer Interfaces - The Hexa Speller. Lecture: Girls Day, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, April 23, 2015

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Peer-Review

Brain Research

List of publications

Accepted, under revision, submitted or in preparation

Forschack, N., Nierhaus, T., Müller, M. M., & Villringer, A. (submitted) Dissociable neural correlates of stimulation intensity and detection in somatosensation.

Al, E., Iliopoulos, F., **Forschack, N.**, Nierhaus, T., Grund, M., Gaebler, M., Motyka, P., Nikulin, V., & Villringer, A. (submitted). Heart-Brain Interactions Shape Somatosensory Perception and Evoked Potentials.

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Forschack, N. (2017) The role of rolandic alpha on somatosensation and its relation to attention. *Department Colloquium , FU Berlin, June 16, 2017*

Forschack, N. (2017) Die Bedeutung rolandischer Alpha-Aktivität in der Somatosensorik und ihr Bezug zu Aufmerksamkeit. *61. Jahrestagung der Deutschen Gesellschaft für Klinische Neurophysiologie und Funktionelle Bildgebung (DGKN), Leipzig, April 28, 2017*

Forschack, N.: The role of attention and alpha rhythm in shaping evoked somatosensory processing. *Max Planck Institute for Human Cognitive and Brain Sciences, Institute Colloquium, Leipzig, November 23, 2015*

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gemäß § 8(2) der Promotionsordnung

Hiermit versichere ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde, und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Ich versichere, dass die vorliegende Arbeit in gleicher oder in ähnlicher Form keiner anderen wissenschaftlichen Einrichtung zum Zwecke einer Promotion oder eines anderen Prüfungsverfahrens vorgelegt wurde.

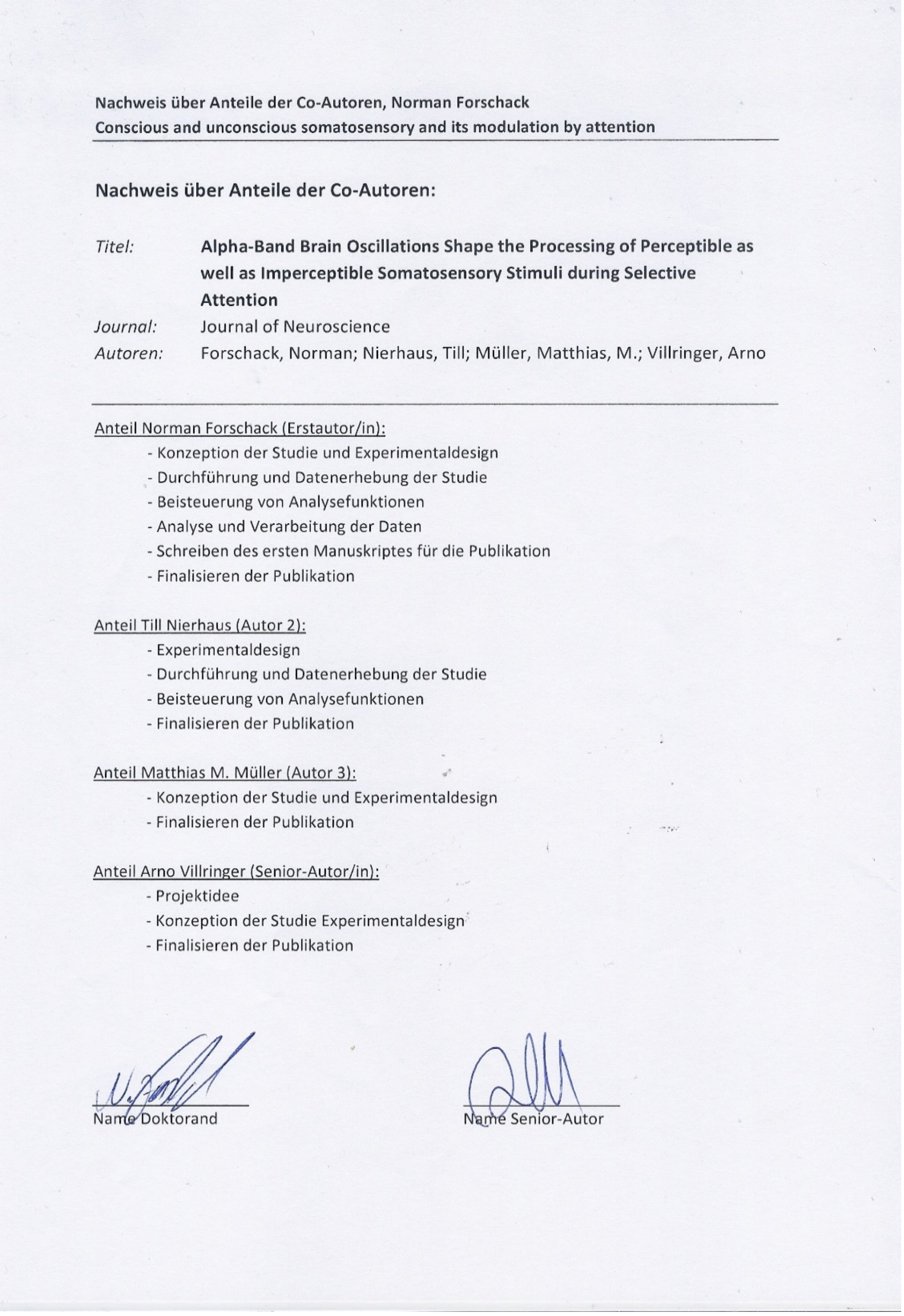
Es haben keine früheren erfolglosen Promotionsversuche stattgefunden.

Die Promotionsordnung der Fakultät für Biowissenschaften, Pharmazie und Psychologie der Universität Leipzig ist mir bekannt und ich erkenne diese an.

Leipzig, den 04. Februar 2019

Norman Forschack

Nachweis über die Anteile der Co-Autoren



Nachweis über Anteile der Co-Autoren, Norman Forschack
Conscious and unconscious somatosensory and its modulation by attention

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Nachweis über Anteile der Co-Autoren:

Titel: **Alpha-Band Brain Oscillations Shape the Processing of Perceptible as well as Imperceptible Somatosensory Stimuli during Selective Attention**
Journal: Journal of Neuroscience
Autoren: Forschack, Norman; Nierhaus, Till; Müller, Matthias, M.; Villringer, Arno

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Anteil Norman Forschack (Erstautor/in):
- Konzeption der Studie und Experimentaldesign
- Durchführung und Datenerhebung der Studie
- Beisteuerung von Analysefunktionen
- Analyse und Verarbeitung der Daten
- Schreiben des ersten Manuskriptes für die Publikation
- Finalisieren der Publikation

Anteil Till Nierhaus (Autor 2):
- Experimentaldesign
- Durchführung und Datenerhebung der Studie
- Beisteuerung von Analysefunktionen
- Finalisieren der Publikation

Anteil Matthias M. Müller (Autor 3):
- Konzeption der Studie und Experimentaldesign
- Finalisieren der Publikation

Anteil Arno Villringer (Senior-Autor/in):
- Projektidee
- Konzeption der Studie Experimentaldesign
- Finalisieren der Publikation

Name Doktorand

Name Senior-Autor