Distilling the neural correlates of conscious somatosensory perception

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Contents

Abstract

The ability to consciously perceive the world profoundly defines our lives as human beings. Somehow, our brains process information in a way that allows us to become aware of the images, sounds, touches, smells, and tastes surrounding us. Yet our understanding of the neurobiological processes that generate perceptual awareness is very limited. One of the most contested questions in the neuroscientific study of conscious perception is whether awareness arises from the activity of early sensory brain regions, or instead requires later processing in widespread supramodal networks. It has been suggested that the conflicting evidence supporting these two perspectives may be the result of methodological confounds in classical experimental tasks. In order to infer participants' perceptual awareness in these tasks, they need to report the contents of their perception. This means that the neural signals underlying the emergence of perceptual awareness often cannot be dissociated from pre- and postperceptual processes. Consequently, some of the previously observed effects may not be correlates of awareness after all but instead may have resulted from task requirements.

In this thesis, I investigate this possibility in the somatosensory modality. To scrutinise the task dependence of the neural correlates of somatosensory awareness, I developed an experimental paradigm that controls for the most common experimental confounds. In a somatosensory-visual matching task, participants were required to detect electrical target stimuli at ten different intensity levels. Instead of reporting their perception directly, they compared their somatosensory percepts to simultaneously presented visual cues that signalled stimulus presence or absence and then reported a match or mismatch accordingly. As a result, target detection was decorrelated from working memory and reports, the behavioural relevance of detected and undetected stimuli was equated, the influence of attentional processes was mitigated, and perceptual uncertainty was varied in a controlled manner. Results from a functional magnetic resonance imaging (fMRI) study and an electroencephalography (EEG) study showed that, when controlled for task demands, the neural correlates of somatosensory awareness were restricted to relatively early activity ($\sim$150 ms) in secondary somatosensory regions. In contrast, late activity ($>$300 ms) indicative of processing in frontoparietal networks occurred irrespective of stimulus awareness, and activity in anterior insular, anterior cingulate, and supplementary motor cortex was associated with processing perceptual uncertainty and reports. These results add novel evidence to the early-local vs. late-global debate and favour the view that perceptual awareness emerges at the level of modality-specific sensory cortices.

Zusammenfassung

Die Fähigkeit zur bewussten Wahrnehmung bestimmt maßgeblich unser Selbstbild als Menschen. Unser Gehirn verarbeitet Informationen auf eine Weise, die es uns ermöglicht, uns der Bilder, Töne, Berührungen, Gerüche und Geschmäcker, die uns umgeben, bewusst zu werden. Unser Verständnis davon, wie neurobiologische Prozesse diese bewusste Wahrnehmung erzeugen, ist jedoch noch sehr begrenzt. Eine der umstrittensten Fragen in der neurowissenschaftlichen Erforschung des perzeptuellen Bewusstseins besteht darin, ob die bewusste Wahrnehmung aus der Aktivität früher sensorischer Hirnregionen entsteht, oder aber die spätere Prozessierung in ausgedehnten supramodalen Netzwerken erfordert. Eine mögliche Erklärung für die widersprüchlichen Ergebnisse, die diesen beiden Perspektiven zugrunde liegen, wird in methodologischen Störfaktoren vermutet, die in klassischen experimentellen Paradigmen auftreten können. Um auf die Wahrnehmung der Versuchspersonen schließen zu können, müssen diese den Inhalt ihrer Wahrnehmung berichten. Das führt dazu, dass neuronale Korrelate bewusster Wahrnehmung häufig nicht sauber von prä- und postperzeptuellen Prozessen getrennt werden können. Folglich könnten einige der zuvor beobachteten Effekte, anstatt tatsächlich bewusste Wahrnehmung widerzuspiegeln, aus den Anforderungen experimenteller Paradigmen entstanden sein.

In dieser Arbeit untersuche ich diese Möglichkeit in der somatosensorischen Modalität. Um zu überprüfen, inwiefern neuronale Korrelate bewusster somatosensorischer Wahrnehmung von den Anforderungen experimenteller Aufgaben abhängen, habe ich ein Paradigma entwickelt, dass die häufigsten experimentellen Störfaktoren kontrolliert. In einer somatosensorisch-visuellen Vergleichsaufgabe mussten die Versuchspersonen elektrische Zielreize in zehn verschiedenen Intensitätsstufen detektieren. Anstatt diese jedoch direkt zu berichten, sollten sie ihre somatosensorischen Perzepte mit gleichzeitig präsentierten visuellen Symbolen vergleichen, die entweder Reizanwesenheit oder -abwesenheit signalisierten. Entsprechend wurde dann eine Übereinstimmung oder Nichtübereinstimmung berichtet. Dadurch wurde die Reizwahrnehmung von Arbeitsgedächtnis und Berichterstattung dekorreliert, die Verhaltensrelevanz detektierter und nicht detektierter Reize gleichgesetzt, der Einfluss von Aufmerksamkeitsprozessen reduziert und die mit der Detektion verbundene Unsicherheit auf kontrollierte Weise variiert. Die Ergebnisse aus einer funktionellen Magnetresonanztomographie (fMRT)-Studie und einer Elektroenzephalographie (EEG)-Studie zeigen, dass die neuronalen Korrelate bewusster somatosensorischer Wahrnehmung auf relativ frühe Aktivität (~150 ms) in sekundären somatosensorischen Regionen beschränkt sind, wenn experimentelle Störfaktoren kontrolliert werden. Im Gegensatz dazu trat späte Aktivität (>300 ms), die auf die Verarbeitung in frontoparietalen Netzwerken hindeutet, unabhängig von der

Reizwahrnehmung auf, und Aktivität im anterioren insulären, anterioren cingulären und supplementärmotorischen Kortex war mit der Verarbeitung von Detektionsunsicherheit und der Berichterstattung verbunden. Diese Ergebnisse liefern neue Erkenntnisse zur Debatte um die Relevanz früher, lokaler vs. später, globaler Hirnaktivität und unterstützen die Ansicht, dass perzeptuelles Bewusstsein in modalitätsspezifischen sensorischen Kortizes entsteht.

List of abbreviations

A1 primary auditory cortex

AAN auditory awareness negativity

ACC anterior cingulate cortex

AIC anterior insular cortex

BA Brodmann area

BMS Bayesian model selection

BOLD blood oxygen level dependent

DCM dynamic causal modelling

ERP event-related potential

FFA fusiform face area

fMRI functional magnetic resonance imaging

GLM general linear model

GNWT Global Neuronal Workspace Theory

IIT Integrated Information Theory

M/EEG magneto-/electroencephalography

NCCs neural correlates of consciousness

NMDA N-methyl-D-aspartate

PFC prefrontal cortex

PPA parahippocampal place area

PPC posterior parietal cortex

RPT Recurrent Processing Theory

RSVP rapid serial visual presentation

S1 primary somatosensory cortex

S2 secondary somatosensory cortex

SAN somatosensory awareness negativity

SMA supplementary motor area

TMS transcranial magnetic stimulation

V1 primary visual cortex

VAN visual awareness negativity

List of original research articles

Study 1

Schröder, P., Schmidt, T. T., & Blankenburg, F. (2019). Neural basis of somatosensory target detection independent of uncertainty, relevance, and reports. *eLife*. 8, e43410. doi: 10.7554/eLife.43410.

Study 2

Schröder, P., Nierhaus, T., & Blankenburg, F. (2021). Dissociating perceptual awareness and postperceptual processing: The P300 is not a reliable marker of somatosensory target detection. *Journal of Neuroscience*. doi: 10.1523/JNEUROSCI.2950-20.2021.

1 Introduction

As you sit down to read these words, a cascade of events is initiated that enable you to make sense of the chain of letters on the page in front of you. Light is reflected from the sheet of paper or emitted from your computer screen to stimulate photoreceptors in your retina. Biochemical processes in these receptors transform the light into electrical signals that travel along the optic nerve to the thalamus and on to the occipital cortex where the primary visual area of the brain is situated. From here, the signal is conveyed to widely distributed brain regions that allow you to interpret the information, integrate it with other incoming signals, and use it to guide your behaviour. However, besides efficient information processing, something more is happening. Somewhere in this chain of processes, the information travelling through your brain gains a subjective quality. There is a feeling to the sensations caused by the light, and this feeling, along with the taste of your last sip of coffee or maybe the loud voice of your neighbour upstairs, determines your subjective experience of this very moment in time (Koch, 2019). In other words, you are conscious of the world around you. The capacity for conscious experience is widely considered the one thing that sets humans, and probably many animals, apart from other information processing entities; it is what makes us special, at least in our own, subjective perception of the world. Yet, its biological basis, the way the soft tissue in our brains gives rise to the multifaceted experiences we have every day, remains poorly understood.

Neurological conditions that influence our subjective experience, as found in split-brain or blindsight patients, have been known for a long time, and they have demonstrated the profound dependence of conscious experience on the integrity of the human brain (Sperry, 1964; Weiskrantz, Warrington, Sanders, & Marshall, 1974). Nonetheless, for much of the twentieth century, it was considered futile or even unscientific to attempt to study consciousness empirically (Seth, 2018). A milestone in the transformation from being a dubious corner of cognitive science to becoming the prolific area of neuroscientific research it is today was set in the early 1990s, when Francis Crick and Christof Koch published their seminal paper arguing for a principled neurobiological approach to the study of consciousness (Crick & Koch, 1990). They suggested to go beyond the hitherto accepted black-box approach and aimed at identifying the neural correlates of consciousness (NCCs): those neural populations, their response properties and connectivity patterns, that correlate with conscious experience and constitute ’the minimal neuronal mechanisms jointly sufficient for any one specific conscious percept’ (Tononi & Koch, 2008). The advance of modern neuroimaging techniques has granted us the opportunity to study these signals non-invasively in humans and although we are still far from understanding why and how consciousness exists at all, we are now able to connect certain brain responses and activity patterns with states of subjective experience. Insights from functional magnetic resonance imaging (fMRI) studies, which provide a high spatial resolution and may identify relevant brain regions, are combined with magneto-/electroencephalography (M/EEG) results that elucidate the temporal dynamics of perception. In addition, invasive recordings in behaving non-human animals contribute a spatially restricted but direct insight into the neural firing patterns underpinning distinct perceptual outcomes. In the last 30 years, these methods have significantly advanced our understanding of the neural processes that lead up to a conscious percept.

Research on the NCCs can be broadly distinguished into two branches that are pursued largely independently. One investigates global states of consciousness, such as coma, general anaesthesia, or dreamless sleep, the other focuses on specific contents of subjective experience, such as the taste of chocolate or the feeling of smooth fabric on the skin (Koch, Massimini, Boly, & Tononi, 2016). In the state-based approach, researchers contrast neural signals during normal wakefulness with those found in altered states of consciousness to identify the neural processes supporting awareness in general. While this approach may give insights into the brain's general capacity to generate a conscious state, it comes with some drawbacks. Most importantly, states of reduced awareness are often linked with profound physiological changes as well as reduced levels of arousal (Laureys, Boly, Moonen, & Maquet, 2009). These and other background processes, such as intact afferent excitation, are necessary for normal consciousness to occur but do not qualify as NCCs (Koch et al., 2016). There are some notable exceptions where fluctuations of consciousness occur within a particular state, for example during periods of sleep with and without dreaming (Siclari et al., 2017), but overall, the distinction between enabling processes and core processes generating awareness remains challenging. Another challenge lies in the correct identification of a patient's state of consciousness. Diagnoses are commonly based on behavioural measures and research has shown that this approach can fail to detect consciousness in unresponsive patients (Owen et al., 2006), further complicating the interpretation of corresponding results (Overgaard & Overgaard, 2010). The alternative approach rests on identifying signals associated with the conscious experience of specific perceptual contents. In the lab, content-specific NCCs (Koch et al., 2016) are usually studied by contrasting experimental conditions in which a particular content is consciously perceived with conditions in which this content is not perceived (detection), or by contrasting conditions in which one content is perceived instead of another (discrimination). Thus, rather than identifying neural processes supporting the conscious state in general, this approach aims at identifying processes supporting the selection of a particular content into conscious experience (Hohwy, 2009). The benefits of this method are twofold: first, the possibility to obtain introspective reports from participants instead of relying exclusively on behavioural measures accounts for the private nature of subjective experience. Second, since different contents of consciousness can be induced in the same person and in a similar context, physiological background conditions can be largely equated, improving experimental control (Overgaard & Overgaard, 2010). If then, the physical stimulus parameters are also held constant, the contrast between conscious and unconscious conditions is thought to isolate exactly those signals that reflect subjective experience.

Previous studies investigating content-specific NCCs have identified a wide range of candidate processes. In the next section, I will review their most important findings and introduce some of the theories they have inspired. Since the neural correlates of perceptual awareness have been studied most extensively in the visual modality, I will start by examining these results in some detail, to illustrate the origin of current models of conscious perception. Then, to arrive at a more comprehensive overview of the most promising candidate NCCs across modalities, I will continue by assessing corresponding results from the auditory and somatosensory modalities and identify similarities that may suggest common underlying mechanisms. Throughout, I will focus on research investigating poststimulus neural responses[1] and, for simplicity, I will use the terms conscious perception, awareness, and experience interchangeably.

1.1 The neural foundations of perceptual awareness

1.1.1 Visual awareness

One of the most productive approaches in studying the neural correlates of conscious perception has been the contrastive method, in which brain responses to consciously perceived stimuli are compared to responses to stimuli that are not consciously perceived. One of the challenges of this method is to create experimental conditions in which the physical stimulation of the senses remains constant, but the participants' awareness thereof varies, allowing researchers to isolate those signals that specifically reflect the subjective experience of sensory contents. Among all sensory modalities, vision is arguably the most obvious candidate to create such conditions, given that a wide range of different stimuli with varying properties and complexity can easily be presented and manipulated on a conventional computer screen. For this reason, and the fact that the visual system is the best researched in perceptual neuroscience, most of the investigation into the neural correlates of awareness has been performed in the visual modality. In the following, I will review the most important findings and introduce selected theories of conscious perception they have inspired. These theories can be broadly classified into three categories based on the

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[1] An important body of research has demonstrated that prestimulus brain states, such as the phase or power of neural oscillations, can influence perception, especially at threshold level stimulus intensities (e.g. Ruhnau, Hauswald, & Weisz, 2014; Samaha, Iemi, Haegens, & Busch, 2020). However, since prestimulus effects merely bias perception but cannot be its generators, for the purpose of this thesis, I will disregard such influences and treat prestimulus effects as a source of noise (but see section 3.2.1 for a discussion of their relevance as precursors of conscious perception).

extent of cortical activation that is believed necessary for the emergence of any one conscious percept: 1) those that assume activity in dedicated local processing modules to be the substrate of perceptual awareness, 2) those that focus on the interaction between early sensory regions and regions at different levels higher up the sensory hierarchy, and 3) those that consider activation of widely distributed networks involving supramodal association cortices to be necessary for conscious perception.

Dedicated sensory processing modules

One of the most straightforward ways to test the causal dependence of conscious experience on the integrity of specific brain regions is to probe awareness in patients who have suffered lesions in these particular regions. Damage to primary visual cortex (V1) results in an inability to consciously perceive the visual world and patients suffering from this condition are deemed cortically blind. However, some of these patients, although they report to lack all visual experience, show above chance performance in visually guided tasks, implying that some visual information continues to be processed unconsciously (Weiskrantz, 1986). This phenomenon is called blindsight, and while its biological foundations remain debated, it suggests that V1 may serve more than a simple relay point for visual input and may instead be involved in the emergence of perceptual experience.

The relevance of early sensory regions for the emergence of conscious perception is supported by fMRI studies that have employed the binocular rivalry paradigm in healthy participants. Binocular rivalry is a form of bistable perception, in which two different images are presented to the left and right eye in the same retinal location. The brain cannot integrate these images and instead periodically switches between them every few seconds, such that the observer sometimes perceives one image and sometimes the other (Blake & Logothetis, 2002). The binocular rivalry paradigm is an elegant way of manipulating subjective experience without changing physical inputs. Associated dynamical changes of perceptual contents have been reported to covary with blood oxygen level dependent (BOLD) responses in V1 (Lee, Blake, & Heeger, 2005; Polonsky, Blake, Braun, & Heeger, 2000), supporting its role in conscious perception. Interestingly, although single unit recordings in monkeys performing the same task have similarly shown that neurons in V1 correlate with the rivalrous percept, only very few V1 neurons are completely silent when their preferred stimulus is perceptually suppressed (Leopold & Logothetis, 1996). This observation suggests that activation of stimulus selective neurons in V1 is not sufficient for the emergence of perceptual experience. In contrast, neurons in extrastriate visual areas, such as inferior temporal cortex, correlate much more reliably with the currently dominant percept and seem to reflect perception beyond ambiguities (Sheinberg & Logothetis, 1997). In humans, the dissociation of activity in V1 and conscious visual percepts has been demonstrated in several fMRI studies. Haynes and Rees (2005) found that the orientation of visual gratings could be decoded from BOLD responses in V1 even when these gratings were visually masked and therefore not consciously perceived. In fact, many visual features that do not result in dissociable percepts elicit differential responses in V1, further suggesting that V1 activity alone is not consciously accessible (Rees, Kreiman, & Koch, 2002). In line with this conclusion, studies using EEG have shown that when attention is controlled for, early visual evoked potentials that are associated with processing in early visual areas (P1 and N1) do not differentiate between seen and unseen stimuli (Railo, Koivisto, & Revonsuo, 2011). Causal evidence comes from a study with quadrantanopic patients with extrastriate lesions. The V1 region in these patients was fully intact and yet, they showed complete blindness in one visual quadrant, demonstrating that V1 integrity alone is not sufficient for conscious perception (Horton & Hoyt, 1991). Conversely, Mazzi, Mancini, and Savazzi (2014) have shown that visual experience might not even be dependent on V1, as demonstrated by transcranial magnetic stimulation (TMS) over posterior parietal regions that resulted in the perception of phosphenes in patients with lesioned V1. Taken together, evidence for V1 as a neural correlate of conscious perception is outweighed by evidence showing little covariation of V1 activity with perceptual contents. Consequently, it is now widely believed that activity in primary visual areas serves a role in unconscious processing upstream of areas determining access to consciousness (Leopold, 2012).

Nonetheless, the relevance of specified processing modules for conscious perception is not entirely off the table. In fact, many studies have shown that the perception of specific visual features is reflected in activity fluctuations in feature-selective visual regions. One of the most prominent examples is found in the selective activation of the fusiform face area (FFA) and parahippocampal place area (PPA) in response to faces and houses, respectively. Tong, Nakayama, Vaughan, and Kanwisher (1998) showed that when faces and houses were presented in a binocular rivalry setting, even though the retinal stimulation never changed, activity in FFA and PPA closely tracked the perceptual switches, each activating when their preferred stimulus became conscious. These activity fluctuations showed a striking similarity to those evoked by physical switches between the two stimuli. Moutoussis and Zeki (2002) have shown similar results using a dichoptic colour fusion paradigm. Given that unconscious stimuli can similarly activate FFA and PPA, these authors argue that it is not the activation of stimulus-specific regions per se that results in conscious awareness but the strength of activation, which they found to be considerably larger for perceived compared to unperceived stimuli. Similar observations have been made for motion perception. In motion induced blindness, a phenomenon in which a stationary target stimulus disappears from vision periodically when surrounded by a moving mask stimulus, disappearance of the target stimulus is associated with a reduction in target specific cortical regions in extrastriate visual area V4 and a concurrent increase in activity in motion-related dorsal regions (Donner, Sagi, Bonneh, & Heeger, 2008). More recently, M. Schneider, Kemper, Emmerling, De Martino, and Goebel (2019) used submillimetre fMRI at ultra-high field strength to show that neural populations in human motion complex are organised in cortical columns that are selectively activated during vertical vs. horizontal visual motion. Interestingly, these same columns showed selective activity increases when ambiguous visual motion stimuli were displayed, and perceptual experience switched from vertical to horizontal motion and vice versa without any changes in retinal input. Collectively, these results suggest that specified regions in the ventral and dorsal visual streams are involved in the generation of conscious visual content.

Findings like these support a modular view on perception, in which different dedicated cortical processing sites or coalitions of neurons (Crick & Koch, 2003) underlie the emergence of different perceptual contents. This account is well reflected in the observation that patients suffering from different neurological conditions affecting perception often show a selective impairment of a particular perceptual feature, such as faces in prosopagnosia, colour in achromatopsia, or motion in akinetopsia (Haque, Vaphiades, & Lueck, 2018). In these conditions, perception of other features is usually unaffected and of course, patients with visual agnosia who show a complete loss of subjective visual experience, retain their capacity to have conscious experience in other modalities. Importantly, each of these conditions is associated with lesions in specific, feature-selective processing sites in the visual processing streams (Haque et al., 2018). This level of functional specialisation seems to suggest that our conscious perception arises from many functionally distinct units or modules (Celesia, 2010) and some even go as far as to conclude that consciousness is not a unified entity as often assumed but instead consists in many distinct microconsciousnesses (Zeki, 2003).

Taken together, some compelling evidence hints at a modular organisation of conscious visual experience. However, this view is far from being universally accepted. In fact, many researchers believe that activity in isolated units is not sufficient for perceptual awareness and point to cases where such activity fails to elicit conscious percepts. For example, Goebel, Muckli, Zanella, Singer, and Stoerig (2001) reported that in patients with V1 lesions, visual stimulation can nevertheless result in activity in ipsilesional areas V4 and V5 that reaches the levels of corresponding activity in the intact hemisphere, and yet fails to evoke any conscious experience of the presented stimuli. Such findings stress the need for more integrative views of conscious perception.

Local recurrent interactions

As reviewed in the previous section, conscious experience of specific visual features is accompanied by activity in feature-selective cortical regions. However, the same conscious experience often breaks down when other regions in the visual processing stream, in particular V1, are damaged. A perspective that may account for the conflicting findings regarding the role of V1 considers the timing of its activation. In a series of experiments, Lamme and colleagues (1998; 2001; 2002) observed that early discharges of V1 neurons in macaques closely mirrored the sensory properties of visual texture stimuli, whereas later responses were modulated by their perceptual features. In a figure ground segregation task, the animals had to detect a texture of oriented line segments (the figure) on a background of orthogonal lines (the ground). The authors found that early transients in V1 were identical for hit and miss trials but a later component of the V1 evoked response at >100 ms was modulated by perception: when monkeys detected the figure, V1 responses showed contextual modulation with different figure and ground response amplitudes, but when they missed the figure, this late contextual modulation vanished (Supèr et al., 2001). Further experiments showed that contextual modulation in V1 is absent under anaesthesia (Lamme et al., 1998) and selectively suppressed when visual backward masking leads targets to go unnoticed (Lamme et al., 2002). Collectively, these findings demonstrate the importance of late activity in V1 for the emergence of visual awareness. Given its timing, this reactivation is believed to result from cortico-cortical feedback from horizontal and backward connections, suggesting that recurrent interactions between V1 and higher-order visual areas play a critical role in conscious perception. This view has been formulated in the Recurrent Processing Theory (RPT, Lamme & Roelfsema, 2000; Lamme, 2006). RPT posits that sensory information is first processed in a feed-forward sweep from low-level to high-level brain areas, which allows for very basic feature extraction but remains unconscious. Conscious perception arises as soon as this feed-forward sweep is consolidated by re-entrant feedback from higher areas to form recurrent loops of activity (Lamme, 2006). Importantly, while activity in high-order regions, for example in prefrontal cortex (PFC), allows for attentional amplification, encoding in working memory, and reporting of perceived stimuli, according to RPT they are not required for the emergence of perceptual awareness. Instead, relatively local recurrent loops within sensory cortices are deemed sufficient (Lamme, 2018).

Since its inception, many studies have found evidence in support of RPT. Using EEG in humans, Fahrenfort, Scholte, and Lamme (2007) have shown that masked and thus, invisible stimuli are propagated to extrastriate areas in a feed-forward sweep similar to that for unmasked stimuli, whereas later components that may be indicative of re-entrant processing are suppressed in the masked condition. Boehler, Schoenfeld, Heinze, and Hopf (2008) have found similar results using MEG and further assert that the awareness-related increase in feedback processing to V1 precedes signals related to attention, suggesting that these are distinct processes. In line with these studies, the earliest event-related potential (ERP) that is consistently found to correlate with awareness across various paradigms is the visual awareness negativity (VAN), a negative potential over occipital-temporal electrodes that occurs at ~200 ms post-stimulus (Eklund & Wiens, 2018; Koivisto & Grassini, 2016; Koivisto & Revonsuo, 2003; Railo, Revonsuo, & Koivisto, 2015). The VAN has been interpreted as a marker of recurrent processing in extrastriate visual cortex and is therefore often taken as evidence in favour of RPT (Förster, Koivisto, & Revonsuo, 2020; Koivisto, Salminen-Vaparanta, Grassini, & Revonsuo, 2016).

FMRI studies using connectivity measures have further demonstrated the association of visual awareness with interactions between regions in striate and extrastriate visual cortex. Haynes, Driver, and Rees (2005) used a metacontrast masking paradigm, in which a visual target stimulus was rendered invisible by presenting a mask in close spatial proximity. They found that the subjective invisibility of masked stimuli was selectively correlated with a decoupling of V1 and fusiform gyrus. Similarly, Fahrenfort et al. (2012) have shown that conscious face perception is associated with increased coupling between FFA and V1 as investigated with psychophysiological interaction analysis.

Causal evidence for the dependence of visual awareness on recurrent interactions in visual cortex comes from TMS studies. By disrupting the processing in visual areas at different time points after stimulus presentation, various studies have demonstrated the importance of late reactivation in V1. Pascual-Leone and Walsh (2001) used TMS pulses on V1 and V5 to test the causal relevance of late responses in V1 for visual motion perception. They found that when the V1 pulse followed the V5 pulse by 5–45 ms, that is after the stimulus had already been processed in V1 and V5 in the feed-forward sweep, perception of a motion phosphene was disrupted. Silvanto and colleagues later confirmed these results by showing that performance on a motion detection task was impaired both if TMS stimulation of V1 preceded or followed the critical time point of V5 activation (Silvanto, Lavie, & Walsh, 2005) and that subthreshold pulses to V5 that alone were insufficient to induce a motion phosphene could result in motion perception when followed by a suprathreshold pulse to V1, resembling a late enhancement of subliminal information that had been signalled back to early striate cortex (Silvanto, Cowey, Lavie, & Walsh, 2005, see also Hurme, Koivisto, Revonsuo, & Railo, 2017). Ro, Breitmeyer, Burton, Singhal, and Lane (2003) used metacontrast masking and found that TMS over V1 at the time of mask processing recovered target perception, which was otherwise suppressed by the mask. Importantly, the suppression of the mask by TMS was greater if the target had been present before mask presentation compared to when it had been absent, suggesting that feedback signals from higher visual areas associated with target processing led to reduced mask processing in V1. All of these results demonstrate that even when the feed-forward sweep is successfully propagated along the visual hierarchy, sensory information does not become conscious until it is consolidated by feedback signals that result in late activity in V1.

There are several reasons why recurrent processing may be a plausible signature of perceptual experience. First, recurrent loops can bind individual features into a coherent scene by reactivating neural populations with different receptive fields in a coordinated fashion to create a unified conscious experience (Lamme, 2018). Moreover, recurrent processing is selective, in that it primarily reactivates those neural populations that have previously been activated in the feedforward sweep (Lamme, 2018; Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008). This selectivity has been suggested to be realised by N-methyl-D-aspartate (NMDA) receptors, which can only be activated when the membrane potential is already depolarised (Blanke & VanDongen, 2009). Through this mechanism, feedback connections may induce synaptic plasticity and create lasting network changes, potentially explaining phenomena such as paired pulse facilitation and suppression (Lamme, 2018). If perceptual awareness indeed depends on feedback activation of NMDA receptors, this might also explain why neurological conditions that affect NMDA receptor signalling, as well as pharmacological NMDA receptor antagonists, such as ketamine, alter conscious experience (Berkovitch, Dehaene, & Gaillard, 2017; Dalmau, Lancaster, Martinez-Hernandez, Rosenfeld, & Balice-Gordon, 2011; Van Loon et al., 2016). Finally, through recurrent excitation, stimulus representations in sensory cortices may be amplified and sustained, making them available to further processing and encoding in working memory (Mashour, Roelfsema, Changeux, & Dehaene, 2020).

In sum, the importance of recurrent processing for visual awareness has been demonstrated in many studies and is supported by a neurobiologically plausible mechanism. However, whether conscious perception and recurrent loops can be mapped one to one remains debated. For example, it has been shown that purely feedforward activity can effectively guide visual behaviour (Koivisto, Kastrati, & Revonsuo, 2014; T. Schmidt & Schmidt, 2009; VanRullen & Koch, 2003) and, conversely, the finding that TMS over posterior parietal cortex (PPC) can induce phosphenes in patients with V1 lesions (Mazzi et al., 2014) suggests that not all visual experience is reliant on late activity in V1. In fact, recurrent processing and awareness seem to occasionally dissociate as observed in gist perception (Tsuchiya & van Boxtel, 2010). Furthermore, early activity associated with local recurrent processing is far from being the only correlate of awareness. For example, target perception in backward masking is reflected in multiple recurrent loops, the first one peaking at 160 ms within visual cortex and then increasingly incorporating more parietal and frontal regions suggesting long-range recurrent interactions (Fahrenfort, Scholte, &

Lamme, 2008). Most studies reporting the VAN also find enhanced activity for conscious stimuli in a later time window, the P300, which is believed to index processing in distributed frontoparietal networks (Eklund & Wiens, 2019; Sergent, Baillet, & Dehaene, 2005). These observations suggest that regions beyond sensory cortices may play an important role in the emergence of conscious perception.

Supramodal cortical networks

Besides activity in sensory cortices, many studies on visual awareness have shown activation of widely distributed frontoparietal networks when stimuli are consciously perceived. For example, Dehaene et al. (2001) found that seen words induce a widespread activation of a left-lateralised network of areas in visual, posterior parietal, and prefrontal regions, whereas activity related to words rendered invisible by masking was largely restricted to visual areas. Likewise, Carmel, Lavie, and Rees (2006) reported greater activity in frontal and posterior parietal regions during the perception of flickering stimuli, and Cignetti et al. (2014) reported higher activation levels in a right frontoparietal network in participants that perceived illusory movements. The role of the PFC in particular has been strengthened by a study using a metacontrast masking paradigm with matched performance levels that found that conscious stimulus perception was specifically associated with increased BOLD activity in the left dorsolateral PFC (Lau & Passingham, 2006). The same region has also been demonstrated to show increased functional connectivity with extrastriate cortex during spontaneous object recognition (Imamoglu, Kahnt, Koch, & Haynes, 2012). More recently, Liu, Yu, Tse, and Cavanagh (2019) investigated a powerful visual illusion called the “double-drift” illusion, in which the direction of motion of a rotating Gabor patch is misperceived, producing mismatches of perceived and physical motion paths of more than 45°. Using fMRI and multivariate decoding, they found that the passively viewed illusory motion path and matched physical control did not share activation patterns in visual cortex but instead could be cross-classified from regions in PFC. Aggregating these findings, a meta-analysis of 19 fMRI studies investigating the change from unconscious to conscious vision in a wide range of experimental paradigms found common activation in a network of regions encompassing not only visual but also temporal, parietal, frontal, and insular cortices (Bisenius, Trapp, Neumann, & Schroeter, 2015), that is areas that are not specific to any one sensory modality. These results further support the view that conscious perception is associated with activation of a wide network of regions, including supramodal association cortices.

Activation of this network is presumed to be reflected in a prominent ERP in the M/EEG signal that is routinely observed to correlate with perceptual awareness: the P300[2], a positive potential over centroparietal electrodes at ~350 ms. Sergent et al. (2005) demonstrated its association with conscious vision in an attentional blink paradigm. The attentional blink phenomenon is observed when two visual target stimuli are successively presented in a rapid visual stream (rapid serial visual presentation, RSVP). Detection of the first target often leads the second target to go unnoticed, providing a good opportunity to measure brain activity for seen and unseen stimuli during identical physical stimulation. Sergent and colleagues asked participants to rate their subjective visibility of the second target and found that the N2 component (i.e. VAN) scaled linearly with visibility whereas the P3a and P3b components showed a non-linear response, which the authors interpreted to reflect stimulus awareness. Similar results have been observed in backward masking (Fu et al., 2017; Lamy, Salti, & Bar-Haim, 2009) and metacontrast masking (Del Cul, Baillet, & Dehaene, 2007), and many more studies have reported the P300 as a correlate of awareness across different experimental paradigms and for various stimulus materials (Boncompte & Cosmelli, 2018; Eklund & Wiens, 2018; Rutiku, Martin, Bachmann, & Aru, 2015; Ye, Lyu, Sclodnick, & Sun, 2019). Collectively, these studies suggest that the neural processes supporting visual awareness occur at relatively late latencies and are unlikely to exclusively originate from visual areas.

Besides EEG and fMRI, intracranial recordings have been used to test the specific relevance of regions in visual and prefrontal areas, respectively. Van Vugt et al. (2018) measured multiunit activity from V1, V4, and dorsolateral PFC in monkeys performing a contrast detection task. Although activity in all three regions differentiated between hit and miss trials, the authors observed that V1 and V4 activity on easy (high contrast) miss trials was similar or even higher than on difficult (low contrast) hit trials. In contrast, activity in dorsolateral PFC reliably dissociated hit from miss trials across all contrast levels. Additionally, this region showed similar late activity for hit and false alarm trials, suggesting a reliable reflection of perceptual reports. To obtain data with high spatiotemporal resolution in humans, Gaillard et al. (2009) recorded brain activity in patients undergoing surgery who were implanted with intracortical electrodes in many different brain regions. They report that in a backward masking paradigm, masked words elicited higher activity than masked blanks in occipital electrodes, whereas unmasked words elicited higher activity than unmasked blanks primarily in frontal electrodes, which they interpret as reflecting unconscious and conscious processing, respectively.

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[2] The P300 is also known as P3 or late positivity and it can be separated into a frontocentral P3a component, associated with involuntary orienting and novelty responses, and a slightly later, centroparietal P3b component, presumed to relate to voluntary target detection (Polich, 2007). It is usually this latter component that is reported to correlate with awareness, but since not all studies make this distinction, I will generally refer to it as the P300.

Finally, the relevance of high-level regions for perceptual awareness is further supported by the fact that disruption of processing in these regions has been shown to compromise the ability to discriminate specific visual features (Candidi, Urgesi, Ionta, & Aglioti, 2008) and alter perceptual thresholds (Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009). In binocular rivalry, the PFC is assumed to be involved in generating perceptual switches (Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Lumer, Friston, & Rees, 1998; Sterzer & Kleinschmidt, 2007), a perspective that implies a causal influence on perceptual contents. Gelbard-Sagiv, Mudrik, Hill, Koch, and Fried (2018) recorded the activity of single neurons in humans and found that perceptual switches were preceded by nonselective activity in frontal cortex as early as 2 s before the switch occurred, followed by stimulus-selective activity in temporal regions 1 s before the switch. The authors conclude that a medial fronto-temporal network is responsible for generating endogenous switches of perceptual experience.

Taken together, there is ample evidence that conscious perception of visual stimuli is associated with a strong activation of neurons in many regions across the cortex and that this late activation can be recorded from the human scalp as a late positive potential, the P300. These observations have inspired an alternative theory of conscious perception, the Global Neuronal Workspace Theory (GNWT, Baars, 1997; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Dehaene & Naccache, 2001). Unlike RPT, GNWT assumes that activity that is restricted to sensory regions and local recurrent loops is not sufficient to generate conscious experience. Instead, any conscious percept is believed to presuppose a non-linear ignition of the global workspace, a set of neural populations that are distributed across the cortex and form a reverberating network that primarily encompasses frontal and parietal regions but may also include sensory cortices or other regions depending on the specific perceptual contents that populate consciousness at any given moment (Mashour et al., 2020). Workspace activation is believed to reflect broadcasting and global accessibility of stimulus information, allowing for flexible cognitive operations, such as working memory, decision making, and action planning. Thus, while RPT is often considered a low-level, sensory theory of conscious perception, GNWT falls within the category of high-level, cognitive theories. Accordingly, while RPT predicts relatively early, sensory correlates of awareness, GNWT predicts a late network activation, in particular, activity in distributed regions in fMRI studies and a non-linear P300 component in M/EEG studies (Dehaene & Changeux, 2011).

As seen above, a wealth of evidence supports the role of high-level association cortices in conscious perception. Nonetheless, some challenges remain. For example, Sandberg et al. (2014) used intermittent presentation of dichoptic stimuli in combination with MEG to dissociate the correlates of perceptual content, stabilisation, and reversals in binocular rivalry. Using decoding, they found that occipital and temporal sources in the VAN time window were most predictive of perception whereas sources in temporal and parietal regions were most predictive of switches. Their results do not support a role for the frontal cortex in perception or perceptual switches. Similarly, using multivariate analysis of MEG signals in a masking paradigm, Andersen, Pedersen, Sandberg, and Overgaard (2016) showed that graded perceptual awareness can be decoded from occipital sources with higher accuracy than from frontal sources during both early (VAN) and late (P300) time windows. Moreover, some studies have found that even unseen stimulus information seems to be processed to the level of perceptual interpretation (Vandenbroucke, Fahrenfort, Sligte, & Lamme, 2014) and can enter late processing stages, as suggested by successful decoding of unconscious stimuli from late M/EEG signals originating from parietal and frontal regions (King, Pescetelli, & Dehaene, 2016; Salti et al., 2015). These findings challenge the rigid distinction between unconscious processing in sensory regions and conscious processing in the global workspace. We must also keep in mind that studies focusing on correlates of awareness that generalise across modalities (Sanchez, Hartmann, Fuscà, Demarchi, & Weisz, 2020) or paradigms (Bisenius et al., 2015) are inevitably biased towards finding amodal correlates of awareness since they disregard specific perceptual contents that might be reflected in content-specific, sensory correlates. Thus, whether conscious visual perception does indeed require activation of a global workspace, remains debated.

1.1.2 Auditory awareness

A unique property of auditory perception is that there is no inherent spatial organisation of incoming signals except for slight interaural time and loudness differences. Thus, in order to make sense of the acoustic world, the brain needs to organise incoming signals into separate auditory streams that accurately represent information emanating from distinct sources (Snyder, Gregg, Weintraub, & Alain, 2012). This property can be used in experimental settings to create ambiguous sound stimuli (Gutschalk & Dykstra, 2014) and auditory illusions (Deutsch, 1990). For example, whether a signal is perceived as one integrated auditory stream or as two separate streams depends on various parameters that can be manipulated experimentally to tease apart neural signals reflecting its physical and perceptual properties, respectively. In auditory streaming experiments, an alternating sequence of high and low pure tones is typically presented as tone triplets with small gaps in between (ABA–ABA). By manipulating the tones' distance in pitch or their loudness difference between the two ears it is possible to create bistable conditions, in which a physically identical signal is sometimes perceived as one integrated stream with a galloping rhythm and sometimes as two separate streams with regular rhythms, for example one of high and one of low pitch (Hill, Bishop, Yadav, & Miller, 2011). Studies that have used this approach in combination with fMRI to study the BOLD correlates of auditory percepts have reported that activity in primary auditory cortex (A1), located in the auditory core region on Heschl’s gyrus (Hackett, 2011), tracks the alternating percepts induced by the ambiguous stimulation (Hill et al., 2011; Schadwinkel & Gutschalk, 2011), suggesting that activity in A1 is sensitive to the perceptual dimension of sound processing. Further evidence for a potential role for A1 in auditory awareness comes from studies employing the continuity illusion, in which an interrupted sound is perceived as continuous if the gap is filled with broadband noise. Both fMRI and MEG investigations in humans have shown that A1 activity indicative of gap processing is suppressed during perception of illusory continuity (Riecke, Van Opstal, Goebel, & Formisano, 2007; Riecke, Esposito, Bonte, & Formisano, 2009). Likewise, electrophysiological recordings in macaques have shown that single neurons in A1 respond to the interrupted but illusory reconstructed stimuli in the same way as they do to continuous stimuli, indicating that the illusory percept is instantiated at the level of A1 (Petkov, O’Connor, & Sutter, 2007). Another animal study has demonstrated that A1 activity in ferrets is predictive of perceptual choices during pitch perception (Bizley, Walker, Nodal, King, & Schnupp, 2013), again suggesting that the transformation from physical to perceptual properties occurs already at the level of A1.

In spite of these results, whether A1 is indeed a substrate of auditory awareness remains debated. Particularly, observations in patients with bilateral lesions in auditory cortex cast doubt on its relevance as an NCC. Although reports of persistent cortical deafness following bilateral temporal infarction exist (Bahls, Chatrian, Mesher, Sumi, & Ruff, 1988), other patients only show selective impairment in the perception of certain acoustic features, such as speech sounds, but maintain a basic capacity for tone detection (Dykstra, Koh, Braida, & Tramo, 2012; Kaga, Shindo, & Tanaka, 1997; although it has been suggested that this ability could be due to recovery processes, see Talwar, Musial, & Gerstein, 2001). Interestingly, one patient with bilateral auditory cortex lesions was found to be unaware of sounds during passive stimulation but regained his awareness of sound on- and offsets when actively listening to them (Engelien et al., 2000). Sound detection under these conditions of directed attention was associated with activity in lateral prefrontal and the spared middle temporal cortex, suggesting that under certain conditions, activity of regions outside auditory cortex is sufficient for conscious perception. Complementary to these observations, many studies have found no covariation of early A1 activity with perception across a range of experimental paradigms (Dykstra, Halgren, Gutschalk, Eskandar, & Cash, 2016; Gutschalk, Micheyl, & Oxenham, 2008; Puschmann, Sandmann, et al., 2013; Puschmann, Weerda, Klump, & Thiel, 2013; Wiegand & Gutschalk, 2012) indicating that activity in A1 alone is likely not sufficient for awareness to emerge.

As in the visual modality, clarity might be gained from considering the timing of A1 activation (K. Meyer, 2011). Using another classic paradigm, informational masking, Wiegand and Gutschalk (2012) have shown that detection of a fixed-frequency target tone sequence presented amidst multi-tone maskers was reflected in increased activity in A1 as revealed by fMRI. However, auditory cortex dipoles fitted to MEG data recorded in another session of the same experiment showed that the difference between detected and undetected targets was not apparent in early A1 potentials but emerged in a later time window, in a negative component peaking at ~180 ms, commonly referred to as the awareness-related negativity or auditory awareness negativity (AAN). The authors speculate that the observed BOLD effects in A1 might be the result of reactivation through feedback from higher-order areas. Other M/EEG studies using auditory streaming (Gutschalk et al., 2005), informational masking (Gutschalk et al., 2008), near-threshold detection (Eklund, Gerdfeldter, & Wiens, 2019; Eklund & Wiens, 2019; Eklund, Gerdfeldter, & Wiens, 2020), bistable pitch perception (Davidson & Pitts, 2014), and figure-ground segregation (Teki et al., 2016) have similarly observed awareness-related effects at ~50–250 ms, consistent with AAN. Although the spatial resolution of M/EEG cannot clearly distinguish between auditory subregions, several authors have speculated that this effect might originate in non-primary auditory cortex (Gutschalk et al., 2005, 2008; Teki et al., 2016), which comprises the belt and parabelt regions directly adjacent to A1 (Hackett, 2011). To test the spatial location of awareness-related potentials directly, Dykstra et al. (2016) recorded activity from intracranial electrodes in a neurosurgical patient performing an informational masking task. They found that target detection was associated with a focal negativity 100–200 ms post-stimulus in electrodes over posterior superior temporal gyrus, compatible with an origin of the AAN in non-primary auditory cortex. Likewise, in an fMRI study on macaques performing a figure-ground segregation task, F. Schneider et al. (2018) found correlates of the animals' percepts in the auditory belt and parabelt and similarly, Kilian-Hütten, Valente, Vroomen, and Formisano (2011) have shown that in humans, ambiguous speech sounds can be decoded from BOLD signals in these regions. Taken together, evidence suggests that non-primary auditory regions in superior temporal cortex may be critically involved in the emergence of conscious auditory perception (Dykstra et al., 2016; Gutschalk & Dykstra, 2014).

The extent to which feedback interactions between primary and non-primary auditory cortex contribute to awareness of sound is less clear, potentially due to the close spatial proximity of core, belt, and parabelt regions, which complicates the separation of respective signals. Some evidence comes from studies on the auditory mismatch negativity, which has been suggested to arise from recurrent interactions between A1, superior temporal gyrus, and inferior frontal gyrus (Auksztulewicz & Friston, 2015;

Garrido et al., 2008). Moreover, it has been suggested that increased feedback connectivity between planum temporale and A1 may be beneficial in ameliorating symptoms in aphasic patients following left-hemispheric stroke (Schofield et al., 2012). However, another study modelling the perception of spectral envelops of sounds in A1, planum temporale, and superior temporal sulcus found no benefit of including backward connections to A1 in their models (Kumar, Stephan, Warren, Friston, & Griffiths, 2007), leaving it unclear in how far feedback to primary auditory fields is indeed necessary for auditory perception. Studies specifically investigating the dependence of auditory awareness on local recurrent interactions by employing dedicated experimental paradigms are currently lacking. Accordingly, although the AAN has been speculated to reflect such interactions based on its latency and distribution (Eklund et al., 2020), and – in analogy to the VAN – is commonly taken to be consistent with RPT (Dykstra et al., 2016; Eklund & Wiens, 2019), direct evidence for this association remains to be established.

One MEG study attempting to elucidate the cortical interactions underlying auditory awareness-related potentials used an informational masking paradigm in which a target of two consecutive tones of the same frequency had to be detected amidst random masker tones (Giani, Belardinelli, Ortiz, Kleiner, & Noppeney, 2015). By means of dynamic causal modelling (DCM), the authors showed that the detection effect at the AAN latency was best explained in terms of intrinsic connectivity changes within auditory cortex. However, because the study did not model subregions within auditory cortex, the nature of these connectivity changes and potential feedback interactions between auditory subregions remains unclear. Interestingly, in this study the AAN was only observed for the second tone in the target sequence, challenging the notion that it reflects awareness of individual tones. Instead, a later sustained deflection, the P3b, reflected target detection of both tones, and DCM suggested that this effect was related to recurrent interactions between auditory cortex and a region in right PPC. This is in line with a number of studies that have found elevated P3b amplitudes for consciously perceived auditory stimuli (Davidson & Pitts, 2014; Dykstra et al., 2016; Eklund & Wiens, 2019; Eklund et al., 2019; Gregg, Irsik, & Snyder, 2014; Gregg & Snyder, 2012; Puschmann, Sandmann, et al., 2013; Shen, Vuvan, & Alain, 2018), with a similar centroparietal distribution as in the visual modality. Intracranial recordings have suggested that the auditory P3b originates in ventrolateral PFC and lateral temporal cortex (Dykstra et al., 2016) but as in the visual modality, its generators likely involve many brain regions, probably also including the PPC (Halgren, Marinkovic, & Chauvel, 1998; Linden, 2005; Soltani & Knight, 2000). Indeed, several studies indicate a role for the inferior parietal sulcus in conscious auditory perception, as it selectively reflects participants' percepts during bistable auditory streaming (Cusack, 2005; Hill et al., 2011) and seems to be involved in auditory figure ground segregation (Teki et al., 2016). Others have found correlates of auditory awareness in widely distributed networks, often including regions of auditory cortex and higher-order areas in frontal, temporal, parietal, cingulate, and insular cortex depending on the specific type of perceptual content (Brancucci, Franciotti, D'Anselmo, della Penna, & Tommasi, 2011; Eriksson, Larsson, Åhlström, & Nyberg, 2007; Kuriki, Numao, & Nemoto, 2016), as well as interactions between auditory and association cortices (Puschmann, Weerda, et al., 2013). Taken together, conscious auditory perception seems to covary with activity in many distributed brain areas including both auditory and supramodal regions.

1.1.3 Somatosensory awareness

The American neurophysiologist Benjamin Libet, who later became famous for his works on free will, was an early pioneer in the neuroscientific study of tactile awareness (Libet, 1993). In the 1960s, he performed experiments investigating the relationship between conscious somatosensory experience and evoked brain responses recorded from the primary somatosensory cortex (S1) of patients undergoing surgery. He observed that electrical target stimuli that were too weak to elicit a conscious percept nevertheless evoked measurable activity in early somatosensory cortex (Libet, Alberts, Wright, & Feinstein, 1967), and conversely, that direct stimulation of S1 could go unnoticed when stimulation intensities were weak (Libet et al., 1964). These findings suggest that activity in early somatosensory cortex is not sufficient for the emergence of a conscious somatosensory percept. However, other studies have found close correspondence between somatosensory experience and activity in S1. In the cutaneous rabbit illusion, participants perceive stimulation at a location that lies between two actually stimulated parts of the forearm, evoking the illusory impression of a hopping rabbit. Blankenburg, Ruff, Deichmann, Rees, and Driver (2006) have investigated this illusion using fMRI and found that the illusory percept was reflected in activity of corresponding somatotopic regions in S1 that was highly similar to that elicited by veridical stimulation. Schwartz, Assal, Valenza, Seghier, and Vuilleumier (2005) report the case of a patient who had a tumour in right S1 and superior parietal gyrus (Brodmann area (BA) 7). While maintaining the capacity to correctly detect the onset of stimuli, this patient was unable to perceive stimulus offsets and instead reported sustained perception of stimuli after they had been removed. The different sensitivity to stimulus on- and offsets was reflected in BOLD activity in the lesioned S1 but not in contralesional S1 or bilateral secondary somatosensory cortex (S2). M/EEG studies investigating the earliest correlates of awareness as markers of the involvement of early somatosensory cortex have found conflicting results. Studies using near-threshold detection tasks, in which stimuli at threshold-level intensities are sometimes detected and sometimes missed, have reported enhanced S1 somatosensory evoked potentials for detected compared to missed stimuli (Hirvonen & Palva, 2016; Jones, Pritchett, Stufflebeam, Hämäläinen, & Moore, 2007; Palva, Linkenkaer-Hansen, Näätänen, & Palva, 2005), whereas studies using alternative tasks typically do not find detection sensitivity in early S1 responses (de Lafuente & Romo, 2005, 2006; Forschack, Nierhaus, Müller, & Villringer, 2020; Schubert, Blankenburg, Lemm, Villringer, & Curio, 2006; Wühle, Mertiens, Rüter, Ostwald, & Braun, 2010; Wühle, Preissl, & Braun, 2011).

The special relevance of S2 on the other hand has repeatedly been demonstrated in various studies using different methods. During vibrotactile target detection, neurons in macaque S2 are the first to show responses predictive of perceptual choice (de Lafuente & Romo, 2006) and similarly, S2 has been demonstrated to contain neurons that specifically signal the perceptual dimension of tactile temporal patterns (Rossi-Pool, Zainos, Alvarez, Diaz-deLeon, & Romo, 2021). In humans, detected targets during paired-pulse stimulation attenuate responses in S2 more strongly than undetected targets, whereas S1 responses are similarly attenuated by detected and undetected stimuli (Wühle et al., 2010, 2011). This is in line with findings from stereotactic EEG recordings showing that S1 shows phasic activity in response to electrical stimulation whereas S2 shows tonic activity, more consistent with perceptual processing (Avanzini, Pelliccia, Lo Russo, Orban, & Rizzolatti, 2018). Neuroimaging studies have shown stronger BOLD responses in S2 (Grund, Forschack, Nierhaus, & Villringer, 2021; Moore et al., 2013) and increased network integration (Weisz et al., 2014) when somatosensory stimuli are detected, altogether suggesting that similar to extrastriate visual regions and non-primary auditory cortex, S2 might be an important node in the neural processes leading up to somatosensory awareness.

As in the visual and auditory modalities, a synthesis of the various findings on S1 and S2 activity during conscious somatosensory perception may be achieved by considering the exact timing of their activation. Sachidhanandam, Sreenivasan, Kyriakatos, Kremer, and Petersen (2013) showed that when mice were trained to detect single whisker deflections, early (<50 ms) responses in S1 barrel cortex were evoked by all stimuli, with no differences between hits and misses, but later responses (50–400 ms) correlated with perceptual reports. Importantly, optogenetic inhibition of the late response significantly deteriorated detection, suggesting a causal role for late S1 activity in driving somatosensory perception. Similarly, Manita et al. (2015) report that tactile surface perception is reflected in reciprocal activation of a cortical loop between S1 and secondary motor cortex and deteriorates when motor cortex input to S1 is optogenetically silenced, demonstrating the crucial dependence of accurate perception on recurrent feedback to S1. These results are in line with studies in both animals and humans that have suggested a crucial relevance of feedback signals to S1 in successful target detection. Using in vivo calcium imaging, it has been shown that choice-predictive activity in S1 is driven by feedback from S2 (Kwon, Yang, Minamisawa, & O'Connor, 2016; Yang, Kwon, Severson, & O'Connor, 2016). A similar mechanism has been suggested to underly the generation of the N1 component in monkeys, elicited upon passive cutaneous stimulation (Cauller & Kulics, 1991), as well as late detection-dependent activity in human S1 (Jones et al., 2007). In M/EEG studies in humans, the somatosensory N140 component over contralateral somatosensory electrodes has repeatedly been found to correlate with awareness (Al et al., 2020; Auksztulewicz, Spitzer, & Blankenburg, 2012; Auksztulewicz & Blankenburg, 2013; Schubert et al., 2006; Forschack et al., 2020; Zhang & Ding, 2010), and it has therefore been suggested to constitute the tactile version of the VAN and AAN (Dembski, Koch, & Pitts, 2021). Using DCM, Auksztulewicz et al. (2012) have shown that the N140 effect can be explained in terms of increased recurrent interaction between S1 and S2 on conscious trials, again suggesting a crucial role for recurrent processing within somatosensory cortex for the emergence of somatosensory awareness. Overall, studies in the somatosensory modality have produced ample evidence in favour of RPT.

The role of higher-level regions in supramodal cortex has been investigated in multiple human and animal studies. Single cell recordings in monkeys have shown that neural signals predictive of perceptual reports emerge as activity spreads across the cortex. In macaques performing detection tasks on vibrotactile stimuli, firing rates of neurons in S1 are unaffected by target detection and instead scale with stimulus strength (de Lafuente & Romo, 2005, 2006). The covariation of firing rates with perceptual reports instead increases with increasing hierarchical levels, starting in S2 and culminating in almost categorical responses in medial premotor cortex (de Lafuente & Romo, 2006). Supporting this observation, target detection in humans has been shown to be associated with increased connectivity between somatosensory and frontal regions (including premotor cortex), suggesting recruitment of a larger recurrent network (Auksztulewicz & Blankenburg, 2013; Hirvonen, Monto, Wang, Palva, & Palva, 2018; Zhang & Ding, 2010). Indeed, neuroimaging studies have identified a wide range of regions that show enhanced activity upon conscious somatosensory perception, including motor areas, anterior insular cortex (AIC), anterior cingulate cortex (ACC), posterior parietal, and prefrontal regions (Allen et al., 2016; Bastuji, Frot, Perchet, Magnin, & Garcia-Larrea, 2016; Bornhövd et al., 2002; Büchel et al., 2002; Grund et al., 2021; Hirvonen & Palva, 2016; Moore et al., 2013). As in the visual and auditory modalities, activation of these regions is accompanied by enhanced P300 amplitudes for detected stimuli over centroparietal electrodes (Al et al., 2020; Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013), suggesting that late activity in distributed cortical networks correlates with somatosensory awareness.

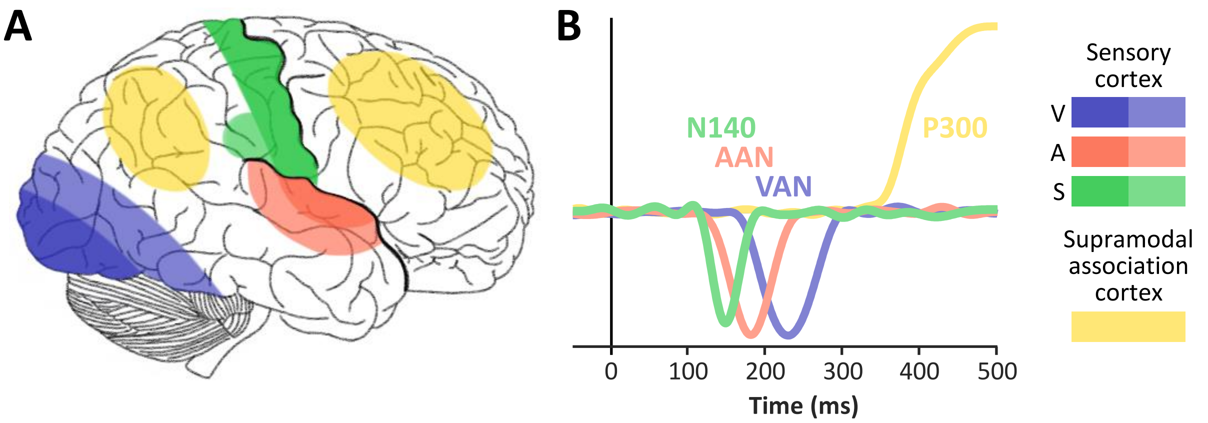


Figure 1: Neural correlates of conscious perception across modalities. A) Spatial. Research on the neural locus of perceptual awareness in the visual (V), auditory (A), and somatosensory (S) modalities has produced similar patterns of results. While some studies have identified activity and local recurrent interactions within sensory cortices as correlates of awareness (darker colours denote primary sensory areas, lighter colours denote non-primary sensory areas), others have found wide-spread network activity that encompasses regions in supramodal association cortices, particularly in the frontal and parietal lobes. **B) Temporal.** M/EEG studies typically find two types of ERPs that correlate with awareness: an early negativity with a sensory-specific topography that likely originates from sensory cortices (time windows and peak latencies are plotted as suggested by Dembski et al., 2021), and a late positivity, the P300, that emerges over centroparietal electrodes and reflects processing in frontoparietal networks.

1.1.4 Summary

Taken together, research in the visual, auditory, and somatosensory modalities has identified highly similar patterns of results (**Figure 1**). While it appears that feed-forward activity in primary sensory regions alone is not sufficient for the emergence of perceptual awareness, the relative importance of later activity in sensory and non-sensory regions remains debated. On the one hand, studies reporting local interactions in sensory cortices and sustained sensory negativities at ~100–250 ms suggest a relatively early, modality-specific correlate of awareness. On the other hand, studies showing activation of widely distributed cortical networks that is reflected in a large centroparietal P300 component imply a late correlate of awareness associated with global availability of information. Which of these candidates truly marks the processes that are both necessary and sufficient for the emergence of a conscious percept remains highly controversial. In fact, the divide between early local and late global NCCs is well reflected in some of the most prominent theories of conscious perception, and importantly, these different theories feature different perspectives on the observed heterogeneity of results. While those that focus on widespread network activity consider the variety of brain regions reported in different studies a hallmark of conscious perception (Dehaene & Changeux, 2011; Mashour et al., 2020), those that argue for the sufficiency of smaller, more specific sets of cortical regions are doubtful as to the validity of the observed network effects and point out problems in the employed methods and interpretations (Boly et al., 2017; Koch et al., 2016). In the next section, I will reassess the presented evidence in light of these problems and explore the possibility that some of the observed effects might not be correlates of awareness after all but instead result from the methodological difficulty of operationalising subjective experience (Aru, Bachmann, Singer, & Melloni, 2012; de Graaf, Hsieh, & Sack, 2012).

1.2 Dissociating perceptual awareness from its precursors and consequences

1.2.1 The problem of introspective reports

As evident from the previous section, numerous studies have found neural correlates of perceptual awareness in regions all across the brain and the primary challenge today consists in consolidating these diverging findings. So far, no consensus has been reached regarding the relevance of early sensory vs. late supramodal brain activity. Both find an abundance of supporting evidence in the literature as well as adamant proponents of theories that make opposing predictions regarding the spatial and temporal scale of expected correlates, placing the early-local vs. late-global debate among the most contested in consciousness science.

Why do the empirical findings observed so far diverge as much as they do? A potential explanation might lie in the realisation that perception rarely occurs in isolation, at least not in experimental settings (Aru et al., 2012; de Graaf et al., 2012). Owing to the private nature of conscious experience, researchers must usually rely on introspective reports, meaning that their participants must tell them about their perceptual experiences, for example by pressing buttons on a keyboard. Although this approach allows categorising conscious and unconscious trials, it entails that perceptual experience is routinely accompanied by many different cognitive processes associated with these reports (Tsuchiya, Wilke, Frässle, & Lamme, 2015). In fact, it has been pointed out that the simple contrast between perceived and unperceived stimuli contains multiple processes that systematically precede or follow conscious perception in most experimental settings but that do not qualify as minimally sufficient and therefore, are not NCCs (Aru et al., 2012). For example, when a participant performs a classical target detection task in the lab, the probability of detecting a target varies with prestimulus cortical excitability, which is influenced by fluctuations in phasic alertness as well as prior expectations regarding the stimulus (Martín-Signes, Pérez-Serrano, & Chica, 2019; Wyart, Nobre, & Summerfield, 2012). At the same time, successfully detecting the target (i.e. consciously perceiving it) triggers a cascade of cognitive processes, including reorientation of attention, perceptual decision making, encoding in working memory, and response se-

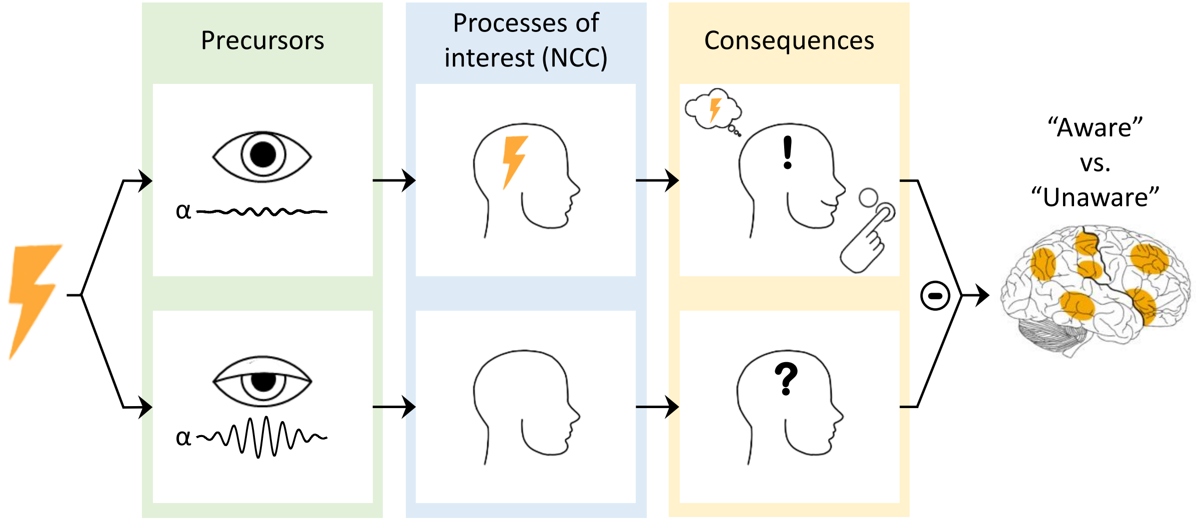


Figure 2: Cognitive processes that correlate with perceptual awareness in experimental settings. In classical target detection tasks, perceptual awareness systematically cooccurs with cognitive processes that act as precursors or consequences of awareness. For example, high levels of alertness and low levels of alpha activity in sensory regions may facilitate target detection. Detected targets in turn resolve uncertainty and initiate decision-, memory-, and report-related processes that differ from those following undetected targets. When contrasting neural responses during conscious and unconscious conditions, all of these processes contribute to the observed effects, such that genuine NCCs cannot unequivocally be identified.

lection. In most experiments, these processes systematically occur for conscious but not unconscious stimuli, such that associated brain activity is conflated when using the contrastive method and may lead to an overestimation of the neural correlates of perceptual awareness (Aru et al., 2012; de Graaf et al., 2012; Pitts, Metzler, & Hillyard, 2014; Tsuchiya et al., 2015) (**Figure 2**). Although this insight seems to suggest a daunting prospect for our neuroscientific understanding of awareness, it also offers a valuable opportunity for reconciliation of the seemingly conflicting literature. In fact, the importance of accounting for potential experimental confounds has been largely acknowledged in recent years and this has led to the development of a range of new creative ways to deal with this problem. Nonetheless, isolating the true neural correlates of conscious perception, unconfounded by task requirements, remains a central challenge in the study of subjective experience and an ongoing source of controversy (Boly et al., 2017; Odegaard, Knight, & Lau, 2017).

1.2.2 Passive stimulation and no-report paradigms

Previous attempts at controlling for task confounds have primarily focused on removing behavioural reports. In so-called no-report paradigms (Tsuchiya et al., 2015), participants either passively view the presented stimuli or are engaged in tasks that do not require explicit reports of the stimuli of interest. Different methods are then used to infer their perceptual experience. As a result, all cognitive processes necessary to execute perceptual reports, such as working memory, perceptual decision making, and motor planning, cease to correlate with awareness, and the contrastive method is expected to reveal a purer NCC. The most straight-forward approach to achieve this is to use suprathreshold stimuli that are task-relevant but do not serve as targets and are therefore not reported. Farooqui and Manly (2018) used a paradigm that resembled the RSVP used in the attentional blink paradigm, but with a significantly slowed rate of stimulus presentation (one stimulus per second) to ensure that participants were fully conscious of all presented images. They found that while target stimuli that were selected for report elicited strong activity in areas of the frontoparietal network, non-target stimuli that were not reported, despite being both conscious and attended, reduced the activity in these areas. Similar results were obtained in a study using intracranial recordings in epileptic patients who performed a simple n-back memory task (Noy et al., 2015). Participants in this study only gave a response when successive stimuli were identical, meaning that in many of the trials, they perceived the stimuli consciously and also encoded them in working memory, but they did not report anything. The authors found that irrespective of the task, the perceived stimuli elicited a robust early response in visual cortex followed by activity in higher visual areas. In contrast, late (>300 ms) responses in frontoparietal electrodes were only present for target stimuli that required a perceptual report and showed little content-specificity, suggesting a profound dependence of these signals on task requirements. Using MEG and multivariate decoding, Marti and Dehaene (2017) found that during RSVP, all stimuli were processed in parallel during the first 150 ms but only stimuli that were identified as targets (and were thus selected for report) elicited late all-or-nothing responses. Interestingly, these authors have interpreted their findings as being consistent with GNWT and seem to suggest that only the target stimuli that were selected for report were consciously perceived. Granted, since presentation times of the stimuli were very brief, the degree of conscious evaluation of each of the stimuli individually cannot be determined with certainty. However, given that participants attended to the stimulus stream and had to (consciously) withhold reports for all non-targets, exclusive conscious access of reported stimuli appears to be an unlikely assumption and alternatively, one could interpret the result as demonstrating a report confound in late activity. Further evidence comes from an fMRI study that measured BOLD activity during the perception of a standing wave of invisibility, a strong backward and forward masking paradigm, in which perception of a target stimulus is reliably suppressed (Tse, Martinez-Conde, Schlegel, & Macknik, 2005). Importantly, the paradigm did not require participants to report their perception, and in line with the assumption that frontoparietal activity is related to postperceptual processing, the results showed that BOLD correlates of target visibility were restricted to regions in extrastriate visual cortex. Finally, in an auditory paradigm, Wiegand, Heiland, Uhlig, Dykstra, and Gutschalk (2018) compared BOLD responses elicited by regular tone patterns when they were either reported or passively listened to. They found that both conditions were associated with activity in auditory regions but activity in a frontal-parietal-insular network was only present when stimuli had to be reported. This is consistent with electrophysiological studies using conditions of passive auditory stimulation, which have found that a widespread P300 response was only present when detected tones were reported, but not when they were passively listened to (Dykstra et al., 2016; Hillyard, Squires, Bauer, & Lindsay, 1971). Overall, studies employing passive suprathreshold stimulation suggest that activity in frontoparietal networks may relate to reporting of perceptual contents and goal completion, but not to the contents themselves. However, since these studies do not control for physical stimulation parameters, the degree to which the observed effects reflect unconscious processing is unclear.

To keep physical stimulation parameters constant while still being able to infer perceptual awareness without explicit reports, Pitts and colleagues employed the inattentional blindness phenomenon (Mack, 2003). In a series of studies, they varied conscious perception by manipulating the relevance of visual target stimuli in three consecutive phases of their paradigm (Pitts, Martínez, & Hillyard, 2012; Pitts, Padwal, Fennelly, Martinez, & Hillyard, 2014; Pitts, Metzler, & Hillyard, 2014; Schelonka, Graulty, Canseco-Gonzalez, & Pitts, 2017; Schlossmacher, Dellert, Pitts, Bruchmann, & Straube, 2020; Shafto & Pitts, 2015). In the first phase, participants performed a distracting secondary task, which left them inattentionally blind of the stimuli of interest. In the second phase, they performed the same task but were previously alerted to the presence of the visual target stimuli, which made them consciously perceive the targets without having to act on them in any way. In the third phase, they performed a task on the target stimuli, such that they were both consciously perceived and reported. In this setting, the late P300 component only reflected target awareness in the third phase of the experiment, when participants reported their perception, but not in the second phase, when stimuli were consciously perceived but not relevant to the behavioural task. In contrast, an earlier negative potential at ~200 ms, consistent with the VAN, correlated with awareness irrespective of task requirements. Similar results were also found using a masking paradigm (Cohen, Ortego, Kyroudis, & Pitts, 2020) as well as auditory stimuli (Schlossmacher, Dellert, Bruchmann, & Straube, 2021), altogether demonstrating that the P300 response is profoundly dependent on task relevance. Other studies have found the association between perceptual awareness and the P300 to be modulated by expectations (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011), response associations (Koivisto et al., 2016), and response criteria (Mazzi, Mazzeo, & Savazzi, 2020), further demonstrating its link to postperceptual processes. Moreover, fast behavioural responses have been shown to occur even before the onset of the P300 (Railo et al., 2015; Ye & Lyu, 2019) and conversely, it has been suggested that a P300 can be elicited in the absence of awareness (Silverstein, Snodgrass, Shevrin, & Kushwaha, 2015; although this study has been criticised on various conceptual and methodological grounds, leaving it somewhat open if the P300, and particularly its later component, the P3b, can indeed be elicited under unconscious conditions, see Naccache, Marti, Sitt, Trübutschek, and Berkovitch (2016)). Collectively, these studies strongly suggest that the P300 is related to cognitive processing of perceptual contents but does not reflect and may not be necessary for the emergence of perceptual awareness, calling its relevance as an NCC into question.

1.2.3 Criticism of no-report paradigms and a way forward

Research demonstrating the task-dependence of late activity in supramodal cortical networks has motivated some researchers to dismiss prefrontal theories of awareness altogether (Boly et al., 2017; Koch et al., 2016). However, it must be noted that the picture is not quite as clear as it seems (Odegaard et al., 2017). In fact, many researchers advocating for cognitive theories of awareness have not been swayed by no-report findings and instead maintain that global ignition or activation of the PFC remains the current best description of perceptual awareness (Mashour et al., 2020; Odegaard et al., 2017; Panagiotaropoulos, Dwarakanath, & Kapoor, 2020). Their criticism is geared towards both methodological and conceptual problems. On the methodological side, it has been argued that conscious but task-irrelevant stimuli might elicit late EEG components with greater temporal variability, leading respective effects to go unnoticed (Boncompte & Cosmelli, 2018). In fact, if perception is not directly inquired, there is no way of knowing if participants consistently perceive the relevant stimuli on every trial, leading to a source of noise that might contribute to the apparent lack of late effects in supramodal regions. More critically, the spatial resolution of both fMRI and EEG is limited to large populations of neurons. Since neurons in PFC are not organised in a retinotopic manner, mass univariate analysis might simply not be sensitive enough to capture effects in these regions (Odegaard et al., 2017). The importance of this argument has been showcased in experiments on binocular rivalry that have used similar paradigms but different measurement and analysis techniques. Frässle, Sommer, Jansen, Naber, and Einhäuser (2014) presented human participants with rivalling motion stimuli and measured their optokinetic nystagmus (characteristic eye movements in the direction of motion) as well as pupil sizes to infer participants' perception without requiring reports. In line with previous no-report studies, they found that with explicit reports, BOLD activity in occipital, parietal, and frontal regions reflected perception but without reports, the effect in frontal regions vanished, yet again implying that activity in the frontal cortex is not necessary for conscious perception. However, using the same approach while measuring spiking activity in monkeys, Kapoor et al. (2020) found that even in the absence of reports, neurons in the inferior convexity of the PFC showed increased firing rates when their preferred stimulus dominated perception. In another animal study, Panagiotaropoulos, Deco, Kapoor, and Logothetis (2012) used a binocular flash suppression task, which employed sudden flashes of salient images of monkey faces to induce exogenous switches of percepts that can be inferred without reports. The results showed that neurons in the lateral PFC of macaques showed feature-selective increases in single unit activity when perceptual switches occurred, again suggesting that neurons in PFC do in fact correlate with conscious content independent of reports. These results strengthen the concern that previous null-effects in prefrontal regions might be due to insufficiently sensitive methods. However, there might be an alternative explanation. Especially in the study by Panagiotaropoulos and colleagues, the sudden and highly salient presentation of monkey faces may have triggered postperceptual processes despite the absence of reports, which could explain the activity in prefrontal regions. Even though neural signals that are related to monitoring and reporting perceptual switches may be attenuated in no-report paradigms, others, such as attentional reorientation and introspection, might persist. This possibility limits the ability of no-report paradigms to truly remove postperceptual processing, and it has been suggested that "no-cognition paradigms" are needed instead (Block, 2019). Besides these methodological concerns, some researchers doubt if unreported stimuli can really be considered conscious at all. In fact, those prescribed to GNWT argue that conscious access of sensory information is a critical part of subjective experience (Mashour et al., 2020) and that only information that can in principle be consciously accessed for report can be considered truly conscious (Frith, 2019). According to these authors, early recurrent activity in sensory regions reflects preconscious processing, whereas late activity in the global workspace, likely encompassing the PFC and potentially indexed by the P300, reflects conscious access (Dehaene et al., 2006). In conclusion, the no-report approach to studying perceptual awareness faces various forms of criticism, meaning that the verdict on the relevance of high-level regions for the emergence of conscious perception is still out.

How could this criticism be addressed? Given that the removal of reports introduces a high level of uncertainty regarding the cognitive processes elicited by a stimulus, a potential solution might be found in experimentally orthogonalising awareness and reports instead of removing reports altogether. If it were possible to completely balance pre- and postperceptual requirements across perceived and unperceived stimuli, such that – ideally – these two conditions would truly only differ in their perceptual outcomes, signals related to precursors and consequences of perception should be controlled for. Accordingly, the contrastive method would identify only those signals that genuinely reflect perceptual awareness, and conscious access would be guaranteed. From an experimental standpoint, this is a challenging endeavour since perception is so intricately linked to its behavioural consequences. Accordingly, not many studies have attempted this approach, but a few examples exist in the literature. Koivisto et al. (2016) introduced a paradigm that uses a go/no-go approach with response reversals to experimentally dissociate ERP correlates of awareness from those reflecting reports. Participants were required to detect low-contrast Gabor patches but the way they reported their perception differed across experimental blocks. In one condition, they pressed a button whenever they had detected the target stimulus, whereas in the other condition, they pressed a button whenever they had not detected the target stimulus. The ERPs for the different conditions suggest that the VAN amplitude was modulated by awareness irrespective of report conditions. The P300 amplitude on the other hand was also modulated by awareness, but with an additional modulation by report requirements, showing larger amplitudes in the go condition than in the no-go condition. The authors concluded that the P300 is generated in a postperceptual stage and is thus unlikely to be causally involved in generating awareness. However, other studies using similar tasks have come to different conclusions. Eklund et al. (2019) attempted to replicate Koivisto et al.'s study in the auditory modality but found that the report condition had no effect on the P300 and instead, both the AAN and the P300 reliably indexed stimulus awareness. Another study by Sanchez et al. (2020) used the go/no-go task with response reversals (although with some variations that may have reintroduced postperceptual processing, especially working memory) as a control condition in their cross-modal decoding study and found that irrespective of the report condition, visual, auditory, and somatosensory stimulus awareness could be cross-decoded from MEG data in late time windows >300 ms. Source analysis suggests that the signals relevant to this late decoding originated from both sensory and frontoparietal network regions. Taken together, previous attempts at orthogonalising conscious access and reports have produced inconsistent results. Interestingly, even in Koivisto et al.'s study, the P300 continued to differentiate conscious from unconscious trials and hence, appears to have signalled more than just reports. It is unclear whether this difference truly reflects conscious access or resulted from other confounding variables. Of particular interest is that the go/no-go task requires participants to use different stimulus-response links in the different task conditions, which have been linked to the P300 (Verleger, 2020). Moreover, both endogenous and exogenous attention may have impacted the results, complicating their interpretation. Another crucial, but unresolved question relates to the generalisability across sensory modalities. As evident from Eklund et al.'s findings, highly similar experimental approaches can lead to different conclusions when moving from the visual to the auditory modality. Given this divergence, the fact that only few studies have examined task-dependence in modalities other than vision poses a problem to general theories of perceptual awareness. Finally, studies attempting to orthogonalise awareness and reports have so far only used M/EEG, leaving it unclear in how far awareness-related activity in frontoparietal networks would be affected by this manipulation. In sum, although some studies have attempted to orthogonalise awareness and reports and have provided interesting first results, their conclusions have been inconsistent and may have been influenced by residual differences in pre- and postperceptual processing.

1.3 Aim of the thesis

The aim of this thesis was to develop an experimental paradigm that provides improved control over potential precursors and consequences of awareness without relinquishing reports and to employ this paradigm to scrutinise the task-dependence of the neural correlates of somatosensory awareness.

I have chosen the somatosensory modality for two reasons: first, the study of somatosensory awareness has so far received the least attention of the modalities reviewed here, and a systematic investigation into the task-dependence of somatosensory NCCs has never been attempted. Second, the somatosensory system offers several characteristics that make it an attractive target for studying the neural basis of perceptual awareness. Somatosensory afferents with known cortical destinations can be stimulated directly, bypassing sensory receptors, and therefore reducing variability in cortical processing. While both S1 and S2 feature multiple somatotopic maps (Blankenburg, Ruben, Meyer, Schwiemann, & Villringer, 2003; Ruben et al., 2001), their anatomical loci on the postcentral bank of the central sulcus and on the upper bank of the Sylvian fissure are readily distinguishable, which sets them apart from the shell-like organisation of subregions in visual and auditory cortices. If, for example, a hand is stimulated, respective somatotopic activations in S1 and S2 occur several centimetres apart (Delhaye, Long, & Bensmaia, 2018) and in almost orthogonal dipoles, allowing even methods with limited spatial resolution to distinguish between these sources (Allison, McCarthy, Wood, Williamson, & Spencer, 1989; Thees, Blankenburg, Taskin, Curio, & Villringer, 2003). Finally, while visual stimuli can be missed simply because participants blinked at the wrong time, this does not occur in somatosensation, making it less susceptible to participants' behaviour.

To dissociate awareness from its precursors and consequences while accounting for previous criticism of no-report paradigms, I developed an experimental task that orthogonalises somatosensory awareness and reports by employing a somatosensory-visual matching procedure. The task equates perceptual reports, behavioural relevance, working memory, and motor responses across conscious and unconscious conditions, mitigates the influence of pre- and post-stimulus attentional selection, and varies physical stimulus parameters, detection probabilities, and expected perceptual uncertainty in a predictable manner, while guaranteeing conscious access from trial to trial. I employed this task in two empirical studies to identify the neural correlates of somatosensory awareness unconfounded by task-demands. In Study 1, I used fMRI to investigate which brain regions correlate with the different processing stages invoked by the task, from physical to perceptual representations and on to the final reports, and to test whether detection-related signals are localised to somatosensory regions or higher-order areas. In Study 2, I used EEG to establish a temporal profile for the transformation observed in Study 1, and to test whether relatively early, modality-specific (N140) or late, supramodal (P300) ERP components correlate with awareness. In the next chapter, I will briefly present the paradigm and employed analysis approach and summarise the empirical studies and their most important findings.

2 Summary of empirical studies

2.1 General methodology

Many studies on somatosensory awareness have used the near-threshold target detection task, as it offers a simple way of varying perceptual outcomes while keeping physical stimulation parameters constant (Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013; Grund et al., 2021; Hirvonen et al., 2018; Jones et al., 2007; Moore et al., 2013; Palva et al., 2005; Zhang & Ding, 2010). Typically, tactile or electrical stimuli are presented to participants' fingers or wrists at an intensity that results in about 50% detection rates – the 50% detection threshold. Participants then report whether they consciously perceived the stimulus or not, for example by pressing a corresponding button on a keyboard. This one-to-one mapping results in covariation of the neural signals that support awareness and those that enable perceptual reports. In fact, the report requirement constitutes only one of many potential confounds that often covary with stimulus perception in experimental settings. In the context of target detection these include:

- **Physical stimulus properties:** Adjusting physical stimulus parameters throughout the course of an experiment can create a bias when on average, detected targets end up having a stronger signal intensity than undetected targets.
- **Prestimulus brain states:** Near-threshold target detection is susceptible to ongoing fluctuations in cortical excitability (e.g. due to changes in endogenous attention or expectations, Melloni et al., 2011; Samaha et al., 2020; Wyart, Nobre, & Summerfield, 2012), which may result in signal differences between detected and undetected targets that are not a direct correlate of target detection but act as a precursor.
- **Oddball effects:** When targets are rarely perceived, detected targets can induce oddball effects, which result in neural signals related to surprise (Linden et al., 1999).
- **Uncertainty:** Detected but not undetected targets can resolve perceptual uncertainty and are likely associated with different introspective processes (de Lafuente & Romo, 2011).
- **Closure of cognitive epochs:** When targets can occur at an unpredictable and unmarked time point, detected targets mark the end of a cognitive epoch but undetected targets do not (Verleger, 2020).

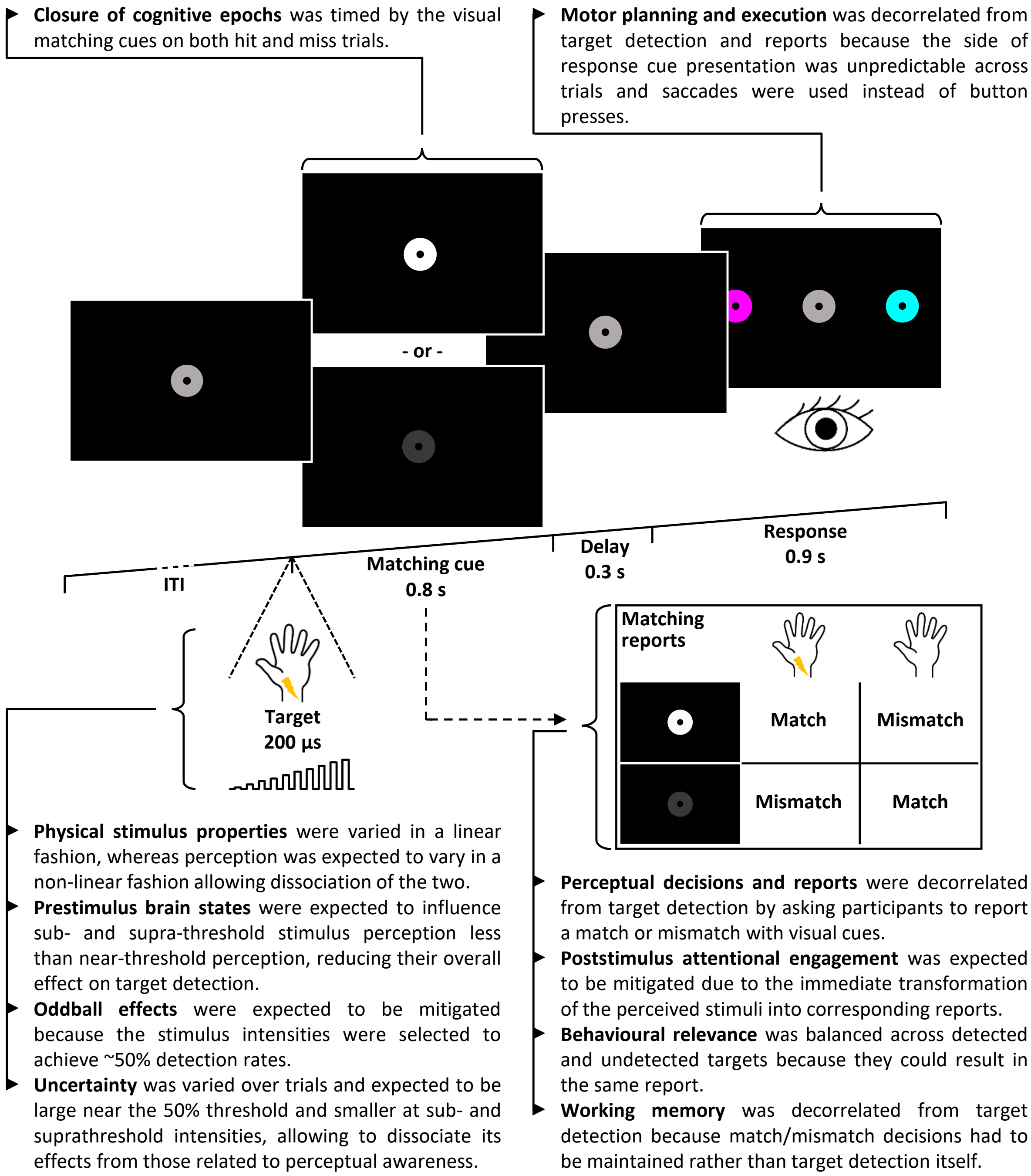
- **Perceptual decisions and reports:** When target detection is reported using a one-to-one mapping between perception and reports, neural processes related to perception, perceptual decision making, and formation of reports cannot be dissociated (Tsuchiya et al., 2015).
- **Post-stimulus attentional engagement:** Detected targets capture exogenous attention, which results in enhanced processing compared to undetected targets (Mena, Lang, & Gherri, 2020).
- **Behavioural relevance:** Target detection is the explicit goal of target detection tasks, such that detected targets have higher behavioural relevance than undetected targets and may trigger reward signals (Farooqui & Manly, 2018; Pitts, Metzler, & Hillyard, 2014).
- **Working memory:** If there is a delay between the stimulation period and the time to respond, participants must hold their decisions in working memory and the working memory content differs between detected and undetected targets when direct reports are used (Rutiku et al., 2015).
- **Motor planning and execution:** When perceptual decisions are consistently mapped to specific motor responses (e.g. a button press whenever a target was detected), the neural responses associated with perceptual awareness cannot be dissociated from those related to preparation and execution of the motor response (Pitts, Metzler, & Hillyard, 2014). For somatosensory studies, if the perceptual receiver and response effector are closely related (e.g. stimulation of one hand and responding with the other hand), cortical interactions in the somatosensory homunculus may result in changes in cortical excitability and thus, alter upcoming stimulus processing (Zagha, Casale, Sachdev, McGinley, & McCormick, 2013).

To isolate the neural correlates of somatosensory awareness, I developed a new version of the somatosensory detection task that largely controls for the above variables by employing an orthogonal visual-tactile matching procedure (**Figure 3**). As in previous studies, participants were required to detect weak electrical target stimuli that were presented to their left median nerves. However, in order to control for pre- and postperceptual processes, several modifications were made: 1. Instead of using threshold intensities only, the target stimuli were presented at ten different stimulus intensity levels that were centred on the 50% detection threshold and individually calibrated to sample the full range of each participant's psychometric function. 2. Instead of directly reporting target detection, participants compared their perception of the electrical target stimuli to simultaneously presented visual matching cues that pseudo-randomly signalled stimulus presence or absence and reported a match or mismatch accordingly. 3. Instead of using button presses, participants reported their match/mismatch decisions by making saccadic eye movements to corresponding colour-coded response cues that switched locations in an unpredictable manner.

This task format offers several advantages over previous detection tasks (for details see **Figure 3**). The intensity variation allowed dissociating physical from perceptual processing stages, varied the expected perceptual uncertainty (as defined by the variability of target detection within each intensity level) in a predictable manner, and reduced oddball effects, as well as the impact of prestimulus brain states on perceptual outcomes (because target detection at sub- or suprathreshold intensities is less volatile than at the perceptual threshold). The visual matching cues triggered closure of cognitive epochs similarly for detected and undetected targets. Further, the matching procedure orthogonalised stimulus awareness and perceptual reports, resulting in equated behavioural relevance and working memory contents across detected and undetected targets, and mitigated the effects of poststimulus attentional capture. Finally, the response format prevented any association of target detection or reports with motor planning and execution.

Taken together, the somatosensory-visual matching task controls for various cognitive variables that occur as precursors or consequences of perceptual awareness in the context of target detection. Many of these variables vary across trials in a predictable or measurable manner, with some showing characteristic response profiles across stimulus intensities and others showing a categorical outcome. These trial-wise fluctuations can be used to construct simple models of the processes expected to occur during task performance. By using these models as regressors in general linear models (GLMs), signatures of different processing stages, from physical to perceptual representations and on to the final reports, can be identified in neuroimaging data. For this purpose, I constructed five trial-wise regressors capturing 1. the trial-wise stimulus intensity as a model of physical stimulation parameters (linear regressor), 2. individual psychometric functions modelling trial-wise detection probability (sigmoidal regressor), 3. categorical target detection as inferred from match/mismatch reports and the matching cues presented on every trial (binary regressor), 4. the slope of individual psychometric functions as a model of expected perceptual uncertainty (inverse U-shaped regressor), and 5. match/mismatch reports (binary regressor).

The advantages of varying stimulus intensity come at the cost of losing the balance of physical stimulus properties across conscious and unconscious conditions. Although a large proportion of trials was presented at stimulus intensities close to perceptual thresholds, resulting in fluctuating perception at identical physical stimulus parameters, trials on the lower and higher ends of the intensity spectrum inevitably created a bias, since stimuli of higher intensities are more likely to be detected than stimuli of



- **Closure of cognitive epochs** was timed by the visual matching cues on both hit and miss trials.
- **Motor planning and execution** was decorrelated from target detection and reports because the side of response cue presentation was unpredictable across trials and saccades were used instead of button presses.
- **Physical stimulus properties** were varied in a linear fashion, whereas perception was expected to vary in a non-linear fashion allowing dissociation of the two.
- **Prestimulus brain states** were expected to influence sub- and supra-threshold stimulus perception less than near-threshold perception, reducing their overall effect on target detection.
- **Oddball effects** were expected to be mitigated because the stimulus intensities were selected to achieve ~50% detection rates.
- **Uncertainty** was varied over trials and expected to be large near the 50% threshold and smaller at sub- and suprathreshold intensities, allowing to dissociate its effects from those related to perceptual awareness.
- **Perceptual decisions and reports** were decorrelated from target detection by asking participants to report a match or mismatch with visual cues.
- **Poststimulus attentional engagement** was expected to be mitigated due to the immediate transformation of the perceived stimuli into corresponding reports.
- **Behavioural relevance** was balanced across detected and undetected targets because they could result in the same report.
- **Working memory** was decorrelated from target detection because match/mismatch decisions had to be maintained rather than target detection itself.

Figure 3: Somatosensory-visual matching task. After a variable intertrial interval (2.5–7 s in the fMRI study, 0.7–1.3 s in the EEG study) participants were presented with an electrical target stimulus at one of ten individually calibrated intensity levels, which they either detected or missed. Simultaneously, a visual matching cue was presented that pseudo-randomly signalled stimulus presence (white disk) or absence (dark grey disk). Participants decided whether the two modalities produced a match or a mismatch and reported their decision after a brief delay by saccading to a peripherally presented colour-coded response cue. Example: When the electrical target was detected and the white matching cue was presented, participants reported a match. Likewise, when the electrical target was missed and the dark grey matching cue was presented, participants also reported a match. Thus, detected and missed targets could result in the same overt report, which decorrelated target detection from various task-related cognitive variables.

lower intensities. To be able to draw meaningful conclusions regarding the neural signatures of conscious somatosensory processing despite this covariation, I employed Bayesian model selection (BMS), which allows principled inference on models that share variance (Stephan, Penny, Daunizeau, Moran, & Friston, 2009). BMS treats models as random variables and computes their group-level posterior probabilities based on the log model evidence computed for each participant, which quantifies a trade-off between model fit and model complexity. The computed posterior probabilities allow identifying which model best explains the observed data even when they share certain features. To implement this approach, I constructed five different GLMs, each defined by one of the regressors of interest. I then used Bayesian GLM estimation to obtain the log model evidence for each participant, model, and measurement unit (voxels in fMRI data, time points x electrodes in EEG data). By running BMS on the resulting log model evidence maps, I obtained exceedance probabilities, quantifying the probability that a particular model explains the data better than any of the other models. I applied this analysis approach to data from an fMRI experiment (Study 1) and two EEG experiments (Study 2) to study the neural locus and temporal dynamics of the processes leading up to somatosensory awareness. For further details on the employed methods, please refer to the original publications attached to this thesis (Schröder, Schmidt, & Blankenburg, 2019; Schröder, Nierhaus, & Blankenburg, 2021).

2.2 Study 1: Neural basis of somatosensory target detection independent of uncertainty, relevance, and reports

Schröder, P., Schmidt, T. T., & Blankenburg, F. (2019). Neural basis of somatosensory target detection independent of uncertainty, relevance, and reports. *eLife*. 8, e43410. doi: 10.7554/eLife.43410.

Studies investigating the neural locus of conscious somatosensory perception have found a wide network of regions to correlate with stimulus awareness, including primary and secondary somatosensory cortices, AIC, ACC, motor regions, as well as wide-spread regions in prefrontal, posterior parietal, and temporal cortices (Allen et al., 2016; Bastuji et al., 2016; Bornhövd et al., 2002; Büchel et al., 2002; de Lafuente & Romo, 2005, 2006; Grund et al., 2021; Jones et al., 2007; Rossi-Pool et al., 2021; Moore et al., 2013). While studies in the visual (Farooqui & Manly, 2018; Frässle et al., 2014) and auditory (Wiegand et al., 2018) modalities suggest that activity in widespread supramodal regions might be related to report requirements rather than awareness, the degree to which the somatosensory target detection network reflects postperceptual processing has not been tested so far. To scrutinise the task-dependence of regions previously found to correlate with awareness, I employed the somatosensory-visual matching task in combination with fMRI. Twenty-seven participants completed four runs of the task while their BOLD responses were measured using a 3T MRI scanner. To find neural correlates of the different processing stages presumed to occur during performance of the task, the five GLMs described above were fitted to the fMRI data of each participant and compared on the group level by means of BMS. The results show a transformation from physical to perceptual processing stages within the somatosensory cortex. While BA 3b and BA 1 of S1 reflected the physical stimulus properties, more posterior regions of S1, including BA 2 and extending into SPL, reflected detection probability, suggesting a first transformation towards perceptual readout within the local hierarchy of S1. This transformation was mirrored in S2, which also showed effects of stimulus intensity but was dominated by a representation of detection probability. In addition, subregions of S2 also showed effects of categorical target detection, indicating that activity in bilateral S2 marks the emergence of stimulus awareness. No area outside of the somatosensory cortices showed systematic effects of stimulus intensity, detection probability, or target detection, suggesting that the neural correlates of somatosensory target detection are restricted to modality-specific sensory regions. In contrast, bilateral AIC and ACC showed strong effects of expected perceptual uncertainty and the left supplementary motor area (SMA) showed sensitivity to perceptual reports. These results suggest that different regions in the commonly reported somatosensory target detection network serve different purposes. While activity in S1 largely reflects physical stimulation parameters and thus, constitutes a precursor of conscious perception, regions of S2 correlate with target detection and may qualify as a true neural correlate of somatosensory awareness. Regions in insular, cingulate, and motor regions seem to be engaged in postperceptual processes that follow from task demands, and supramodal regions in PFC and PPC cease to correlate with target detection altogether, making it unlikely that they underlie the emergence of perceptual experience.

2.3 Study 2: Dissociating perceptual awareness and postperceptual processing: the P300 is not a reliable marker of somatosensory target detection

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While fMRI is well suited to study the spatial location of brain regions supporting awareness, M/EEG studies are commonly used to investigate the timing of awareness-related signals. Different regions in the sensory hierarchy show characteristic response latencies, such that the temporal dynamics of sensory processing may be indicative of the hierarchical level a stimulus must reach in order to become conscious (de Lafuente & Romo, 2006). Studies testing the timing of somatosensory awareness by means of M/EEG have reported awareness-related potentials starting from ~90 ms onwards (Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013; Schubert et al., 2006). Most commonly, the somatosensory N140 over contralateral central electrodes and the P300 over centroparietal electrodes are found to show increased amplitudes for consciously perceived stimuli (Al et al., 2020; Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013; Forschack et al., 2020; Schubert et al., 2006; Zhang & Ding, 2010). In the visual and auditory modalities, several studies have suggested that the P300 results from report requirements (Cohen et al., 2020; Pitts, Metzler, & Hillyard, 2014; Schlossmacher et al., 2021), whereas earlier sensory negativities have been suspected to reflect attentional processes (Mena et al., 2020; Pitts, Metzler, & Hillyard, 2014). So far, studies that test the task-dependence of early and late ERP correlates of somatosensory awareness are lacking. To fill this gap and establish a temporal profile for the stimulus transformation observed in Study 1, I employed the somatosensory-visual matching task in combination with EEG. Twenty-four participants completed the experiment while their EEG was recorded from a 64-channel BioSemi system. To further test the dependence of awareness-related ERP responses on report requirements, this study also included a control experiment, in which 22 additional participants were subjected to an identical stimulation procedure but reported their perception directly rather than giving match/mismatch reports. Moreover, to ensure the validity of the BMS approach, I included two control models in the analysis, a null model, including only an intercept regressor, and a cue model, modelling the white/dark grey matching cue presented on every trial. As expected, the null model outperformed all other models in the baseline period, when no effects are to be expected, and the cue model best explained the signal in occipital electrodes, where visual processing is likely reflected. Regarding the experimental models, results from the matching task show that early ERP responses indicative of stimulus processing in S1 (P50) were best explained by the intensity model, suggesting processing of physical stimulus properties at this latency. The detection probability model first explained the data at ~100 ms, likely reflecting processing in S2. The first effect of categorical target detection was observed at the N140 latency. This effect was relatively brief and preceded by an effect of stimulus intensity, potentially suggesting a transformation from physical to perceptual representations at this latency. Finally, a broadly distributed P300 component occurred for both detected and undetected trials and was best explained by the stimulus intensity and detection probability models but not by the target detection model. Data from the control experiment using direct reports confirmed the intensity effect in the P50 and detection effect in the N140 component. In addition, a strong effect of target detection was observed in the late P300 component which showed enhanced amplitudes for detected compared to missed targets. Interestingly, the uncertainty and report models did not explain the data well in either of the experiments suggesting that corresponding processes are not well reflected in stimulus-locked EEG data. Overall, the results suggest that while very early ERP components reflect physical stimulus processes and thus, constitute precursors of conscious perception, the N140 component reflects stimulus awareness and is only marginally affected by report requirements. In contrast, the late P300 shows a profound task-dependence as it only reflected stimulus awareness when target detection directly correlated with reports and could otherwise be elicited even when target stimuli were missed. Therefore, late activity following target detection is likely not a true correlate of somatosensory awareness but instead reflects postperceptual processing.

3 Discussion

The aim of this thesis was to scrutinise the relevance of early brain activity in sensory cortices vs. late activity in widespread supramodal networks for the emergence of somatosensory awareness. Using a novel somatosensory detection task in combination with fMRI and EEG, I have shown that – when controlled for its most common precursors and consequences – the neural correlates of somatosensory awareness were restricted to regions in somatosensory cortex. Within the first 150 ms of stimulus processing, a transformation from physical to perceptual representations occurred, with S1 primarily reflecting stimulus intensity and S2 showing sensitivity to target detection. These effects were reflected in the amplitudes of the P50 and N140 components, respectively. Later activity in supramodal association cortex did not show correlation with awareness. Instead, regions in the anterior insula, cingulate, and supplementary motor areas were sensitive to perceptual uncertainty and reports. Frontoparietal processing as indexed by the P300 occurred for both detected and undetected targets, indicating association with task requirements. Thus, our studies provide evidence in favour of the early sensory view of conscious perception and suggest that late activity in supramodal regions reflects postperceptual processing, but not perceptual awareness per se.

3.1 From physical to perceptual stimulus processing in the somatosensory system

The results of our two studies are in good correspondence and collectively imply that somatosensory stimuli undergo a transformation from physical to perceptual processing stages within somatosensory cortices. The P50 component is commonly assumed to reflect processing in BA 1 of S1 (Allison et al., 1989; Allison, McCarthy, & Wood, 1992; Hämäläinen, Kekoni, Sams, Reinikainen, & Näätänen, 1990; Yamashiro et al., 2019), suggesting that the intensity effects observed in S1 in our fMRI study and at the P50 latency in our EEG study reflect the same underlying process. Previous studies have similarly shown that activity in S1 shows a more or less linear scaling with stimulus intensity (Forschack et al., 2020; Backes, Mess, Van Kranen-Mastenbroek, & Reulen, 2000; Ferretti et al., 2003; Jousmäki & Forss, 1998; Lin et al., 2003; A. J. Nelson, Staines, Graham, & McIlroy, 2004; Timmermann et al., 2001; Torquati et al., 2002), altogether confirming a reflection of physical stimulus properties in the early responses in S1. Both the P100 (Allison et al., 1989, 1992; Yamashiro et al., 2019) and N140 (Frot & Mauguière, 2003; Gijsen, Grundei, Lange, Ostwald, & Blankenburg, 2021; Ostwald et al., 2012) have been suggested to originate from bilateral S2. Given that the P100 in our study showed a transition from an intensity effect to an effect of detection probability, whereas the N140 was the first to show an effect of target detection, this correspondence may suggest a serial emergence of the intensity, detection probability, and detection effects in S2 observed in our fMRI study. Virtually all of the studies showing a linear intensity effect in S1 have also observed activity in S2, but the relationship of S2 activity with stimulus intensity is less clear. While some have found S2 activation upon suprathreshold stimulation regardless of stimulus properties (Backes et al., 2000; Ferretti et al., 2007; A. J. Nelson et al., 2004), consistent with a role in stimulus detection, others have reported some degree of intensity modulation, with saturation points at varying intensity levels (Jousmäki & Forss, 1998; Lin et al., 2003; Timmermann et al., 2001; Torquati et al., 2002). One study found a sigmoidal activation profile very similar to that observed in large parts of S2 in our study, but with an inflection point near the pain threshold and thus, at much higher intensity levels (Timmermann et al., 2001). These results may suggest that activity in S2 can adapt to task demands, as has previously been observed in S2 responses in macaques (Romo, Hernández, Zainos, Lemus, & Brody, 2002). However, another study has shown that the variable response properties may instead be explained in terms of subregions within S2, as they observed a posterior compartment that scaled with stimulus intensity and an anterior compartment that activated regardless of intensity level and possibly subserved stimulus detection (Ferretti et al., 2003), a finding that is well in line with our results. Taken together, evidence suggests a representation of physical stimulus parameters in S1, and variable stimulus representations in S2, including one reflecting target detection.

Both fMRI and EEG measure the activity of large populations of neurons and are therefore not directly informative regarding the underlying response properties of single cells. Thus, our studies cannot resolve how exactly the transformation from intensity to detection sensitivity is computed on the neuronal level. However, some insight may be gained from comparing our results with studies that have recorded single unit activity from intracranial electrodes in behaving animals. Several studies suggest that neurons in S1 increase their firing rates with increasing stimulus intensities, indicating that the intensity effect observed in our data may result from rate coding in S1, and hence, may reflect the response dynamics of individual neurons in this region (de Lafuente & Romo, 2005; Lankarany, Al-Basha, Ratté, & Prescott, 2019). However, other studies recording from S1 neurons in rats have found that not only firing rates but also the number of activated neurons increased with stimulus intensity (Glazewski & Barth, 2015; Zhang et al., 2011), suggesting that population coding may also play a role in the observed intensity effects in S1. In contrast, surprisingly little is known about single neuron responses to intensity variations in S2. One study measured single unit activity in S2 in response to stimuli of different intensities in macaques performing a detection task and observed that S2 firing rates increased with increasing stimulus intensities and were predictive of the animals' behavioural choices (de Lafuente & Romo, 2006). Unfortunately, no information regarding trial-to-trial response variability was provided in this study, leaving it open whether the recorded neurons indeed showed a linear increase in firing rates or could have been better described by a sigmoidal or even categorical detection function. However, another study from the same lab used a temporal pattern discrimination task, in which macaques were trained to discriminate between regular and irregular tactile stimulus patterns (Rossi-Pool et al., 2021). In this study, the authors report that spiking activity in different subpopulations in S2 reflected either the physical stimulus parameters or the categorical choice outcome. These results support the coexistence of different neural populations within S2, reflecting physical and perceptual stimulus dimensions, respectively. In our data, we similarly observed a coexistence of linear and categorical response profiles in S2, and additionally, we found a sigmoidal response, reflecting the probability of target detection. What it means for a population of neurons to reflect the probability of target detection may not be directly apparent. In this context it is of note that sigmoidal population functions have been shown to naturally emerge from populations of neurons that possess variability in their firing thresholds (Wilson & Cowan, 1972) or prestimulus membrane depolarisation (Marreiros, Daunizeau, Kiebel, & Friston, 2008). If single neurons constitute binary units that are either active or inactive, depending on whether the noisy postsynaptic input crosses their individual depolarisation thresholds or not, the population as a whole implements a sigmoidal activation function of linearly varying input. Downstream neurons with larger receptive field sizes that integrate responses from such populations would then collectively exhibit response dynamics close to all-or-none firing (**Figure 4A**), linking the sigmoidal population response to detection probability. Indeed, receptive fields in S2 neurons greatly vary in size (Fitzgerald, Lane, Thakur, & Hsiao, 2006), such that such a transformation could in principle occur in this region. However, given that both fMRI and EEG are primarily sensitive to fluctuations in local field potentials and thus, the input to neuronal populations as well as their local intracortical processing (Buzsáki, Anastassiou, & Koch, 2012; Logothetis, 2003), how exactly our observations can be mapped to changes in neuronal firing rates needs further investigation. Granted this constraint, the above considerations may imply that the transformation from physical to perceptual stimulus properties observed in the somatosensory system could rely on a hierarchical transformation from rate coding in S1 and subregions of S2, to a first population code characterised by a distribution over thresholds with non-zero variance, to a final population code that exhibits all-or-nothing response dynamics. Clearly, these suggestions are highly speculative and require experimental validation. However, at the very least, the evolution of response profiles observed in our studies may constrain models of the cellular mechanisms that can plausibly underlie the transformation from physical to perceptual stimulus representations in the somatosensory hierarchy. Exactly which populations or mechanisms subserve conscious experience in this process, and what role feedback connections may play in the transformation remains an open question.

3.2 Neural correlates of somatosensory awareness

3.2.1 Activity in primary somatosensory cortex reflects precursors of awareness

Both our fMRI and EEG results suggest that activity in S1 does not differentiate between detected and undetected targets (**Figure 4B, C**). The fMRI results suggest that a posterior portion of S1 correlated with a sigmoidal function reflecting detection probability, which might indicate a first transformation towards perceptual readout. However, the detection probability model predicts the same level of activation for detected and undetected targets of the same intensity, and thus, marks a preperceptual processing stage. Therefore, our results strongly suggest that S1 should not be considered part of the somatosensory NCC. This conclusion is in line with several previous studies that have not observed awareness-related activity in early S1 responses using various measurement techniques in both humans and animals (Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013; de Lafuente & Romo, 2005, 2006; Forschack et al., 2020; Grund et al., 2021; Moore et al., 2013; Schubert et al., 2006; Wühle et al., 2010, 2011; Zhang & Ding, 2010). However, some studies have observed very early detection effects in S1 responses (Hirvonen & Palva, 2016; Palva et al., 2005). Given that these studies used near-threshold stimulation, it is possible that their results reflect the influence of prestimulus brain states on upcoming stimulus detection (Palva et al., 2005). In fact, it has been demonstrated that prestimulus activity in S1 (Moore et al., 2013; Schubert, Haufe, Blankenburg, Villringer, & Curio, 2009) as well as its integration within a larger network of regions (Frey et al., 2016) can predict access to consciousness of upcoming near-threshold stimuli and these differences in baseline activity result in altered stimulus evoked responses (Stephani, Hodapp, Jamshidi Idaji, Villringer, & Nikulin, 2021). Such perceptual biases are certainly informative regarding potential precursors of awareness and their study may aid in characterising the neural prerequisites of access to conscious perception (see e.g. Ruhnau et al., 2014). However, given their influence on poststimulus effects, disentangling these precursors from true NCCs in near-threshold studies is challenging. Paradigms that employ a wider range of stimulus properties, as employed here, may therefore constitute a valuable alternative for isolating the neural correlates of perceptual awareness from its precursors.

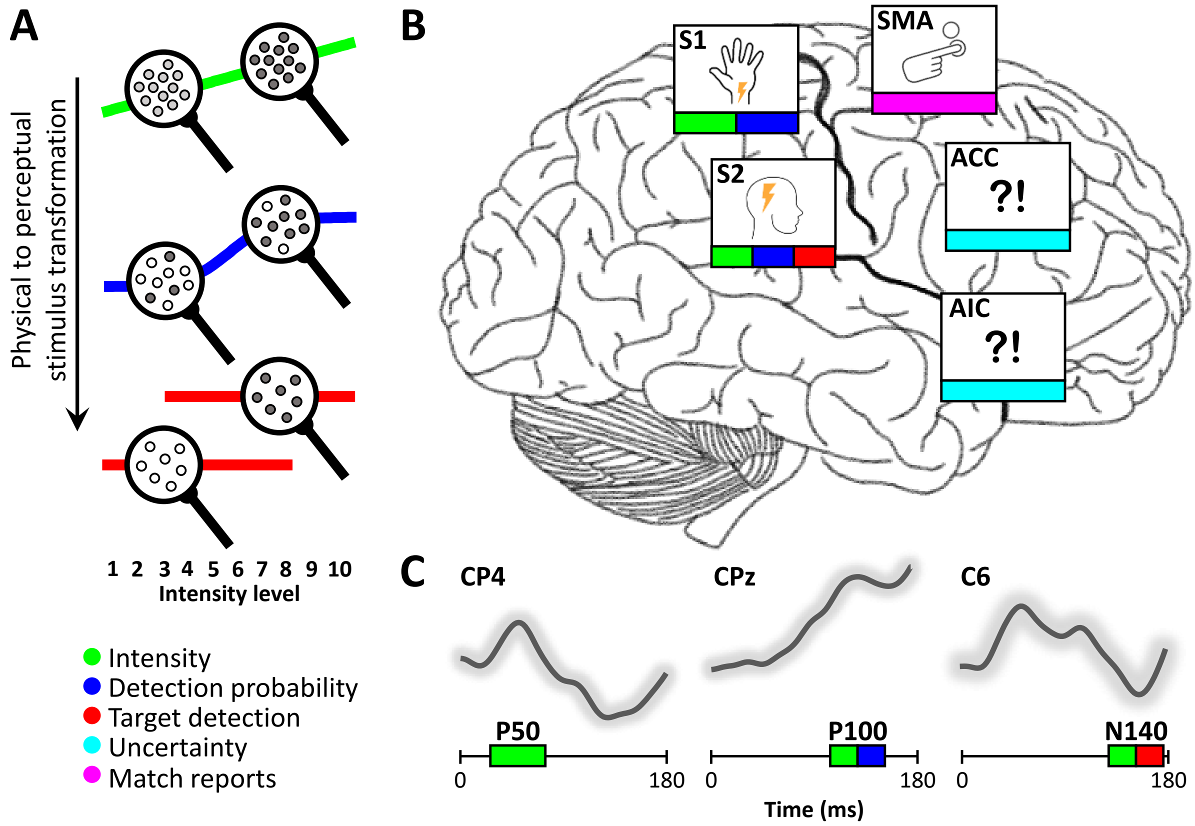

Figure 4: Results summary. A) Hypothetical cellular responses. During the matching task, a conversion from physical to perceptual stimulus processing stages occurred in somatosensory regions. The observed population activity may have resulted from a hierarchical transformation from rate to population coding, which culminates in all-or-nothing responses reflecting stimulus awareness as downstream neurons with increasing receptive field sizes integrate upstream responses. The circles within the magnifying glasses represent single neurons in different neural populations that signal stimulus intensity (green), detection probability (blue), or categeorical target detection (red). Darker shading of the circles indicates higher firing rates. **B) fMRI results.** While BOLD responses in S1 largely reflected physical stimulus properties (stimulus intensity), S2 showed multiple response profiles and constituted the only region showing an effect of categorical target detection. ACC and AIC as part of the salience network showed the highest activity on trials near perceptual thresholds when stimulus uncertainty was high. SMA activity reflected match/mismatch reports. Activity in prefrontal and posterior parietal regions did not show covariation with any of the employed models. **C) EEG results.** The early P50 component was modulated by stimulus intensity, confirming processing of physical stimulus properties in early S1 responses. Effects of detection probability were first observed in the P100 component and the earliest response reflecting categorical target detection occurred in the N140 component at ~150 ms. Both of these components have been suggested to originate from S2 (Allison et al., 1992; Frot & Mauguière, 2003). Later components were strongly modulated by task requirements and likely reflect postperceptual processing.

3.2.2 Activity in secondary somatosensory cortex correlates with awareness independent of task requirements

The only effects of categorical target detection during the matching task occurred in S2 and at the latency of the N140 component (**Figure 4B, C**). Similar detection effects have previously been observed in S2 in the form of increased BOLD responses (Grund et al., 2021; Moore et al., 2013), prolonged processing (Wühle et al., 2010, 2011), enhanced ERPs (Al et al., 2020; Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013; Forschack et al., 2020; Schubert et al., 2006; Zhang & Ding, 2010), increased firing rates (de Lafuente & Romo, 2006), and more effective network integration (Weisz et al., 2014). Moreover, disruption of S2 integrity has been reported to compromise awareness of tactile stimulation (Hanada et al., 2020; S. Meyer et al., 2016). Our results suggest that this relatively early, modality specific activity can occur largely independently of task requirements and therefore qualifies as a true correlate of conscious somatosensory perception. This adds to evidence from the visual and auditory modalities indicating that – when report requirements are accounted for – perceptual awareness manifests at the level of non-primary sensory cortices (Noy et al., 2015; Tse et al., 2005; Wiegand et al., 2018).

The most critical challenge for activity in sensory cortices as a correlate of awareness is its possible dependence on attentional processes. Awareness-related negativities in particular have been plagued by the question to what extend they might reflect stimulus-related attention rather than awareness per se, and thus constitute precursors or consequences of conscious perception (Aru et al., 2012; Mashour et al., 2020; Pitts, Metzler, & Hillyard, 2014). Although it appears clear that attention and awareness are closely related – we usually see, hear, or feel what we attend to and vice versa – the exact relationship between these two concepts remains highly controversial. While most researchers agree that attention and conscious perception are in principle distinct processes that rely on distinct neural mechanisms (Baars, 1997; Koch & Tsuchiya, 2007; Maier & Tsuchiya, 2020; Tallon-Baudry, 2012), the question of necessity has not yet been conclusively answered. While some believe attention to be strictly necessary for conscious perception (Cohen, Cavanagh, Chun, & Nakayama, 2012; Dehaene et al., 2006), others claim a double dissociation between the two, arguing that attention can occur in the absence of awareness and, crucially, that awareness can occur in the absence (or near-absence) of attention (Koch & Tsuchiya, 2007; Lamme, 2018; Matthews, Schröder, Kaunitz, Van Boxtel, & Tsuchiya, 2018; Van Boxtel, Tsuchiya, & Koch, 2010). Despite this conflict, the fact that attentional processes can profoundly impact what is consciously perceived is undisputed. This is unequivocally demonstrated in inattentional blindness phenomena, where a primary attention-demanding stimulus or task prevents secondary, unattended stimuli from reaching awareness (Mack, 2003). Besides this endogenous, top-down form of attention, the general level of attention, phasic alertness, has also been shown to alter perceptual thresholds (Martín-Signes et al., 2019). Moreover, unattended but salient stimuli can capture exogenous, bottom-up attention (Itti & Koch, 2000; Parkhurst, Law, & Niebur, 2002), boosting stimulus processing. Importantly, all of these different types of attention are generally associated with increased signals in sensory regions (Eimer & Forster, 2003; Johansen-Berg, Christensen, Woolrich, & Matthews, 2000; Mangun, Buonocore, Girelli, & Jha, 1998; Mena et al., 2020; Woldorff et al., 1993). Crucially, activity in S2 as well as the N140 component have previously been demonstrated to be modulated by endogenous and exogenous attention (Eimer & Forster, 2003; Johansen-Berg et al., 2000; Mena et al., 2020), making it all the more important to carefully dissociate the effects of attention from those of conscious perception. In our studies, we aimed to reduce the influence of prestimulus endogenous attention and phasic alertness by presenting target stimuli at different intensity levels, assuming that detection of stimuli at clearly sub- or supraliminal intensities would be largely unaffected by fluctuations in attention. The effects of exogenous attention captured by a detected target stimulus were reduced by the requirement to quickly compare the visual and somatosensory percepts, which we assumed to discourage reflective attentional engagement with the perceived target. The comparison between the matching task and the direct report task in our EEG study suggests that this approach was at least in part successful, given that detection effects were strongly reduced in the matching task. This was especially true for components that are known to be sensitive to manipulations of attention, including the P100 (Eimer & Forster, 2003) and P300 (Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto & Revonsuo, 2007). However, it is clear that our task manipulations merely reduced the effects of attention but may not have eliminated them entirely. Indeed, the N140 detection effect in the matching task was slightly reduced compared to that in the direct report task, suggesting that this component, too, was to some degree altered by task requirements. Accordingly, some uncertainty remains regarding the question whether the observed detection effects in S2 and in the N140 component truly reflect awareness or constitute residual effects of endogenous or exogenous attention. In the visual modality, previous studies that have attempted to control for attentional processes more directly have commonly employed 2×2 designs that manipulate awareness and attention independently. These studies tend to find that attention and awareness rely on different neural mechanisms (Chen, Wang, Yu, & Liu, 2017; Watanabe et al., 2011; Wyart, Dehaene, & Tallon-Baudry, 2012; Wyart & Tallon-Baudry, 2008) and, crucially, that the VAN, which may be interpreted as the visual analogue of the N140 (Dembski et al., 2021), specifically reflects awareness, not attention (Koivisto, Revonsuo, & Lehtonen, 2006; Koivisto et al., 2009; Koivisto & Revonsuo, 2007) and can be distinguished from the attention-related potential

N2pc (Bola, Paź, Doradzińska, & Nowicka, 2021; Woodman & Luck, 2003). To date, similar investigations in the somatosensory and auditory modalities have yet to be performed. However, given the evidence from the visual modality and the relative robustness of our detection effects towards task manipulations, it appears that activity in S2 at ~150 ms post stimulus is the current best candidate marker of stimulus awareness during somatosensory target detection.

3.2.3 Activity in supramodal cortical networks reflects consequences of awareness

We did not observe any reliable correlates of target detection in regions outside the somatosensory cortices or at late latencies commonly associated with processing in frontoparietal networks. We thus confirm previous research that has suggested that activity in frontoparietal networks is likely associated with task relevance, reports, and goal completion (Cohen et al., 2020; Farooqui & Manly, 2018; Frässle et al., 2014; Noy et al., 2015; Pitts et al., 2012; Pitts, Padwal, et al., 2014; Pitts, Metzler, & Hillyard, 2014; Schelonka et al., 2017; Schlossmacher et al., 2020, 2021; Shafto & Pitts, 2015; Wiegand et al., 2018) and we offer two extensions to this conclusion: first, our studies are the first to demonstrate that late frontoparietal network activity dissociates from perceptual awareness in the somatosensory modality, suggesting that previous observations may generalise across modalities. Second, our task manipulation did not rely on passive stimulation or no-report paradigms but instead orthogonalised stimulus awareness and reports. Accordingly, we ensured equal relevance of perceived and unperceived stimuli, such that the absence of detection effects in supramodal regions or the P300 cannot be explained in terms of increased signal variability due to reduced processing. Moreover, by obtaining reports in all conditions we ascertain the perceptual outcome on every trial, such that noise resulting from incorrectly classified trials is minimised. Finally, our paradigm ensured trial-to-trial conscious access, such that previous suggestions, which have assigned early sensory negativities to preconscious or at most phenomenally conscious states and late positivities to proper conscious access (Dehaene et al., 2006), are not supported by our results. We thus validate and extend previous results from no-report studies, while overcoming several points of criticism that have so far limited their conclusiveness.

Many different brain areas in frontal, parietal, temporal, and even subcortical regions are assumed to contribute to the P300 waveform (Halgren et al., 1998; Linden, 2005; Soltani & Knight, 2000). This diversity likely reflects the many different cognitive processes that produce activity in the P300 time range (Verleger, 2020; Yamaguchi & Knight, 1991) and underlies the composite nature of the signal. Besides the well-known subcomponents P3a and P3b (Polich, 2007), it has recently been suggested that the P300 might contain a third component that reflects awareness even in the absence of reports. Sergent et al.

(2021) found that although the typical P300 vanished when participants no longer reported their perception of auditory target vowels, they could still decode target presence from late time windows, when a sustained negativity occurred instead of the P300. Crucially, the late responses during passive listening could be used to decode perception during an active condition, which the authors interpret as showing a late “correlate of awareness per se“, which is normally hidden in the P300 response. Moreover, they found that the data in this late time window were best explained by a non-linear “bifurcation model” (similar to our detection model), which they interpret as reflecting a late all-or-none signal marking access to awareness. Although interesting, it is unclear how these results can be reconciled with previous studies that have used passive auditory stimulation but have not found late negativities to correlate with awareness (Dykstra et al., 2016; Hillyard et al., 1971). The study makes no reference to the AAN, although the onset of the reported late negativity (~250 ms) as well as the central (although slightly more posterior) topography may suggest certain similarities. Interestingly, source localisation showed that regions involved in the passive task constituted a reduced version of the network involved in the active task. Although the authors interpret the subnetwork as reflecting mostly activity in IFG, they acknowledge that the projected sources were so close to temporal cortex that alternatively, they might have resulted from spill-over from auditory regions, especially given the imprecision of EEG source reconstruction. However, even if the observed effects were attributed to late activity in sensory regions, the reported all-or-none effect is clearly at odds with our results. While Sergent and colleagues find their bifurcation model to dominate the signal from 250 ms onwards, we only found very restricted effects of categorical target detection, and no such effects in the P300 time range or in typical P300 source regions. Whether this difference can be attributed to differences in the employed models or differences in the tasks remains to be tested. However, the fact that in their passive task participants were still occasionally asked whether they had perceived the auditory stimulus may have prompted covert decision processes, resulting in yet another postperceptual dichotomisation. Studies employing similar methods but circumventing the pitfalls of no-report paradigms by orthogonalising awareness and reports, may aid in determining whether the auditory P300 indeed contains a subcomponent reflecting awareness independent of reports or merely results from uncontrolled task demands.

3.3 The role of supramodal regions in perceptual tasks

Although the study by Sergent et al. (2021) comes to different conclusions regarding the correlates of awareness, it bears a striking resemblance to our results in another respect. Similar to our fMRI study, Sergent and colleagues found that the brain region most likely involved in reporting perceptual contents is the SMA. The fact that they found report-related SMA activity using EEG whereas we did not observe any report effects in our EEG data may be due to the more complex reports in the matching task, which required integrating two stimuli and may have resulted in increased temporal variability of the decision process. In our control experiment, however, reports were much simpler, and we observed a prominent P300 effect reflecting these reports. Although we have no direct evidence that this effect originated from SMA, a previous study on somatosensory target detection source-localised the P300 effect to a medial central cluster encompassing bilateral SMA (Auksztulewicz & Blankenburg, 2013). Crucially, our results show that merely balancing motor responses does not provide a sufficient control for such report-related activity, given that motor responses in the direct report task were completely dissociated from detection. Thus, studies showing ostensibly perception-related signals in motor regions (Auksztulewicz & Blankenburg, 2013; de Lafuente & Romo, 2005, 2006; Malejko et al., 2018) must be carefully examined for potential effects of report requirements that may confound analyses beyond mere motor planning effects.

In addition to the SMA, we also observed task-related activity in AIC and ACC, which correlated with our model of perceptual uncertainty. The AIC and ACC commonly coactivate in perceptual tasks (Sterzer & Kleinschmidt, 2010) and they have been suggested to form a salience network, which tags salient events and initiates further processing (Menon & Uddin, 2010). Importantly, both of these regions have previously been implied in processing decision uncertainty (Gorka, Nelson, Phan, & Shankman, 2016; Stolyarova et al., 2019). The model used here defined uncertainty in terms of stimulus characteristics: stimuli close to perceptual thresholds were expected to be sometimes detected and sometimes missed, and thus, result in more uncertain perceptual decisions than stimuli that were clearly sub- or suprathreshold. Or put simply: the task was expected to be more difficult around threshold intensities. Activity in AIC and ACC has previously been shown to correlate with task difficulty and perceptual ambiguity (Deary et al., 2004; Lamichhane, Adhikari, & Dhamala, 2016; Philiastides & Sajda, 2007). Such observations have prompted the view that these regions are involved in attentional control mechanisms and switching of attentional sets (Bissonette, Powell, & Roesch, 2013; Eckert et al., 2009; Luks, Simpson, Feiwell, & Miller, 2002; S. M. Nelson et al., 2010). These control processes allow the allocation of additional resources under conditions of increased perceptual or behavioural demands, possibly by coordinating the switch between the default mode network and the central executive network (Goulden et al., 2014). The dependence of AIC function on task demands becomes particularly apparent when comparing different studies that have used similar stimuli but imposed different behavioural requirements on participants. Christensen, Ramsøy, Lund, Madsen, and Rowe (2006) asked participants to rate the clarity of their visual percepts of backward masked stimuli while measuring fMRI. They found that activity in AIC increased with increasing stimulus visibility. In contrast, Deary et al. (2004) similarly employed visual backward masking but asked participants to perform a discrimination task which became harder the more the presented backward masks suppressed their visual percepts. In this behavioural context, AIC activity decreased with increasing stimulus visibility, and thus, showed the opposite response profile. Our task falls in the middle between these behavioural protocols, as it resulted in the most difficult decisions in the middle of the employed range of stimulus intensities, and accordingly, the strongest AIC/ACC activity on these trials. Sterzer and Kleinschmidt (2010) have taken the aforementioned results to imply that AIC and ACC generate heightened sensory alertness, which can be triggered by either stimulus or task characteristics, and which allows more effective integration of sensory information. Indeed, a study by Sadaghiani, Hesselmann, and Kleinschmidt (2009) has shown that prestimulus activity in these regions facilitates detection of near-threshold auditory stimuli, and similar prestimulus effects have been observed in the somatosensory modality (Boly et al., 2007; Hirvonen & Palva, 2016). Altogether, these studies provide compelling evidence that AIC and ACC do not reflect somatosensory awareness (Bastuji et al., 2016; Büchel et al., 2002; Grund et al., 2021) or even awareness in general (Craig, 2009) as has previously been suggested but instead may regulate attentional control and boost sensory processing depending on task demands.

The involvement of PFC and PPC is less clear in our studies since none of our tested models showed effects in these regions. However, given that they are among the most commonly reported brain regions in studies on perceptual awareness (Mashour et al., 2020; Rees et al., 2002), it is worth considering why we did not observe such activity. If we assume that EEG signals in the P300 time range to some degree reflect activity in PPC and PFC (Halgren et al., 1998; Linden, 2005; Soltani & Knight, 2000), our data may suggest that experimental effects in PPC and PFC in the fMRI study were not absent because there was no task-related activity in these regions but because the processes computed here were equated across experimental conditions. Looking back at our experimental design, candidate processes include perceptual decision making, working memory, and more generally, processes related to behavioural relevance, all of which were largely equated in the matching task. Indeed, both prefrontal and posterior parietal regions are known to be involved in perceptual decision making (Heekeren, Marrett, & Ungerleider, 2008) and working memory (D'Esposito, Postle, & Rypma, 2000; Lara & Wallis, 2015; T. T. Schmidt, Schröder, Reinhardt, & Blankenburg, 2021; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002), which may explain their routine activation in perceptual tasks. Further, a previous study has shown that frontoparietal areas activated when stimuli defined as targets were detected, but the same regions deactivated when equally attended and conscious stimuli were presented that did not serve as targets (Farooqui & Manly, 2018). These results suggest that behavioural relevance and goal completion may similarly contribute to seemingly perception-related activity in frontoparietal areas. Nonetheless, even if it should eventually turn out that PFC is not causally involved in awareness of visual, auditory, or somatosensory stimuli, this does not exclude the possibility that it underlies other, potentially non-sensory contents of consciousness. For example, the subjective experience of confidence, closely related to the concept of metacognition, has been suggested to reside in PFC (Fleming & Dolan, 2012; Shekhar & Rahnev, 2018) as well as processes related to emotion awareness (Phillips, Drevets, Rauch, & Lane, 2003). Interestingly, studies using intracranial electrical stimulation, which apply currents directly to the brain, rarely show any concrete sensory experiences when prefrontal regions are stimulated (Fox et al., 2020) but can result in various emotional experiences and experiences of conceptual thought (Fox et al., 2018; Raccah, Block, & Fox, 2021). Thus, although PFC may not be a universal correlate of awareness, subregions in PFC may well underlie the emergence of these specific types of experiences.

3.4 Implications for theories of conscious perception

Our studies have identified correlates of somatosensory awareness in relatively early, somatosensory cortical regions and are thus compatible with theories of conscious perception that focus on activation of dedicated processing modules in sensory pathways (Celesia, 2010; Koch et al., 2016; Zeki, 2003), as well as those stressing the importance of cortical interactions at the level of sensory cortices (Lamme, 2006). Detection effects in the somatosensory N140 component have previously been attributed to recurrent interactions between S1 and S2 (Auksztulewicz et al., 2012; Auksztulewicz & Blankenburg, 2013), indicating that awareness of a somatosensory stimulus may result from increased feedforward and feedback processing between these two regions. This account suggests that the detection effect in S2 observed in our fMRI study may have been the result of more effective feedforward processing. Interestingly, we did not observe a corresponding detection-related increase in activity in S1, which one might expect if feedback signalling were enhanced for perceived targets. Previous studies have in fact reported detection-related feedback enhancement to result in late depolarisation in S1 (Auksztulewicz et al., 2012; Jones et al., 2007; Kwon et al., 2016; Yang et al., 2016), but no such effects were apparent in our fMRI data. However, neither of our studies directly tested changes in connectivity associated with target detection, and it is certainly possible that our methods were simply not sensitive enough to detect subtle alterations in S1 depolarisation resulting from potential feedback interactions. Thus, at this point the relevance of the S2–S1 feedback pathway for target detection in our studies cannot be conclusively determined. Nonetheless, the detection effect observed in the N140 component is in line with previous studies suggesting local recurrent processing as a potential NCC and provides further evidence that awareness-related negativities, possibly reflecting this recurrency, can persist when task requirements are controlled for.

In contrast, we have not found any involvement of supramodal regions in the emergence of somatosensory awareness, and thus, our studies do not provide evidence for theories that assume global broadcasting of information to be necessary for awareness (Dehaene et al., 2006) or theories presuming a privileged role for PFC (Brown, Lau, & LeDoux, 2019; Lau, 2007). Instead, we corroborate the view that such late global activity reflects postperceptual processing. Indeed, it appears that global availability, or rather the neural activity believed to reflect global availability, is not a defining characteristic of conscious content. Instead, the restriction of correlates of awareness to sensory regions seems to conflict with the idea that conscious perception has a high-order cognitive quality. It has previously been suggested that there might be two correlates of conscious perception, one reflecting the phenomenal quality of a percept and one reflecting conscious access, which is characterised by global availability of information that serves as input to further cognitive processing such as working memory and action (Block, 2005). On the neural level, these two processes have been hypothesised to be reflected in local recurrent processing in sensory regions and global recurrent processing involving frontoparietal networks, respectively (Mashour et al., 2020). However, in the matching task, we ensured that consciously perceived stimuli were accessed and subjected to further cognitive processing, and yet, we found no evidence for a global correlate of awareness. Thus, our results do not support a neuronal distinction between phenomenal and access consciousness. It must be noted, however, that results such as ours cannot exclude a role for supramodal regions in perceptual awareness altogether. As previously mentioned, the neuronal organisation in these regions, and in PFC in particular, might prevent relevant activity from being detected when using coarse methods such as fMRI and M/EEG. Instead, invasive recordings of single cells or populations of neurons or multivariate analyses might be necessary to uncover awareness-related signals in these areas. This possibility is certainly the most important limitation of most previous studies on the task dependence of supramodal correlates of awareness and – although we generally expect the simplicity of the stimuli used here to reduce the requirement for complex multivariate representations – it is left largely untouched by our results. Likewise, as has previously been pointed out (Odegaard et al., 2017), a few studies showing null-effects in prefrontal regions do not falsify theories postulating their necessity. However, even if more sensitive measurements or analysis techniques may eventually prove the role of supramodal regions for awareness, this does not change the fact that at present, much of the literature has not sufficiently accounted for potential task confounds, and therefore, the validity of corresponding studies regarding the question of necessity is limited. This is especially important given that GNWT, a theory that is heavily built on evidence presenting large univariate effects, continues to be the most popular theory of awareness in the field (Michel et al., 2018). Clearly, studies using classical experimental paradigms have made a tremendous contribution to our understanding of the neural processes underlying the emergence of awareness and cognition in general. However, by re-evaluating this literature through the lens of potential precursors and consequences of awareness we may gain the unique chance to consolidate seemingly conflicting lines of evidence and advance the collective effort to find the true neural correlates of awareness.

3.5 Is awareness all-or-none or graded?

Although we expected effects related to stimulus awareness to be reduced in the matching task compared to previous, less controlled paradigms, it is quite striking just how restricted our detection effects were. Especially the EEG study revealed a drastic reduction of categorical detection effects in the matching task compared to the control experiment. However, also the detection effects in the fMRI study were surprisingly limited when we consider that the conscious percept of a stimulus is often described as a non-linear, threshold-crossing, all-or-nothing event (Dehaene & Changeux, 2011; Del Cul et al., 2007; Mashour et al., 2020; Sergent & Dehaene, 2004). This observation offers an alternative – albeit speculative – interpretation of our results that takes the subjective dimension of our task into account. For instance, it is safe to assume that subjective experience differs between detected and missed stimuli of the same intensity level. At the same time, the subjective experience of detected stimuli at near-threshold intensities and at clearly suprathreshold intensities is likely to also differ. This means that neither the intensity nor the detection model perfectly captured the perceptual experience of the target stimuli. Crucially, however, the differences in experience would be expected to covary with stimulus intensity and therefore correlate positively with both the intensity and the detection probability models, at least for detected stimuli. Accordingly, these two models may have captured some neuronal variability related to such graded experiences. Since the goal of the matching task was to decorrelate awareness and reports, explicit subjective awareness or intensity ratings were not an option in our experiments. However, previous studies that have used such ratings have shown that not only does perceptual experience change with changing stimulus intensities (Malejko et al., 2018; Muniak, Ray, Hsiao, Dammann, & Bensmaia, 2007) – which is rather trivial – but that awareness itself might have a graded rather than dichotomous nature, at least for low-level sensory features (Derda et al., 2019; Jimenez, Grassini, Montoro, Luna, & Koivisto, 2018; Overgaard, Rote, Mouridsen, & Ramsøy, 2006; Tagliabue, Mazzi, Bagattini, & Savazzi, 2016). In the somatosensory modality, a previous EEG study has shown that even the subjective experience of stimuli of identical intensity can vary parametrically and that this parametric variation correlates with the amplitudes of the N140 and P300 components (Auksztulewicz & Blankenburg, 2013). Interestingly, in our EEG study we observed widespread effects of intensity and detection probability in the P300 time range. Although the P300 amplitude is known to be sensitive to stimulus intensity (Mizukami, Kakigi, & Nakata, 2019; Polich, Ellerson, & Cohen, 1996), such that this result was not overly surprising, the possibility that some of this variance may have been related to graded perceptual experience could potentially rehabilitate the relevance of late EEG activity for somatosensory awareness. As discussed above, the P300 is a composite signal that likely originates from multiple brain regions (Halgren et al., 1998; Linden, 2005; Soltani & Knight, 2000). Therefore, it is somewhat curious that the two models that best explained the P300 in our EEG study, the stimulus intensity and detection probability models, were found to exclusively show effects in primary and secondary somatosensory cortices in our fMRI study. Whether these regions indeed generated the intensity-modulated P300 responses in the EEG study or if, instead, the relevant source activity was not amenable to fMRI cannot be determined with certainty. However, the fact that the P300 is a high-amplitude sustained signal makes it unlikely that no corresponding activity would be measurable with fMRI. Moreover, the P300 topography closely resembled that of the P100, which is believed to originate from S2 (Hämäläinen et al., 1990; Yamashiro et al., 2019). Thus, S2 dipoles could in principle generate a signal consistent with the observed P300 topography. The time course of S2 activity is certainly compatible with such sustained effects, as it has been shown to exhibit tonic activity lasting >300 ms following median nerve stimulation (Avanzini et al., 2018). Finally, we would not be the first to report awareness-related effects at the P300 latency in sensory regions (Sanchez et al., 2020). Taken together, while we cannot say for sure that the intensity and detection probability effects in the P300 were in any way reflective of graded perceptual experiences or that these effects originated from somatosensory regions, the available evidence in principle allows for this interpretation. In fact, two-alternative forced choice tasks as employed here and in many other studies might artificially dichotomise sensory activity through decision-related top-down stabilisation (Meindertsma, Kloosterman, Nolte, Engel, & Donner, 2017). Further research that controls for task demands while allowing for more continuous measures of awareness is warranted to shed light on this issue and could add to the ongoing debate surrounding the question whether awareness is graded, all-or-none, or both (Bachmann, 2013; Overgaard et al., 2006; Sekar, Findley, & Llinás, 2012; Windey, Vermeiren, Atas, & Cleeremans, 2014).

3.6 Open questions, future directions, and conclusions

The results presented in this thesis provide evidence for a correlate of somatosensory awareness in S2 and lend support to the view that relatively early, sensory-specific brain activity underlies the emergence of conscious perception. While these findings may further the early-local vs. late-global debate, several open questions remain.

First, it is unclear whether S2 serves as a general correlate of somatosensory awareness or specifically as a correlate of simple electrical target detection as employed here. S2 is subdivided into four cytoarchitectonic regions in the parietal operculum (OP1–4), each of which has different cellular characteristics and connectivity profiles (Eickhoff, Schleicher, Zilles, & Amunts, 2006). Neurons in these regions feature relatively large, bilateral receptive fields (Delhaye et al., 2018; Fitzgerald et al., 2006) that respond to various forms of tactile stimulation (Burton & Sinclair, 1990; Pruett, Sinclair, & Burton, 2001; Sinclair & Burton, 1993) and are strongly interconnected with both primary somatosensory and higher-order cortical areas (Burton, Fabri, & Alloway, 1995; Cipolloni & Pandya, 1999; Liao & Yen, 2008). This functional anatomy suggests highly integrative processing in S2, which could point to its role as a somatosensory processing hub that transforms somatosensory information into behaviourally relevant outcomes. However, whether awareness of different, more complex stimulus features would similarly be reflected in S2 activity or would require the recruitment of higher-order regions akin to feature-selective regions in the visual streams, requires further investigation. Combining the matching task employed here with more complex stimuli, such as tactile patterns or even objects could constitute a valuable step in that direction.

Further, it is currently unclear how awareness-related negativities in different modalities relate to each other and if they reflect the same underlying processes. Although the VAN, AAN, and N140 have all been suggested to arise from local recurrent processing in sensory cortical areas (Auksztulewicz et al., 2012; Eklund et al., 2020; Koivisto et al., 2016), their exact neural underpinnings and anatomical bases are not completely understood. Dembski et al. (2021) have recently proposed that the VAN, AAN, and N140 (or somatosensory awareness negativity, SAN) could be considered instantiations of a "general awareness negativity", marking a mechanism that is general to awareness but specific to certain kinds of conscious content. They note that studies investigating specific kinds of content are predisposed to finding activity in sensory regions but whether there are any modality-independent processes that bring these sensory contents into awareness remains unclear. Our findings as well as previous results from no-report paradigms imply that the search for such modality-independent correlates of awareness must be conducted very prudently to not conflate potential supramodal awareness-related activity with postperceptual processes. Likewise, studies that generalise across sensory modalities (Sanchez et al., 2020) or stimulus types (Bisenius et al., 2015) need to be interpreted with this problem in mind. A related question concerns the interaction of neural processes directly reflecting perceptual awareness with background processes. These may comprise not only those supporting general arousal, such as an intact reticular activating system (Parvizi & Damasio, 2003), but also activity related to maintaining a task set, a process that is commonly assumed to involve the PFC (Banich et al., 2000; Forstmann, Brass, Koch, & Von Cramon, 2005). Thus, even if prefrontal activity might not be directly reflective of conscious contents, its integrity could still be necessary for these contents to enter conscious awareness. Previous studies that have attempted to test such a causal involvement by perturbing activity in PFC suggest that it may indeed have some effect on perceptual thresholds (Del Cul et al., 2009) but the relevance of this finding in terms of necessity has not been sufficiently explored, and observations in patients with lesions in PFC have so far been inconclusive (Boly et al., 2017; Odegaard et al., 2017).

Finally, although the early-local vs. late-global debate has important implications for some theories of awareness, it has less bearing on others. For example, the integrated information theory (IIT, Oizumi, Albantakis, & Tononi, 2014; Tononi, Boly, Massimini, & Koch, 2016) does not make explicit claims about where in the brain activity should correlate with awareness. Instead, it attempts to identify fundamental properties of subjective experience and uses these properties as constraints on physical systems that can plausibly account for them (Tononi, 2015). Although there are some ideas on why, in this framework, certain brain regions may or may not contribute to conscious experience, there is no clear mapping between conscious and unconscious processing in sensory vs. supramodal regions, per se. Rather, the degree of conscious experience depends on the degree to which a system possesses integrated information (and this is true for all physical systems, not just brains). Although the theory is beginning to be tested in real-world neuroimaging data (Haun et al., 2017; Kim et al., 2018), how neural activity satisfying the requirements for conscious experience according to IIT might interact with other cognitive processes arising from task demands or if this is even a relevant question in this context is largely unexplored.

So far, it seems that evidence suggesting task dependence of NCCs in high-order association cortices has done little to convince scientists subscribed to prefrontal theories of awareness (Mashour et al., 2020; Odegaard et al., 2017). Has the early-local vs. late-global debate reached a stalemate? In the most extreme sense, sensory theories find themselves having to prove that conscious experience is possible without any involvement of higher-order regions, which seems impossible given the limited coverage and resolution of available measurement techniques. In contrast, cognitive theories need to prove that no conscious experience of any kind is possible without involvement of these regions, which again, seems impossible given the sheer number of conceivable conscious contents and the limited accessibility of subjective experience without potentially confounding interrogation. It is questionable whether such a strict distinction is productive in any way, especially considering that it might turn out to be impossible to fully dissociate awareness from its precursors and consequences. After all, our everyday conscious experience is closely intertwined with and sculpted by its relevance for our behaviour. Nonetheless, this does not mean that attempts to disentangle the neural processes supporting the different aspects of this experience are futile. As I have shown here, by varying cognitive variables associated with a simple detection task in a controlled manner, we can characterise brain activity beyond simple detection contrasts. Similar approaches may narrow the field of candidate neural signals that can plausibly underlie the awareness of specific perceptual contents and refine our understanding of the neural mechanisms of subjective experience. To reach this goal, it may be fruitful to focus less on the question of whether late activity in widespread supramodal networks frequently cooccurs with or even alters conscious contents, and instead ask the question: is it truly necessary? When it comes to the awareness of simple electrical pulses to the wrist, our studies suggest that the answer might be: no.

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Appendix

Original publication of Study 1

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RESEARCH ARTICLE

Neural basis of somatosensory target detection independent of uncertainty, relevance, and reports

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Abstract Research on somatosensory awareness has yielded highly diverse findings with putative neural correlates ranging from activity within somatosensory cortex to activation of widely distributed frontoparietal networks. Divergent results from previous studies may reside in cognitive processes that often coincide with stimulus awareness in experimental settings. To scrutinise the specific relevance of regions implied in the target detection network, we used functional magnetic resonance imaging (n = 27) on a novel somatosensory detection task that explicitly controls for stimulus uncertainty, behavioural relevance, overt reports, and motor responses. Using Bayesian Model Selection, we show that responses reflecting target detection are restricted to secondary somatosensory cortex, whereas activity in insular, cingulate, and motor regions is best explained in terms of stimulus uncertainty and overt reports. Our results emphasise the role of sensory-specific cortex for the emergence of perceptual awareness and dissect the contribution of the frontoparietal network to classical detection tasks.

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Introduction

The target detection task is a standard paradigm to study the neural correlates of perceptual awareness. In the near-threshold detection task, participants are presented with stimuli at intensities close to their individual detection thresholds, resulting in detection rates of ~50%. Neural responses underlying detected and undetected targets can then be contrasted at identical physical stimulation parameters to identify the neural correlates of conscious access.

In the somatosensory domain, research on this task has identified a range of areas that correlate with target detection. These include the thalamus, primary (SI) and secondary (SII) somatosensory cortices, motor areas, the anterior insular cortex (AIC), anterior cingulate cortex (ACC), as well as posterior parietal and prefrontal regions (**Auksztulewicz et al., 2012**; **Bastuji et al., 2016**; **Allen et al., 2016**; **Bornhövd et al., 2002**; **Büchel et al., 2002**; **de Lafuente and Romo, 2005**; **de Lafuente and Romo, 2006**; **Frey et al., 2016**; **Hirvonen and Palva, 2016**; **Jones et al., 2007**; **Moore et al., 2013**). This diversity of findings parallels results from the visual and auditory modalities (e.g. **Carmel et al., 2006**; **Eriksson et al., 2007**; **Rees et al., 2002**) and underlies the idea that perceptual awareness emerges when local information is propagated from sensory cortices to higher order brain regions to elicit a reverberating network of broadcast activity (**Baars, 1997**; **Dehaene et al., 2006**).

While a complex network activation may seem a suitable candidate to explain a complex phenomenon such as perceptual awareness, the functional specificity of the identified regions remains largely unknown. One problem that complicates the interpretation is that classical target detection tasks not only probe perceptual awareness but involve a range of correlated cognitive processes that may confound classical contrastive analyses (**Aru et al., 2012**; **de Graaf et al., 2012**). In the context of the somatosensory near-threshold detection task, four aspects are particularly problematic: 1. perception of near-threshold stimuli is difficult, and resolution of associated uncertainty and introspective processes may differ between detected and undetected targets (***de Lafuente and Romo, 2011***). 2. Target detection is the explicit behavioural goal of the task and therefore, detected targets have higher behavioural relevance than undetected targets (***Farooqui and Manly, 2018***). 3. Target detection is directly mapped to overt reports that allow for assessment of participants' trial-by-trial perception (***Tsuchiya et al., 2015***). 4. Overt reports are often communicated with button presses by one hand while stimulation occurs on the other hand, which may affect cortical excitability in homologue regions of the sensorimotor homunculus (***Zagha et al., 2013***). All these variables potentially contribute to the commonly observed network activation and dedicated experimental paradigms are warranted to scrutinise its functional specificity for target detection and accordingly, somatosensory awareness.

Here, we used functional magnetic resonance imaging (fMRI) on a novel somatosensory detection task that explicitly varies stimulus uncertainty and controls for behavioural relevance, overt reports, and motor responses. To distinguish BOLD responses reflecting target detection from those indicating concomitant processes, we fit simple behavioural models to our fMRI data, capturing trial-wise physical stimulus intensity, target detection, detection probability, expected uncertainty, and overt reports, respectively. We dissociate corresponding representations in the brain by means of Bayesian Model Selection (BMS, Stephan, Penny, Daunizeau, Moran, & Friston, 2009), which determines which model best explains the data in every voxel of the brain based on model evidence maps. Building on insights from the visual modality (***Farooqui and Manly, 2018***; ***Frässle et al., 2014***; ***Koch et al., 2016***), we hypothesise that BOLD responses associated with target detection are restricted to somatosensory regions, whereas activity in the frontoparietal network reflects cognitive processes that follow from task requirements.

Results

Experimental paradigm

Participants performed a two-alternative forced choice somatosensory detection task on electrical pulses administered to their left median nerves inside the fMRI scanner (see ***Figure 1*** and Materials and methods for a detailed description of the task design). To vary stimulus uncertainty, we presented stimuli at ten different intensity levels that were individually adjusted to sample the full dynamic range of each participant's psychometric function from 0 to 100% detectability. Accordingly, stimuli presented near individual 50% detection thresholds were expected to be associated with higher uncertainty (as defined by larger trial-by-trial variability in target detection) than clearly sub- or supraliminal stimuli. To balance behavioural relevance and overt reports across detected and undetected targets, instead of directly reporting target detection, participants were required to match their perception of somatosensory target stimuli against simultaneously presented visual cues that signalled stimulus presence or absence. As a result, detected and undetected targets could result in the same overt report (match or mismatch), making them equally relevant for the task. Finally, to avoid motor response-related activation of cortical hand representations, instead of giving manual responses, participants responded with saccades to peripheral response cues. We analysed 3T fMRI data of n = 27 participants who performed 4 runs of 100 experimental trials each.

Behaviour

Participants detected 52.25 ± 11.65% (mean ± standard deviation) of targets. Note that targets were presented on every trial and only the stimulus intensity was individually manipulated to render targets sub- or supraliminal. Therefore, the detection rate was identical to the hit rate and false alarms or correct rejections could not occur. As expected, participants' target detection varied with stimulus intensity, resulting in characteristic sigmoidal psychometric functions (***Figure 2***). A Bayesian equivalence of the paired-sample t-test suggests strong evidence for shorter reaction times for detected than undetected targets (detected: 352.11 ± 50.98 ms, undetected: 363.88 ± 55.97 ms, difference: 11.77 ± 14.84 ms, BF10 = 88.01). To test if the task manipulation successfully dissociated target detection from overt reports, we computed Bayesian tests of association for all participants and found that none of the participants showed positive evidence for an association between the two

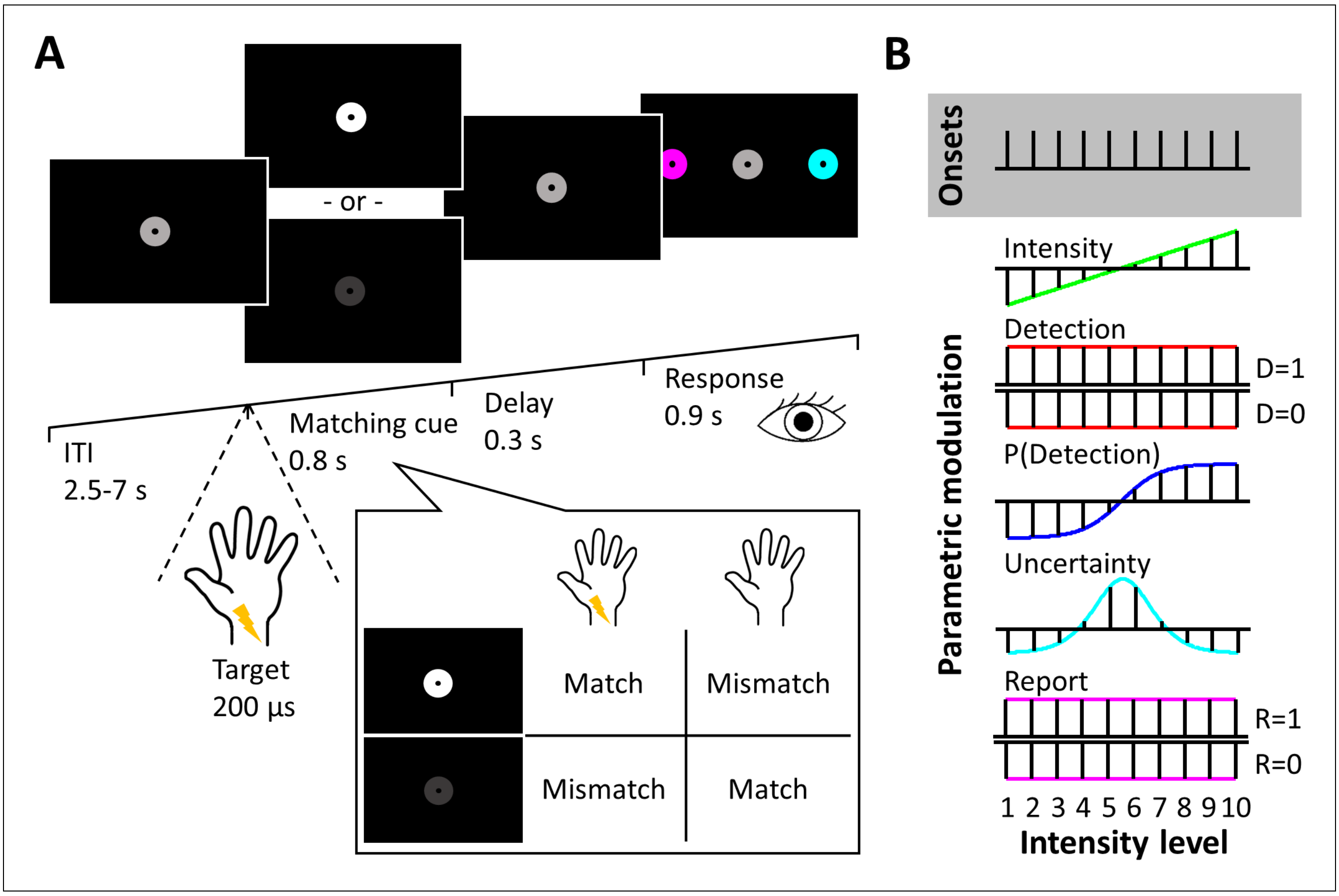

Figure 1. Experimental design. (**A**) Trial design. After a variable intertrial interval of 2.5–7 s, electrical target stimuli and visual matching cues were presented simultaneously. A white matching cue signalled stimulus presence, a dark grey matching cue signalled stimulus absence. After a short delay, participants reported a match or mismatch between the cue and their somatosensory percept by selecting one of two colour-coded disks with a saccadic eye movement. Example: If participants detected the target and saw a white matching cue, they would report a match. Likewise, if they did not detect the target and saw a dark grey matching cue, they would also report a match, resulting in the same behavioural relevance of detected and undetected targets and orthogonalisation of target detection and overt reports. (**B**) Graphical depiction of experimental regressors plotted against stimulus intensity levels. Five stimulus and behavioural dimensions of our task were specified as parametric regressors on trial onsets: physical stimulus intensity, target detection, detection probability, expected uncertainty, and overt reports.

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variables (all BF10 <.5). In contrast, we found positive evidence for independence for all participants (BF01 >4) except one (BF01 = 2.62).

fMRI

From our paradigm, we extracted five experimental regressors to identify brain regions that process the various stimulus and behavioural dimensions of the task: linear stimulus intensity, binary target detection, detection probability, expected uncertainty, and overt reports (***Figure 1B***). The shared variance in some of these regressors (intensity, detection, detection probability) would result in multicollinearity issues and unstable beta estimates in classical regression analyses. To overcome this problem, we separated the regressors into different models and performed Bayesian model comparison to determine which regressor best explained the data over and above shared variance. To this end, the experimental regressors were incorporated in five different general linear models (GLMs) as parametric regressors on trial onsets, each of which constituted a specific hypothesis of expected BOLD responses. We then estimated the models using the first-level Bayesian GLM estimation as implemented in SPM12 (***Penny et al., 2007***). The resulting model evidence maps were subjected to random effects BMS to obtain one exceedance probability (EP) map per model, indicating the voxel-wise probability that a particular model explained the data better than any of the other models (**Rosa et al., 2010**; **Stephan et al., 2009**). To extract only those voxels where one model clearly outperformed all other models, we thresholded these maps at EP $\geq$ .99 and further inspected only those voxels that exceeded this threshold. When models are expected to share a lot of probability mass due to correlated regressors, they may be too similar in the variance they explain to outperform each other sufficiently to exceed a desired EP threshold. To avoid such model dilution (**Hoeting et al., 1999**), in a first step, we combined the intensity, detection, and detection probability models into a model family (+family) and performed BMS on the family level (**Penny et al., 2010**) to define regions of interest (ROIs), in which the +family yielded EP $\geq$ .99. The +family models were then assessed individually within these ROIs. The uncertainty and report models on the other hand were not expected to share variance with any of the other models and were therefore assessed in a whole-brain analysis.

The +family defined ROIs in contralateral right SI extending into right superior parietal lobule (SPL), bilateral SII extending into posterior insular cortices, as well as left superior frontal gyrus (SFG), left inferior parietal lobule (IPL), and left visual area V3 (**Figure 3A**). Within these regions, the intensity model was the best model in the anterior part of the right SI cluster (peak voxel [38, −40, 66], peak EP = .96), primarily spanning areas 3b, 1, and 2. Further intensity representations were found in regions of bilateral SII, in particular the most anterior and posterior edges of the right SII cluster (anterior: peak voxel [54, −6, 4], peak EP = .90; posterior: peak voxel [62, −34, 22], peak EP = .98) and the medial part of left SII (peak voxel [−46, –34, 22], peak EP = .90). The detection probability model best explained data in the posterior part of right SI (primarily area 2) extending into SPL (peak voxel [34, −50, 62], peak EP = .99), as well as large regions of bilateral SII (right: peak voxel [56, −16, 20], peak EP = .99; left: peak voxel [−60, –36, 20], peak EP = .98). Finally, the binary detection model was the best model in superior and inferior parts of the right SII cluster (superior: peak voxel [62, −20, 30], peak EP = .95; inferior: peak voxel [52, −22, 8], peak EP = .96) and in mostly lateral regions of left SII (peak voxel [−62, –36, 26], peak EP = .93). Further detection-sensitive regions were found in left SFG (peak voxel [−26, 56, 22], peak EP = 1), left IPL (peak voxel [−50, –58, 46], peak EP = 1), and left V3 (peak voxel [−12, –80, −16], peak EP = 1). Within SI, the spatial distribution of voxels explained by the intensity and detection probability models, respectively was found to follow the known cytoarchitectonic subdivisions of the anterior parietal cortex (**Figure 3—figure supplement 1**). In SII on the other hand, voxels with sensitivity to intensity, detection probability, and detection did not show an apparent organisation along the cytoarchitectonic subdivisions of the parietal operculum.

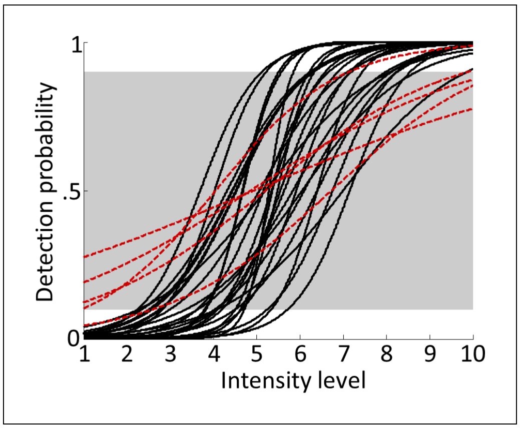

Figure 2. Psychometric functions. Logistic functions were fitted to each participant's behavioural data during the main experiment and averaged across runs to obtain continuous models of individual psychometric functions. Note that although the shape of the psychometric function can vary considerably across participants, due to the individually adjusted stimulus intensities, the resulting curves were normalised to span 0–100% detection probability from intensity levels 1 to 10. Red dashed lines show fitted psychometric functions of five participants that failed to reach ≤10% detection probability for intensity level 1 or ≥90% detection probability for intensity level 10 (outside the grey-shaded area) and were therefore excluded from all further analyses.

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The following source data is available for figure 2:

Source data 1. Target detection rates for all intensity levels.

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Having established regions that were well explained by the +family models, we further examined the underlying model parameters. To this end, we extracted beta estimates of the respective experimental regressors from individual BMS peaks and computed Bayes factors quantifying the evidence that these estimates systematically deviated from zero on the group level. Since the model selection procedure does not account for directionality of the underlying effects (i.e. both positive and negative parameter estimates may contribute to the model evidence), we imposed this second constraint

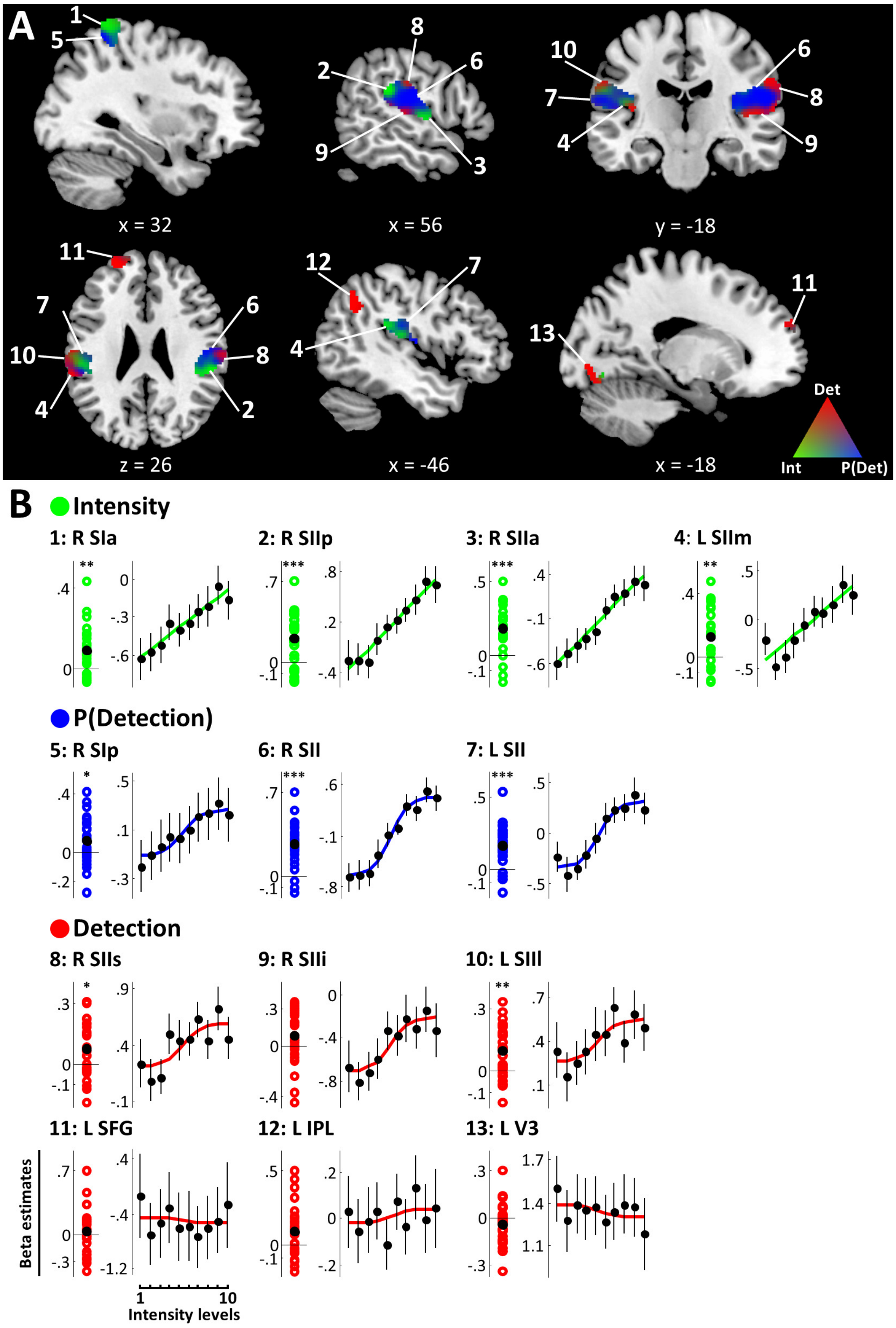

Figure 3. +family models. (**A**) BMS results (ROI analysis). EPs of the +family models are displayed within +family ROIs. RGB values indicate model EPs: The corners of the RGB triangle correspond to EP = 1 signifying a clear winner of the BMS, whereas intermixed colours indicate similar EPs for respective models. Intensity (green), P(Detection) (blue), Detection (red). k ≥ 50 voxels. (**B**) Beta estimates and stimulus response profiles. Left panels: Beta estimates of the winning models' experimental regressors were extracted from individual BMS peak voxels.

Figure 3 continued on next page

Figure 3 continued

Each coloured circle corresponds to one participant's beta estimate. Black circles mark group means. Asterisks indicate evidence for a deviation from zero: *BF >3, **BF >20, ***BF >150. Right panels: beta estimates for different intensity levels were extracted from regions of interest and plotted to provide SRPs. For visualisation, fitted representations of the winning models are plotted along with the beta estimates. Error bars represent the standard error of the mean. Somatosensory regions show representations of stimulus intensity, detection probability, and binary target detection, which are reflected in their SRPs. Detection-sensitive regions in prefrontal, posterior parietal, and visual areas do not show systematic relationships with stimulus intensity.

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The following source data and figure supplement are available for figure 3:

Source data 1. Beta estimates for clusters defined by the +family models.

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Figure supplement 1. Distribution of models in cytoarchitectonic subregions of SI and SII.

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on the identified regions to detect systematic variation across participants and thus, systematic association of the behavioural regressors with the observed BOLD activity. To visualise these associations, we extracted stimulus response profiles (SRPs). SRPs show the fitted activity of a region as a function of stimulus intensity and can provide a visual representation of the model fit. Regions that are well explained by models featuring a systematic relationship with stimulus intensity (intensity, detection, detection probability, uncertainty) were expected to show a response profile visibly reflecting this relationship. Regions that are explained by models with no such relationship on the other hand (report) were expected to show no systematic differences in BOLD responses across stimulus intensities.

All regions explained by the intensity model showed strong (R SIa: BF10 = 33.94; L SIIm: BF10 = 81.58) or very strong (R SIIp: BF10 = 385.13; R SIIa: BF10 = 6114.09) evidence for a positive regression weight of the intensity regressor indicating a positive relationship of stimulus intensity and BOLD responses in these regions (***Figure 3B***, ***Table 1***). This result is reflected in the SRPs of intensity-sensitive regions, which show a linear response increase with increasing stimulus intensity (***Figure 3C***). Likewise, positive regression weights for the detection probability regressor in SI and SII were confirmed with positive (R SIp: BF10 = 3.04) and very strong evidence (R SII: BF = 232795.89, L SII: BF = 7961.84) and, correspondingly, these regions show sigmoidal SRPs. For the binary detection regressor, positive regression weights were exclusively found in bilateral SII (R SIIs: BF = 8.63; L SIIl: BF = 96.7). Parameter estimates in all other regions explained by the detection model failed to yield positive evidence for a systematic deviation from zero (R SIIi: BF = 1.36; L SFG: BF = .31; L IPL: BF = 2.84; L V3: BF = .65), indicating that in these regions the response to target detection was not systematic across participants. Accordingly, the sigmoidal shape of the SRP that would be expected from an area showing a categorical response to target detection (recall that target detection averaged over trials and plotted against stimulus intensity amounts to the psychometric function) is less pronounced in these regions.

The uncertainty model yielded EP $\geq$.99 in bilateral superior medial gyrus (SMG) extending into ACC (peak voxel [2, 30, 40], peak EP = 1) and bilateral AIC (right: peak voxel [36, 22, -6], peak EP = 1; left: peak voxel [−34, 18, –8], peak EP = 1) (***Figure 4A***, ***Table 1***). Very strong evidence confirms positive beta estimates in all these regions (SMG/ACC: BF10 = 366797.07; R AIC: BF10 = 453.09; L AIC: BF10 = 479302.70), and the respective SRPs show a clear inverse U-shaped function, suggesting that these areas exhibit the strongest activity for targets close to detection thresholds, when expected uncertainty is highest (***Figure 4B***).

Finally, the report model fit best in left supplementary motor area (SMA) (peak voxel [−2, 8, 64], peak EP = 1), right supramarginal gyrus (SMarG) (peak voxel [60, -34, 44], peak EP = 1), and left thalamus (peak voxel [−6, –16, 10], peak EP = 1) (***Figure 5A***, ***Table 1***). Of these, SMA was found to be the only region showing beta estimates that reliably deviated from zero (SMA: BF10 = 65.14). Beta estimates extracted from left thalamus and right SMarG did not yield positive evidence for an effect (L Thal: BF10 = .22; R SMarG: BF10 = .23) and these regions' sensitivity to overt reports is therefore considered unsystematic. As expected from the lack of association between overt reports and target

Table 1. Brain regions showing EP $\geq$ .99 for any of the tested models.

For the +family models the .99 EP threshold was applied on the family level and individual peak EPs are reported for every model. k $\geq$50 voxels. Betas of experimental regressors extracted from individual BMS peaks are reported as mean ± SEM. ACC: anterior cingulate cortex, AIC: anterior insular cortex, IPL: inferior parietal lobule, SI: primary somatosensory cortex, SII: secondary somatosensory cortex, SFG: superior frontal gyrus, SMA: supplementary motor area, SMarG: supramarginal gyrus, SMG: superior medial gyrus. a: anterior, p: posterior, i: inferior, s: superior, m: medial, l: lateral.

Cluster size	Region	Peak MNI (x,y,z)			Peak EP	Beta	BF10
Intensity							
247	R SIa (BA 3b, 1, 2)	38	−40	66	.96	.09 ± .02	33.94
276	R SIIp	62	−34	22	.98	.18 ± .03	385.13
213	R SIIa	54	−6	4	.90	.20 ± .04	6114.09
212	L SIIm	−46	−34	22	.90	.13 ± .03	81.58
Detection probability							
71	R SIp (BA 2)	34	−50	62	.99	.08 ± .03	3.04
932	R SII	56	−16	20	.99	.27 ± .04	232795.89
602	L SII	−60	−36	20	.98	.17 ± .03	7961.84
Detection							
189	R SIIi	52	−22	8	.96	.09 ± .04	1.36
76	R SIIs	62	−20	30	.95	.08 ± .03	8.63
128	L SIIl	−62	−36	26	.93	.10 ± .02	96.70
116	L SFG	−26	56	22	1	.04 ± .05	.31
66	L IPL	−50	−58	46	1	.09 ± .03	2.84
72	L V3	−12	−80	−16	1	−.04 ± .02	.65
Uncertainty							
664	SMG/ACC	2	30	40	1	.33 ± .04	366797.07
127	R AIC	36	22	−6	1	.22 ± .03	453.09
70	L AIC	−34	18	−8	1	.22 ± .05	479302.70
Report							
132	L SMA	−2	8	64	1	−.12 ± .03	65.14
71	L Thalamus	−6	−16	10	1	−.01 ± .02	.22
51	R SMarG	60	−34	44	1	.02 ± .04	.23

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detection, SRPs in these areas did not reflect a systematic relationship with stimulus intensity (***Figure 5B***).

Discussion

To scrutinise the neural processes underlying somatosensory target detection in humans, we employed an experimental paradigm that explicitly dissociates target detection from stimulus uncertainty, behavioural relevance, overt reports, and motor responses. Using Bayesian Model Selection on the acquired fMRI data, we observe a transformation from physical to perceptual representations as the target is propagated through the somatosensory hierarchy. This transformation primarily occurred in SI and SII, whereas expected uncertainty was represented in insular and cingulate regions and overt reports were processed in supplementary motor cortex. Our analysis reveals large overlap with the previously identified target detection network but assigns functional specificity to the involved regions.

SI is the first cortical region to receive somatosensory input from the contralateral body side. It is subdivided into four somatotopic maps, areas 3a/b, 1, and 2, that are organised along an anterior-

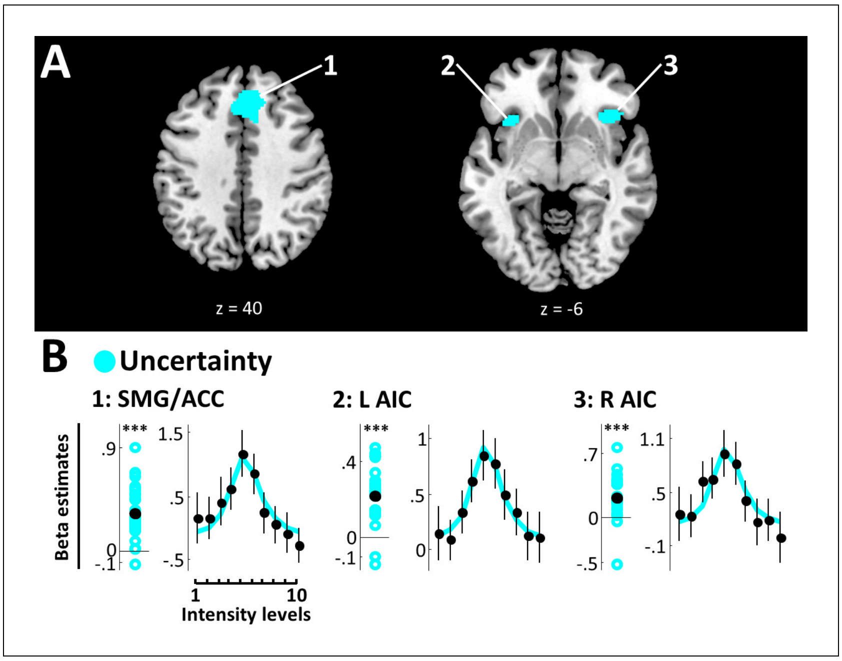

Figure 4. Uncertainty model. (**A**) BMS results (whole-brain analysis). Voxels with EP ≥.99 for the uncertainty model are displayed. Expected uncertainty best modelled data in bilateral SMG/ACC and bilateral AIC. k ≥50 voxels. (**B**) Beta estimates and stimulus response profiles. Beta estimates of the winning models' experimental regressors (left panels) and SRPs (right panels) are displayed as in ***Figure 3***. *BF >3, **BF >20, ***BF >150. SMG/ACC and AIC show positive beta estimates and clear inverse U-shaped SRPs, confirming a representation of stimulus uncertainty.

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The following source data is available for figure 4:

Source data 1. Beta estimates for clusters defined by the uncertainty model.

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posterior axis on the postcentral gyrus and increase in their hierarchical level (***Delhaye et al., 2018***; ***Felleman and Van Essen, 1991***). Our analysis suggests that during somatosensory target detection, contralateral areas 3b, 1, and anterior parts of area 2process the physical stimulus intensity, whereas more posterior parts of area 2, extending into adjacent SPL, represent the probability to detect a target. Previous research has been ambiguous regarding the role of SI for target detection. Some studies found no difference in SI responses for detected and undetected targets (***de Lafuente and Romo, 2005***; ***Schubert et al., 2006***; ***Wühle et al., 2010***; ***Wühle et al., 2011***) and are in line with a representation of physical stimulus properties. Others have reported stronger SI evoked magneto-/electroencephalography responses for detected compared to missed stimuli (***Hirvonen and Palva, 2016***; ***Jones et al., 2007***; ***Palva et al., 2005***). Interestingly, most studies reporting early detection-related effects in SI used the classical near-threshold detection task, whereas those that did not find effects in SI typically used alternative approaches (varying stimulus intensities: ***de Lafuente and Romo, 2005***; ***de Lafuente and Romo, 2006***; backward masking: ***Schubert et al., 2006***; paired-pulse paradigms: ***Wühle et al., 2010***, ***Wühle et al., 2011***). As target detection at perceptual threshold changes with fluctuations in cortical excitability (***Boly et al., 2007***; ***Frey et al., 2016***; ***Moore et al., 2013***; ***Schubert et al., 2009***; ***Weisz et al., 2014***), this dissociation raises the question, whether differentiable SI responses for detected and undetected near-threshold stimuli are in fact markers of stimulus awareness or rather the result of background processes that may facilitate or attenuate target detection depending on pre-stimulus brain states (***Schubert et al., 2006***). In our data, we do observe a transformation of stimulus representations in SI as the stimulus is propagated up the local hierarchy. However, although the detection probability model captures some perceptual properties of the stimulus and may constitute a first step towards perceptual readout, it does not explicitly differentiate between detected and undetected trials and importantly, predicts the same

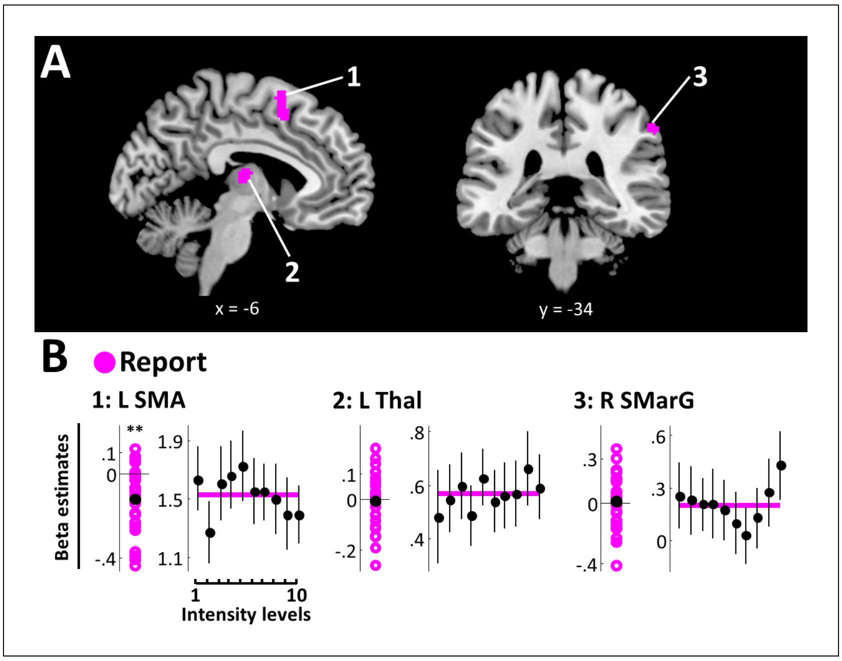

Figure 5. Report model. (**A**) BMS results (whole-brain analysis). Voxels with EP ≥.99 for the report model are displayed. Overt reports best modelled data in left SMA, left thalamus, and right SMarG. k ≥50 voxels. (**B**) Beta estimates and stimulus response profiles. Beta estimates of the winning models' experimental regressors (left panels) and SRPs (right panels) are displayed as in ***Figure 3***. *BF >3, **BF >20, ***BF >150. L SMA is the only report region that shows beta estimates that systematically deviate from zero. None of the identified report regions show systematic relationships with stimulus intensity, as expected from the lack of association between overt reports and target detection.

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The following source data is available for figure 5:

Source data 1. Beta estimates for clusters defined by the report model.

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level of activation for threshold stimuli, regardless of whether they were perceived or not. Therefore, our results do not support detection-sensitivity in SI.

Responses in bilateral SII mirror the transformation from stimulus intensity to detection probability in SI and importantly, they also show an effect of binary target detection in adjacent regions. The distribution of these effects did not align with the cytoarchitectonic subdivisions of the parietal operculum, whose distinct functional roles remain largely elusive. The less pronounced somatotopy and large interindividual variability in SII (***Eickhoff et al., 2006a***; ***Sanchez Panchuelo et al., 2018***) may have concealed the exact organisation of the observed effects and further studies are needed to ascertain the specific functional topology. Nonetheless, the relevance of region SII for somatosensory target detection is well documented in the literature. It exhibits stronger somatosensory evoked potentials (***Auksztulewicz et al., 2012***; ***Wühle et al., 2010***; ***Wühle et al., 2011***), increased spike rates (***de Lafuente and Romo, 2006***), stronger BOLD-signal changes (***Moore et al., 2013***), and increased network integration (***Weisz et al., 2014***) when stimuli are detected compared to when they are missed. Our findings are in line with intracortical recordings in monkeys (***de Lafuente and Romo, 2006***) showing that SII neurons are the first to be predictive of perceptual decisions. Previous studies have further shown that SII integrates information from different body parts (***Goldin et al., 2018***), indexes unexpected somatosensory stimuli (***Chen et al., 2008***) and stimulus omissions (***Andersen and Lundqvist, 2019***), and can adapt to task requirements (***Romo et al., 2002***). In combination with the observed shift from physical to perceptual representations in our study, evidence suggests that SII might be a central relay point at which behaviourally relevant stimuli are transformed into perceptual outcomes.

Expected uncertainty, here defined as susceptibility to perceptual fluctuations, best explained the data in SMG/ACC and AIC. These regions are commonly referred to as the salience network, which is involved in conflict monitoring, reorienting of attention, and introspective processes (**Menon and Uddin, 2010**) and, interestingly, was found to be sensitive to perceptual ambiguity (**Lamichhane et al., 2016**). Importantly, both ACC and insular cortex have previously been implied in somatosensory target detection (**Bastuji et al., 2016**; **Boly et al., 2007**; **Büchel et al., 2002**; **Hirvonen and Palva, 2016**; **Moore et al., 2013**). The insula in particular has been assigned a pivotal role in interoceptive inference (**Seth, 2013**) and awareness (**Craig, 2009**; **Critchley et al., 2004**), although recent research suggests that activity in AIC might reflect interoceptive sensitivity and learning rather than subjective experience per se (**Canales-Johnson et al., 2015**). In light of our results and given the fact that interoceptive signals, such as the heartbeat, are often faint signals, future research may benefit from combining measures of perceptual uncertainty (e.g. **Garfinkel et al., 2015**) with neuroimaging techniques to reconcile interoceptive processing with insular response properties. With regard to its role in somatosensory perception, the AIC has further been demonstrated to show strengthened backward connectivity with somatosensory cortex upon mismatch detection (**Allen et al., 2016**). Considering that in our study AIC particularly activated for hard-to-detect stimuli, these findings suggest that – although it does not generally reflect target detection – AIC may exert top-down modulation on somatosensory cortex to facilitate somatosensory processing.

The primary objective of the target detection task is to uncover neural processes underlying the emergence of perceptual awareness. Our results identify responses in somatosensory cortex as the best correlates of perceptual awareness and are in line with previous research emphasising the role of dedicated sensory regions for both visual (**Boehler et al., 2008**; **Hurme et al., 2017**; **Pascual-Leone and Walsh, 2001**; **Ress et al., 2000**) and somatosensory awareness (**Auksztulewicz et al., 2012**; **Jones et al., 2007**). However, this view is not unopposed and especially the role of prefrontal cortex (PFC) remains a topic of intense debate. While opponents argue that activity in PFC is an artefact of report requirements and behavioural relevance (**Boly et al., 2017**; **Brascamp et al., 2015**; **Farooqui and Manly, 2018**; **Frässle et al., 2014**; **Koch et al., 2016**; **Pitts et al., 2014**; **Tsuchiya et al., 2015**), proponents uphold that PFC has been demonstrated to code perceptual content even in passive paradigms (**Panagiotaropoulos et al., 2012**) and that null-findings in PFC may be the result of insufficient sensitivity in the methods (**Odegaard et al., 2017**). Ours is the first study to explicitly dissociate stimulus awareness from overt reports and behavioural relevance in the somatosensory domain and while we can only draw conclusions to the extent of the stimuli and methods used in this study, our findings do not support reliable representations of somatosensory awareness in PFC.

Importantly, we did not find strictly detection-related responses in posterior parietal cortex either, a result that conflicts with the 'posterior hot zone' theory of conscious perception (**Koch et al., 2016**) but is in line with an earlier finding suggesting that posterior parietal activation is related to goal completion but not stimulus awareness (**Farooqui and Manly, 2018**). Given that we controlled for goal completion effects in our study by equating behavioural relevance across detected and undetected targets, we may conclude that the correlates of target detection are largely restricted to dedicated sensory processing sites when controlled for common task requirements.

The aim of the current study was to experimentally dissociate target detection from four potentially confounding processes and hence, preclude these processes as root causes of detection-related neural activity. 1. Stimulus uncertainty: By varying stimulus intensities across trials, we implicitly tested for specific response profiles that occur in regions reflecting target detection. Specifically, these regions were expected to show low activity for low, subthreshold stimulus intensities and high activity for high, suprathreshold stimulus intensities. Since uncertainty, no matter if subjective or objective uncertainty measures are used, decreases for high-intensity stimuli, we can exclude uncertainty related processes as the driving force of activity in regions showing such a response profile. 2. Behavioural relevance: In order to perform the task, participants had to report a match or mismatch between their target perception and a visual matching cue. Since detected and undetected targets were found to occur equally often for match and mismatch reports, the two perceptual outcomes were equally relevant for the task and thus, differences in behavioural relevance are unlikely to have caused the observed detection-related activity. 3. Overt reports: As mentioned in point 2, overt reports were independent of target detection and are therefore unlikely to have caused detection-related effects. However, participants might still form a covert but explicit decision regarding the presence or absence of the target prior to making the match/mismatch decision, which could potentially confound the observed detection effects. Two reasons speak against this interpretation: First, the task imposed a time constraint that required participants to form their decisions fast. Therefore, the task could best be solved by directly comparing the two input modalities without engaging intermediate steps, a strategy, that was verbally confirmed by a majority of participants after the experiment. Second, the only areas that showed reliable and systematic covariation with target detection were regions in bilateral SII. An explicit internal decision regarding the absence or presence of a target stimulus would be expected to involve supramodal processes (because the same decision can be made on stimuli from different modalities) and therefore recruit higher order association cortices. Since this was not the case, we consider it unlikely that the detection effects observed in SII were induced by explicit perceptual decisions. Nonetheless, rapid low-level perceptual decision processes cannot be completely excluded and alternative approaches, such as no-report paradigms (***Tsuchiya et al., 2015***), may aid in disentangling their impact. 4. Motor responses: Participants gave their reports by making saccades to peripheral response cues. None of the observed detection effects overlap with regions commonly observed during saccadic eye movements (***Ettinger et al., 2008***; ***Kimmig et al., 2001***) and effects in SI were localised to hand areas and far removed from eye representations in the somatosensory homunculus. Changes in cortical excitability due to motor responses are therefore unlikely to have affected the results. In conclusion, we consider the detection-related responses observed in bilateral SII to be largely free of the addressed experimental confounds.

A theoretical framework that accommodates awareness-related responses in sensory cortices is the recurrent processing hypothesis of conscious perception, which argues that perceptual awareness emerges when feedforward signals from early sensory cortex are consolidated by re-entrant feedback (***Lamme, 2006***). Such a mechanism might account for the early transformation from stimulus intensity to detection probability that we observed in SI and in fact, previous research on somatosensory target detection suggests that stimulus awareness is best captured in recurrent interactions between SI and SII (***Auksztulewicz et al., 2012***; ***Cauller and Kulics, 1991***; ***Kwon et al., 2016***; ***Yang et al., 2016***). However, these earlier studies have used simpler versions of the detection task and studies employing methods with high temporal resolution in combination with rigorous experimental control are warranted to scrutinise the functional specificity of recurrent processing for somatosensory awareness.

Another open question concerns the relationship between target detection and subjective experience. Clearly, subjective experience of a detected target at near-threshold intensities is not identical to that of a stimulus at much higher intensities and thus, it is not well modelled by the detection model. Likewise, subjective experience can vary for stimuli at identical physical stimulus intensities and thus, it is not well modelled by the intensity or detection probability models. To address the subjective dimensions of our task, we would require trial-by-trial awareness ratings (and likewise, confidence ratings to evaluate metacognitive aspects of uncertainty). In the current investigation, we did not acquire such ratings because, although they would endow us with a better model of subjective experience, they would also reintroduce the requirement for explicit reports on the stimuli and result in higher relevance of detected compared to undetected targets. However, building on the results of the current study and the opportunities offered by the Bayesian analysis approach, incorporating such subjective reports and probing underlying neural responses may be a promising avenue for future research. In fact, it has been shown that subjective somatosensory awareness is parametrically encoded in connectivity patterns between somatosensory and higher order regions (***Auksztulewicz and Blankenburg, 2013***). This line of research could potentially consolidate experimental findings arguing for local versus global perspectives.

In summary, our findings dissect the functional contribution of different regions in the target detection network and advocate more complex experimental paradigms to dissociate neural responses reflecting conscious access from those supporting collateral functions. Note, however, that this is not to say that frontal and posterior parietal areas do not contribute to the full phenomenal experience of the task. We should keep in mind that although the somatosensory detection task allows for an operationalisation of basic stimulus awareness, detection of simple electrical targets is a simplistic reduction of what constitutes the richness of our everyday conscious perception.

Certainly, cognitive processes such as attention and introspection considerably influence our experience and may even alter perceptual contents and likewise, detection of more complex stimuli, such as tactile motion or objects may require additional cognitive resources further downstream the somatosensory hierarchy. Having said that, when it comes to the perceptual integration of somatosensory stimuli as simple as electrical pulses to the wrist, our data suggest that activity in secondary somatosensory cortex is the best correlate of perceptual success.

Materials and methods

Participants

Thirty-two healthy, right-handed volunteers with normal or corrected-to-normal vision completed the experiment. Data of five participants were excluded from the sample because they did not show stable psychometric functions (for more details see Behavioural data analysis and ***Figure 2***), leaving data of 27 participants that entered the analyses (18 females, nine males, age range: 19–38). All participants gave written informed consent prior to the experiment and received a monetary reimbursement for their participation. The study was approved by the local ethics committee at the Freie Universität Berlin and complied with the Human Subjects Guidelines of the Declaration of Helsinki.

Procedure

All participants completed a 30-min training to familiarise with the electrical stimulation and ensure full understanding of the task. In the beginning of the fMRI scanning session, individual psychometric functions were determined to obtain appropriate stimulus intensities for the main task (see Stimulus intensities). Following this ~9 min procedure, all participants completed four runs of the target detection task, each lasting 12.6 min. On each run, 100 experimental trials were presented in random order, interspersed with 10 null events, in which participants fixated throughout the trial without visual or electrical stimulation. The number of trials presented at each intensity level followed a normal distribution to maximise the number of trials with intensities close to detection threshold. This procedure resulted in a total of 400 experimental trials per participant with 64 trials each for the threshold intensity levels 5 and 6, and 16 trials each for the lowest and highest intensity levels 1 and 10.

Trial design

Each trial was preceded by a variable fixation period of 2–7.5 s, during which participants fixated on a central fixation point, surrounded by a grey disk (***Figure 1A***). The trial started with the presentation of an electrical pulse at one of ten predetermined stimulus intensity levels, which was either detected or missed by the participant. Simultaneously, the grey fixation disk changed its luminance to either white or dark grey, serving as the visual matching cue. A white disk signalled stimulus presence, a dark disk stimulus absence. The two luminance levels of the matching cues as well as the intermediate luminance level presented during fixation were clearly discernible and lasted for 0.8 s. Participants compared their somatosensory percepts (target detected or missed) to the visual matching cues (signalling stimulus presence or absence) and decided on a match or mismatch between the two modalities (***Figure 1A***, inset). After a delay of 0.3 s, participants reported their decision by making a saccade to one of two peripherally presented, colour-coded disks, representing a match or mismatch, respectively. If participants failed to give their responses within 0.9 s, the fixation disk briefly turned red signalling a missed trial.

Importantly, the matching cues were counterbalanced over intensity levels and randomised across trials, resulting in about 50% match and 50% mismatch reports for each intensity level. As a result, any associations of overt reports with stimulus intensity or stimulus detection were eliminated. Likewise, the specific sides on which the colour-coded response cues were presented alternated over trials and were counterbalanced over intensity levels and matching cues to preclude systematic lateralisation of the motor responses. The specific colour code (i.e. the mapping between pink/cyan colours and match/mismatch reports) was counterbalanced across participants.

Stimulus intensities

Stimulus intensities for the target detection task were drawn from individual psychometric functions that were determined prior to the main experiment. While lying in the MRI scanner, participants were presented with 15 stimulus intensities differing by increments of 0.1 mA and centred on initial estimates of individual 50% detection thresholds (obtained by testing several intensities manually). Each intensity level was repeated 20 times resulting in a total of 300 pulses that were presented in random order. On each trial, participants indicated if they had felt the stimulus or not by pressing one of two buttons. A logistic function with two parameters (50% detection threshold and slope at detection threshold) was fitted to the data yielding a continuous model of the individual psychometric function (***Wichmann and Hill, 2001***). This model was used to obtain estimates of the stimulus intensities resulting in 1% detection probability (T01), 50% detection probability (the individual detection threshold, T50), and 99% detection probability (T99). The 10 stimulus intensities used in the main experiment were spaced equidistantly around T01 (set as intensity level 2) and T99 (set as intensity level 9). This procedure accommodates individual variation in the shape of psychometric functions and was used to ensure a complete sampling of each participant's dynamic range even in case of small drifts in detection thresholds. On average, the procedure yielded initial thresholds of T01 = 1.84 ± .53 mA, T50 = 2.40 ± .69 mA, and T99 = 2.96 ± .92 mA (mean ± standard deviation).

Stimuli and materials

Electrical stimuli were generated as analogue voltage signals using a waveform generator (DT-9812, Data Translation, Bietigheim-Bissingen, Germany) controlled with Matlab (The MathWorks, Inc, Natick, MA, RRID:SCR_001622). A bipolar constant current stimulator (DS5, Digitimer, Hertfordshire, UK) converted the voltage signal into direct current monophasic square wave pulses of 200 µs duration and administered the stimuli to the left median nerve via MR-compatible adhesive electrodes (GVB-geliMED GmbH, Bad Segeberg, Germany). Responses were recorded using an MR-compatible eye tracker (EyeLink 1000, SR Research Ltd, Mississauga, Ontario, Canada, RRID:SCR_009602). Gaze direction was evaluated online and a response was registered as soon as the gaze remained within the response area for 200 ms. Stimulation and response collection were implemented in Matlab using the Psychophysics (***Brainard, 1997***, RRID:SCR_002881) and EyeLink (***Cornelissen et al., 2002***) toolboxes.

fMRI scanning procedure

All participants were scanned at the Center for Cognitive Neuroscience Berlin using a 3T Siemens Tim Trio MRI scanner equipped with a 32-channel head coil. T2*-weighted images were acquired using an echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, voxel size = 3×3×3 mm3, matrix = 64×64, 37 slices, 20% gap, flip angle = 70°). 378 volumes were obtained on each experimental run. T1-weighted structural images were acquired for coregistration using a 3D MPRAGE sequence (TR = 1900 ms, TE = 2.52 ms, voxel size = 1×1×1 mm3, FOV = 256×256 mm2, 176 slices, flip angle = 9°). Including preparation time, estimation of the psychometric function, four experimental runs, and the structural scan, scanning time summed up to approximately 1.5 hr.

Data analysis

Behavioural

Behavioural data analysis was performed with Matlab. Models of individual psychometric functions were obtained by fitting logistic functions to the behavioural data of all runs. An average psychometric function was determined for each participant by taking the mean of the fitted detection thresholds and slopes for individual runs. From these average psychometric functions, each participant's fitted detection probabilities for intensity levels 1 and 10 were determined. Five participants, whose detection probabilities were >10% for intensity level 1or <90% for intensity level 10, were excluded from further analysis because for these participants, sampling of the full dynamic range of their psychometric functions was not successful (potentially due to pronounced drifts in detection thresholds, changes in response criteria, or inaccurate reports) (***Figure 2***). Differences in reaction times between detected and undetected targets were assessed using a Bayesian equivalent of the paired t-test (***Krekelberg, 2019***), and the Bayes factor quantifying the evidence for a mean deviation from zero (BF10) is reported. To test if target detection and match/mismatch reports were indeed independent, we calculated Bayesian tests of association (**Johnson and Albert, 2006**) between these two variables for every participant and report Bayes factors for association (BF10) and independence (BF01). Following the guidelines by **Kass and Raftery (1995)** we consider 1 < BF < 3 negligible, 3 < BF < 20 positive, 20 < BF < 150 strong, and 150 < BF very strong evidence.

FMRI

FMRI preprocessing and data analysis were performed with SPM12 (www.fil.ion.ucl.ac.uk/spm, RRID: SCR_007037) and custom Matlab scripts. Functional images were realigned using six parameter rigid body transformation to account for head motion, corrected for differences in slice acquisition time, and normalised to standard MNI space using SPM's unified segmentation. Structural images were coregistered to the mean functional image and white matter (WM) and cerebrospinal fluid (CSF) masks were stored for later analysis. Spatial smoothing was not performed prior to the first-level analysis because the Bayesian GLM approach estimates the smoothness of experimental effects from the data using spatial priors (**Penny et al., 2005**) (for information on smoothing of evidence maps and beta images, see below).

Five trial-wise experimental regressors were extracted from the paradigm: 1. The linear stimulus intensity modelling physical stimulus properties, 2. binary target detection as inferred from participants' reports and the presented matching cues modelling an all-or-nothing response to detected targets, 3. detection probability as modelled by individual psychometric functions, 4. expected stimulus uncertainty modelled as the slope of individual psychometric functions (an inverse u-shaped function), and 5. binary match/mismatch responses as a model of overt reports (**Figure 1B**). Five different GLMs were then constructed, each incorporating one of the five experimental regressors: each GLM contained one onset regressor modelling all trial onsets. This onset regressor was parametrically modulated by a z-scored experimental regressor. Z-scored reaction times were added as a further parametric regressor to ensure that differences in model fit could not result from variations in reaction times. Temporal derivatives, motion parameters, as well as the first five principal components explaining variance in the white matter and cerebrospinal fluid signals, respectively were added as nuisance regressors. All models were fitted to each participant's fMRI data using the first-level Bayesian estimation procedure as implemented in SPM12. As spatial prior, we used the recommended Unweighted Graph Laplacian prior, which softly constrains effects to be similar in neighbouring voxels (where the strength of the constraint for each regressor is estimated from the data). With this procedure, we obtained posterior probability maps (**Penny et al., 2005**) for every participant and model, along with free energy approximations to the model evidence in the form of whole-brain voxel-wise log evidence maps (**Penny et al., 2007**). These evidence maps were smoothed with an 8 mm FWHM Gaussian filter, resampled to $2\times2\times2$ mm^3 voxel size, and subjected to voxel-wise random effects BMS resulting in one EP map per model for group-level inference (**Rosa et al., 2010**; **Stephan et al., 2009**). Voxels showing EP $\geq$.99 for any model were considered voxels of interest. Since the models were identical except for their experimental regressors, differences in model evidence could only arise from differences in the experimental regressors. Note that we did not include an explicit null model because voxels that were not well explained by any of the models would simply not yield high EPs.

To prevent model dilution for models explaining shared variance, we combined the intensity, detection, and detection probability models into one model family, which adjusts their prior expectation. We call this family the +family because their respective experimental regressors correlate positively with stimulus intensity. We then performed family-level BMS (**Penny et al., 2010**) on the +family, the uncertainty model, and the report model using the .99 EP threshold. Voxels in which the +family explained the data with high probability were defined as ROIs and stored as a +family mask. We then reran the BMS procedure on voxels within the +family mask, this time only comparing the intensity, detection, and detection probability models to determine their individual contributions to the model family fit. To assess the impact of the employed spatial prior and smoothing parameters on the overlap of effects, we repeated the analyses, once using a global shrinkage prior (which does not constrain the smoothness of the data) in the GLM estimation, and once using a 4 mm FWHM smoothing kernel on the evidence maps used for BMS. Neither of these methods considerably reduced the overlap of effects and we report the results using the original parameters. Since we were interested in the behaviour of well-defined regions, we only considered clusters of k $\geq$50 voxels as regions of interest in all analyses.

Next, we tested the beta estimates of the winning models' experimental regressors for systematic deviation from zero. For this purpose, we obtained one group mask for each ROI from the group level EP maps. For the +family models, these masks included all voxels within the .99 EP family clusters in which the respective model scored higher EPs than the other +family models. For the uncertainty and report ROIs, masks were extracted at the .99 EP level. Within each group mask, we determined the subject-level probability peak of the model defining that ROI for every participant (calculated as the ratio of model evidence for that model over the summed model evidence across all models). We then extracted individual beta estimates from these peaks using the beta images of the respective winning models that were previously obtained from the first-level Bayesian GLM estimation and tested their deviation from zero using the Bayesian equivalent of a one-sample t-test (***Krekelberg, 2019***).

To extract SRPs, we defined a new GLM with ten onset regressors, one for each intensity level. Again, the model contained reaction times and all nuisance regressors from the main analysis and was fit to the fMRI data using the first-level Bayesian estimation scheme. The resulting beta images were smoothed at 8 mm FWHM and resampled to $2 \times 2 \times 2$ mm^3. For each ROI (as defined by the main analysis), beta estimates for the ten intensity regressors were then extracted from 4 mm radius spheres, centred on the previously identified individual model probability peaks. For each intensity level, the mean beta estimate across the sphere was saved for every participant and the mean beta estimates across participants were plotted as a function of intensity level, yielding SRPs for each region. This way of defining individual spheres ensures their centres lie within the ROI while accommodating individual variation in exact peak locations.

Finally, we examined the distribution of voxels best explained by the different models of the +family across the known cytoarchitectonic subregions of primary and secondary somatosensory cortex (***Eickhoff et al., 2006b***; ***Geyer et al., 1999***; ***Grefkes et al., 2001***). To this end, we determined which of the +family models yielded the highest exceedance probability in the group level BMS for each voxel within the identified SI and SII ROIs. For each cytoarchitectonic subregion (BA 3b, 1, 2, OP1-4), we then determined the proportion of voxels labelled by the respective +family models to obtain a descriptive summary of the BMS results across regions.

All anatomical coordinates are provided in MNI space. We used the SPM Anatomy Toolbox (***Eickhoff et al., 2005***, RRID:SCR_013273) for anatomical reference where possible and MRIcron (www.mccauslandcenter.sc.edu/mricro/mricron, RRID:SCR_002403) to display fMRI results.

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Author contributions

Pia Schröder, Conceptualization, Data curation, Software, Formal analysis, Funding acquisition, Validation, Investigation, Visualization, Methodology, Writing—original draft, Project administration, Writing—review and editing, Interpretation of results; Timo Torsten Schmidt, Conceptualization, Investigation, Writing—review and editing, Interpretation of results; Felix Blankenburg, Conceptualization, Resources, Supervision, Funding acquisition, Project administration, Writing—review and editing, Interpretation of results

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Additional files

Supplementary files

- Transparent reporting form

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Data availability

In accordance with EU's General Data Protection Regulation we are unable to share raw fMRI data. However, single subject log evidence maps and group posterior probability maps have been uploaded to figshare (https://doi.org/10.6084/m9.figshare.7347167.v1) and posterior probability maps can be directly inspected on Neurovault (https://neurovault.org/collections/4496/). Analysis code is available on GitHub (https://github.com/PiaSchroeder/SomatosensoryTargetDetection_fMRI; copy archived at https://github.com/elifesciences-publications/SomatosensoryTargetDetection_fMRI).

The following datasets were generated:

Author(s)	Year	Dataset title	Dataset URL	Database and Identifier
Schröder P	2018	Somatosensory target detection	https://neurovault.org/collections/4496/	Neurovault, 4496
Schröder P	2018	Neural basis of somatosensory target detection	https://doi.org/10.6084/m9.figshare.7347167.v1	Figshare, 10.6084/m9.figshare.7347167.v1

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Behavioral/Cognitive

Dissociating Perceptual Awareness and Postperceptual Processing: The P300 Is Not a Reliable Marker of Somatosensory Target Detection

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A central challenge in the study of conscious perception lies in dissociating the neural correlates of perceptual awareness from those reflecting its precursors and consequences. No-report paradigms have been instrumental in this endeavor, demonstrating that the event-related potential P300, recorded from the human scalp, reflects reports rather than awareness. However, these paradigms cannot probe the degree to which stimuli are consciously processed from trial to trial and, thus, leave open the possibility that the P300 is a genuine correlate of conscious access enabling reports. Here, instead of removing report requirements, we took the opposite approach and equated postperceptual task demands across conscious and unconscious trials by orthogonalizing target detection and overt reports in a somatosensory detection task. We used Bayesian model selection to track the transformation from physical to perceptual processing stages in the EEG data of 24 male and female participants and show that the early P50 component scaled with physical stimulus intensity, whereas the N140 component was the first correlate of target detection. The late P300 component was elicited for both perceived and unperceived stimuli and was not substantially modulated by target detection. This was in stark contrast to a control experiment using a classical direct report task, which replicated the P50 and N140 effects but additionally showed a strong effect of target detection in the P300 time range. Our results demonstrate the task dependence of the P300 in the somatosensory modality and show that late cortical potentials dissociate from perceptual awareness even when stimuli are always reported.

Key words: Bayesian model selection; electroencephalography; P300; perceptual awareness; somatosensory; target detection

Significance Statement

The time it takes for sensory information to enter our conscious experience can be an indicator of the neural processing stages that lead to perceptual awareness. However, because many cognitive processes routinely correlate with perception, isolating those signals that uniquely reflect perceptual awareness is not a trivial task. Here, we show that late electroencephalography signals cease to correlate with somatosensory awareness when common task confounds are controlled. Importantly, by balancing report requirements instead of abolishing them, we show that the lack of late effects cannot be explained by a lack of conscious access. Instead, we propose that conscious access occurs earlier, at ~150 ms, supporting the view that early activity in sensory cortices is a neural correlate of conscious perception.

Introduction

Whether the neural processes giving rise to conscious perception originate in sensory cortices or higher-order regions is a longstanding debate. In the somatosensory modality, the event-related potentials (ERPs) N140 over contralateral somatosensory electrodes and P300 over centroparietal electrodes show enhanced amplitudes for consciously perceived stimuli (Schubert et al., 2006; Auksztulewicz et al., 2012), whereas very early components, such as the P50, seem to reflect physical stimulus properties (Forschack et al., 2020). These findings are consistent with studies in the visual and auditory modalities that have similarly reported awareness-related negativities at ~200 ms over modality-specific electrodes and late positivities at ~350 ms over centroparietal electrodes (Sergent et al., 2005; Eklund et al., 2019).

Despite this agreement, recent years have seen a rigorous debate centering on the question of whether these potentials truly reflect awareness or are instead associated with precursors or consequences of conscious perception (Melloni et al., 2011; Aru et al., 2012; Pitts et al., 2014; Rutiku et al., 2015; Naccache et al., 2016; Cohen et al., 2020; for a recent review, see Förster et al., 2020).

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While early negativities have been suspected to reflect attentional processes rather than awareness (Pitts et al., 2014), the P300 has been found to be sensitive to expectations (Melloni et al., 2011), attention (Koivisto et al., 2006), and the timing of reports (Ye and Lyu, 2019). In a series of studies, Pitts and colleagues have demonstrated that the visual P300, in particular its later subcomponent P3b, ceases to index awareness when stimuli are conscious but not reported, that is, when they have no behavioral relevance to the task (Pitts et al., 2014; Cohen et al., 2020; Schlossmacher et al., 2020). These findings suggest that the P300 reflects postperceptual processing rather than perceptual awareness per se. However, two questions are still outstanding: First, because no-report paradigms do not directly inquire participants' subjective experience, it remains unclear to what extent the presented stimuli are consciously processed and whether the neural processes that otherwise allow sensory information to become accessible for conscious report can accurately be captured. In this context, it has been criticized that failure to detect a P300 for conscious but task-irrelevant stimuli may be due to increased temporal variability of the elicited components (Boncompte and Cosmelli, 2018), a lack of conscious access, or even a failure to correctly identify conscious stimuli (Mashour et al., 2020). Indeed, studies using more active manipulations of reports have been inconclusive regarding the task dependence of the P300, showing a dependence on reports in vision (Koivisto et al., 2016) but not in audition (Eklund et al., 2019; but see Schlossmacher et al., 2021). This leads to the second question: do findings from visual studies generalize across sensory modalities? So far, studies testing the task dependence of the P300 are scarce in the auditory and completely lacking in the somatosensory modality, prohibiting final conclusions regarding the general relevance of early and late ERP markers of perceptual awareness.

The goal of our study was to address these questions and scrutinize the task dependence of early and late ERP correlates of perceptual awareness in the somatosensory modality. To control for task demands while guaranteeing conscious access, we used a somatosensory-visual matching task that orthogonalized target detection and perceptual reports, leading to equated behavioral relevance, working memory, and attentional capture of detected and undetected stimuli. To track the transformation from physical to perceptual processing stages, we constructed simple behavioral models capturing various task dimensions and evaluated them using time-resolved Bayesian model selection (Stephan et al., 2009). Based on a previous fMRI study (Schröder et al., 2019) and insights from the visual modality, we hypothesized that (1) very early potentials (P50) reflect physical stimulus properties, (2) the somatosensory N140 correlates with target detection independent of task requirements, and (3) the P300 reflects postperceptual processes and only differentiates between hits and misses when reports correlate with detection but not when report requirements are controlled for.

Materials and Methods

Participants

Participants were recruited from the student body of the Freie Universität Berlin and from the general public. All participants reported to be healthy with no history of neurologic or psychiatric disorders, were right-handed, and had normal or corrected-to-normal vision. Twenty-eight participants completed the main experiment (matching task). Data of 3 participants were excluded because they did not show stable psychometric functions (see Behavior and Fig. 2), and data of another participant were excluded because of strong motion-related artifacts in the EEG recordings leading to the exclusion of >50% of trials. Thus, data of 24 participants entered the analyses (19 females, 5 males, age range: 19-37 years). Another 23 participants completed a control experiment using a classical detection task (direct report task). From this dataset, data of 1 participant were excluded because of unstable psychometric functions, leaving data of 22 participants that entered the analyses (12 females, 10 males, age range: 21-42 years). All participants gave written informed consent before the experiment and received a monetary reimbursement or course credits for their participation. The study was approved by the local ethics committee at the Freie Universität Berlin and complied with the Human Subjects Guidelines of the Declaration of Helsinki.

Experimental design

Matching task. In the main experiment, participants performed a two-alternative forced choice somatosensory detection task on electrical median-nerve stimuli while their EEG was recorded (Fig. 1*A*). Each trial was preceded by a variable intertrial interval, during which participants had to fixate on a central gray fixation disk. Following the intertrial interval, an electrical target stimulus was delivered at 1 of 10 intensity levels. The intensity levels were individually calibrated to sample the full dynamic range of each participant's psychometric function from 0% to 100% detectability (see Stimuli and apparatus). Accordingly, physical stimulus properties, detection probability, and perceptual uncertainty associated with target detection varied from trial to trial. Presentation of the electrical target pulse was accompanied by a simultaneous change in the fixation disk's brightness to either white or dark gray. This change in brightness served as a visual matching cue, which signaled target presence (white) or absence (dark gray). Participants were instructed to compare their somatosensory percept (electrical pulse detected or not detected) to the visual matching cue (signaling target presence or absence) and decide whether the two modalities produced a match (e.g., electrical pulse detected and white matching cue presented) or a mismatch (e.g., electrical pulse detected and dark gray matching cue presented; Fig. 1*A*, left box). Electrical pulses were presented on every trial and only their intensity levels varied, rendering them subliminal or supraliminal. Target detection for the highest and lowest intensity levels was expected to be relatively stable (~0% detection probability at intensity level 1 and ~100% detection probability at intensity level 10), whereas detection at intermediate intensity levels was expected to fluctuate from trial to trial. In contrast, the two brightness levels of the matching cue were clearly discernible. This ensured that electrical target detection could be directly inferred from the combination of the matching cues presented on each trial and the participant's match or mismatch reports. After a brief delay, in which the fixation disk returned to its original brightness, two color-coded response cues were presented to the left and right of the fixation disk. Participants reported their match/mismatch decisions by making a saccade to the corresponding response cue (the color codes were counterbalanced across participants). Their gaze was evaluated online, and a response was registered as soon as the gaze remained within the response area for 0.2 s, which was signaled to the participant by a brief increase in the selected response cue's size. The next intertrial interval began as soon as a response was logged or once the allotted response time had elapsed. In this case, the fixation disk briefly turned red, signaling a missed trial. The presented matching cues and the specific sides on which the color-coded response cues were presented were counterbalanced across intensity levels, and trials were presented in random order. All participants completed 6 blocks of 200 trials (~10 min per block), resulting in 1200 trials per participant. The number of trials per intensity level followed a normal distribution, such that the number of trials at intensity levels near the 50% detection threshold was maximized (with 192 trials each for the threshold intensity levels 5 and 6 and 48 trials each for the lowest and highest intensity levels 1 and 10). Before the main experiment, participants completed a 30 min training, in which they were required to achieve at least 90% accuracy on a run with superthreshold stimuli to ensure full understanding of the task and a low error rate in the main experiment.

Direct report task. To assess the influence of task requirements on early and late ERP correlates of somatosensory target detection, we ran a control experiment, in which participants performed a direct report task, comparable to classical detection tasks. The stimulation protocol, visual displays, and all other experimental parameters were identical to the main experiment, and only the task instructions differed to produce hit/

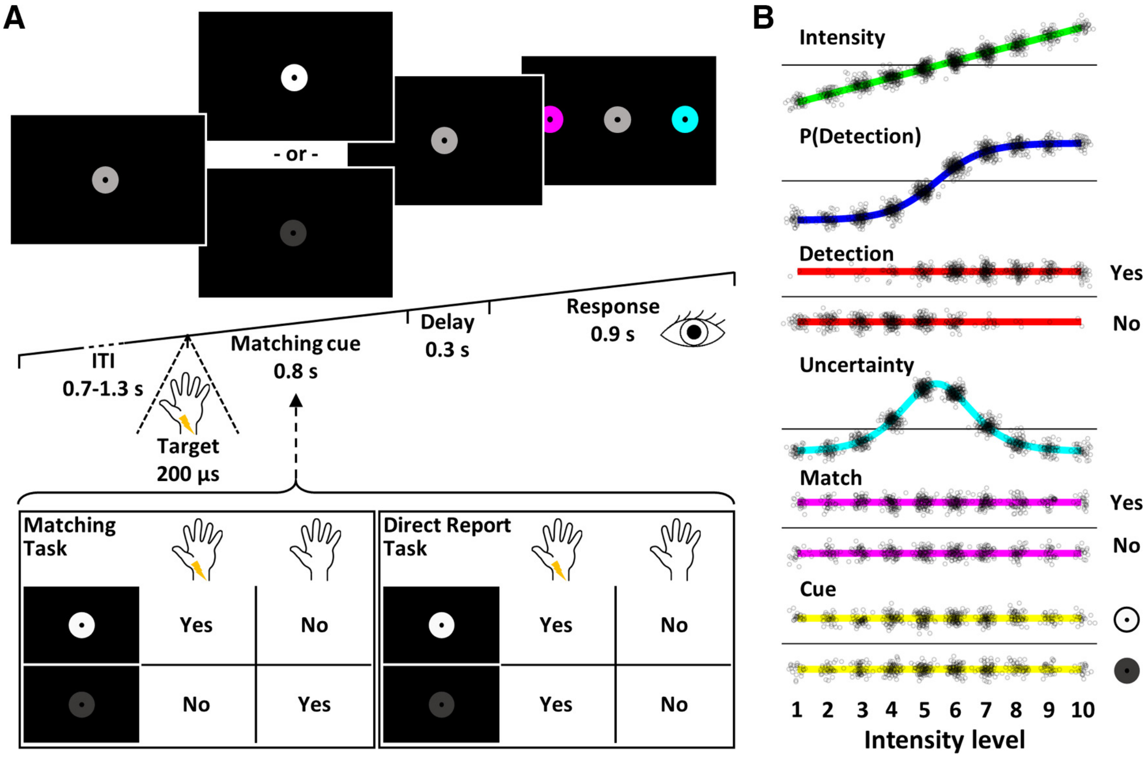

Figure 1. Experimental design. ***A***, Trial design. Following a variable intertrial interval, participants received an electrical target pulse at 1 of 10 intensity levels, which they either detected or missed. At the same time, the fixation disk changed its brightness to serve as the visual matching cue, which signaled target presence (white) or target absence (dark gray). In the matching task, participants compared their somatosensory percept to the matching cue and decided whether the two modalities matched or not (left box). In the direct report task, participants ignored the identity of the matching cue and merely decided whether they had detected a target pulse or not (right box). After a brief delay, they reported their decision by making a saccade to one of two peripherally presented, color-coded response cues. The selected cue briefly increased in size, signaling that the response was logged, and the next trial began. ***B***, Experimental regressors. EEG responses were modeled with seven different GLMs that were compared using BMS. Each experimental GLM contained an intercept regressor and one of six experimental regressors modeling stimulus intensity, detection probability, target detection (hit vs miss), expected uncertainty, matching reports (match vs mismatch), and matching cues (white vs dark gray). An additional null model contained the intercept regressor only. Small black circles represent individual trials of 1 participant. Please note that although the detection probability regressor is computed from the detection regressor, the two models differ in their behavior within intensity levels: for example, looking at the predictions for trials at intensity level 5, the detection probability model predicts the same activation level for all targets of that intensity level, regardless of whether they were detected or missed, whereas the detection model predicts categorically higher activity for detected than missed trials. Thus, the detection model assumes a nonlinear, all-or-none response for detected stimuli, whereas the detection probability model assumes a graded response. Further note the intensity-biased distribution of trials in the detection regressor, which leads to correlations between models and prohibits classical GLM analysis.

miss reports instead of match/mismatch reports. Participants were similarly presented with electrical target stimuli and concurrent matching cues, but they were informed that the fixation disk's change in brightness merely indicated the timing of a potential target stimulus, with no relevance of the direction of change. Thus, instead of reporting match/mismatch decisions, they directly reported whether they had perceived the target stimulus or not by saccading to the corresponding color-coded response cue (Fig. 1*A*, right box).

Task comparison. Because of the different report requirements, the two tasks offered different levels of experimental control. In both experiments, the selected intensities ensured an overall detection rate of ~50%, such that detected stimuli were not expected to produce oddball effects. Likewise, because of the randomization, participants could not predict which response cue would be presented on which side, so that they could not prepare a motor response early in the trial in either experiment. However, in the direct report task, target detection directly correlated with overt reports, behavioral relevance, working memory, and attentional capture. In contrast, in the matching task, the use of counterbalanced matching cues resulted in a decorrelation of target detection and overt reports. Importantly, since detected and undetected targets could result in the same overt report, their behavioral relevance and ensuing working memory were equated. Finally, the multimodal nature of the task required participants to split their attentional resources between somatosensory and visual inputs and quickly combine the extracted information into corresponding reports. As a result, signal differences related to poststimulus attentional capture were expected to be minimized. Thus, the contribution of postperceptual processing to the hit versus miss contrast was expected to be considerably attenuated in the matching task compared with the direct report task.

Stimuli and apparatus. Target pulses were generated as analog voltage signals using a waveform generator (DT-9812, Data Translation), converted to direct current monophasic square wave pulses of 200 µs duration by a constant current stimulator (DS5, Digitimer), and delivered via adhesive electrodes (GVB-geliMED) attached to the left wrist to stimulate the median nerve. Stimuli were delivered at 10 individually calibrated intensities that were determined from participants' psychometric functions. The psychometric functions were estimated before the experiments using the threshold estimation procedure described by Schröder et al. (2019), which accommodates between-subject variation in detection thresholds and criteria (estimated 1%, 50%, and 99% detection thresholds: matching task: T01 = 1.88 ± 0.79 mA, T50 = 2.53 ± 0.75 mA, T99 = 3.18 ± 0.91 mA; direct report task: T01 = 2.38 ± 0.78 mA, T50 = 2.88 ± 0.82 mA, T99 = 3.38 ± 0.91 mA [mean ± SD]). Stimulus presentation was implemented in MATLAB (The MathWorks, RRID:SCR_001622) using the Psychophysics toolbox (Brainard, 1997) (RRID:SCR_002881). For response collection, participants' gaze was measured using an SMI RED-m remote eye tracker (120 Hz, Sensomotoric Instruments) and SMI's iView X SDK.

EEG recording and preprocessing. EEG data were recorded from 64 electrodes placed according to the extended 10-20 system (ActiveTwo, BioSemi). Four additional electrodes recorded vertical (vEOG) and horizontal (hEOG) eye movements. Preprocessing steps included high-pass filtering at 0.01 Hz (data of 1 participant in the control experiment were high-pass filtered at 0.5 Hz to remove excessive sweat artifacts), downsampling from 2048 Hz to 512 Hz, and rereferencing to the common average. Eye blinks were removed from the data using adaptive spatial filtering based on individual blink templates computed from the vEOG (Ille et al., 2002). The continuous data were cut into epochs from −50 to 600 ms relative to stimulus onset. All epochs were visually inspected for artifacts, and artifactual trials were removed (on average, 5.20% in the main experiment and 6.48% in the control experiment). The artifact-free, epoched data were then low-pass filtered at 40 Hz and baseline corrected using a baseline from −50 to −5 ms. All preprocessing and data analyses were performed using SPM12 (www.fil.ion.ucl.ac.uk/spm; RRID:SCR_007037) and custom MATLAB scripts. EEGLAB's topoplot function was used to plot topographies (Delorme and Makeig, 2004) (RRID:SCR_007292).

Statistical analysis

Behavior. Logistic functions were fitted to the behavioral data of each experimental block to obtain continuous models of the underlying psychometric functions (Wichmann and Hill, 2001). For each participant, the estimated slope and threshold parameters were then averaged across blocks to obtain one psychometric function per participant. Estimated detection probabilities <10% for intensity level 1 and >90% for intensity level 10 were defined as inclusion criteria. The rationale behind these criteria was that minimum and maximum detection probabilities outside these margins would indicate an incomplete sampling of the individual psychometric function (possibly because of changes in detection thresholds, response criteria, or erroneous reports). In the main experiment (matching task), data of 3 participants and in the control experiment (direct report task), data of 1 participant were excluded based on these criteria (see Fig. 2). Differences in mean psychometric functions between tasks, which could be indicative of altered stimulus processing, were tested by running a Bayesian equivalent of the two-sample *t* test on the estimated 50% threshold and slope parameters. Differences in reaction times between hits and misses were tested using a Bayesian equivalent of the paired-sample *t* test (Krekelberg, 2019). For all *t* tests, Bayes factors in favor of a difference are reported (BF10). To test whether the matching task successfully dissociated target detection from overt reports, Bayesian tests of association (Johnson and Albert, 1999) were performed on these variables for each participant in the matching task and Bayes factors for independence are reported (BF01, i.e., Bayes factors in favor of the null hypothesis). Following the recommendations by Kass and Raftery (1995), we consider $1 \leq \text{BF} < 3$ negligible, $3 \leq \text{BF} < 20$ positive, $20 \leq \text{BF} < 150$ strong, and $150 \leq \text{BF}$ very strong evidence. All descriptive statistics are reported as mean ± SD, except where otherwise noted.

EEG. Neuronal processing of the somatosensory stimulus was expected to undergo a transformation from physical to perceptual stages and on to the final reports. To track this transformation in the EEG signals and identify the latency at which awareness-related potentials occur, we constructed five GLMs. Each contained an intercept regressor and a trialwise experimental regressor capturing a variable of interest (Fig. 1*B*): (1) intensity: the stimulus intensity level presented on each trial as a model of physical stimulus properties (linear regressor); (2) P(detection): the individual psychometric functions modeling trialwise detection probability (sigmoidal regressor); (3) detection: categorical target detection which was inferred from match/mismatch reports and matching cues in the main experiment and explicitly reported in the control experiment, modeling a nonlinear response expected to index awareness (binary regressor); (4) uncertainty: the slope of individual psychometric functions modeling the expected uncertainty associated with target detection (inverse U-shaped regressor); and (5) match: matches and mismatches between target detection and visual matching cues, which were explicitly reported in the main experiment and inferred from hit/miss reports and matching cues in the control experiment (binary regressor). Although participants did not engage with the matching cue in the direct report task and did not form match/mismatch reports, we still included the match model (as defined by the alignment of participants' hit/miss reports with the matching cues presented on every trial) in the analysis of both experiments to ensure that any differences in results would be attributable to differences in the data and not to differences in the model spaces. In addition to the five models of interest, we included two further GLMs as control models to validate the approach: (6) cue: a visual control model that was defined by the white or dark gray matching cues to demonstrate specificity of the results to electrodes over somatosensory and visual cortices, respectively (binary regressor); and (7) null: a control model that contained only the intercept regressor to ensure that model selection would correctly dismiss experimental models when no effects were expected (i.e., no effects in the baseline period).

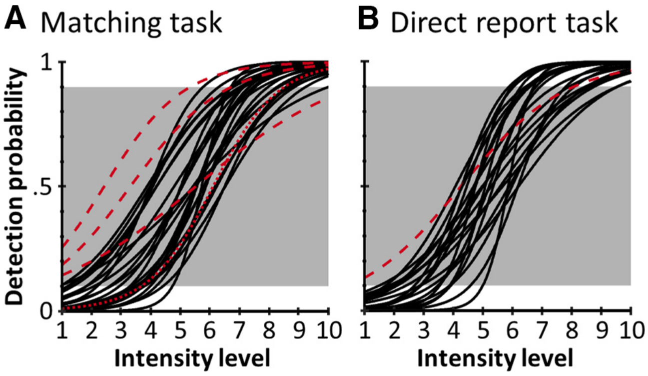

Figure 2. Psychometric functions in the matching task (***A***) and the direct report task (***B***). Black lines indicate the individual block-averaged psychometric functions of participants included in the final samples (matching task: $n = 24$; direct report task: $n = 22$). The psychometric curves are plotted as a function of intensity level, not intensity in mA, to normalize across participants. Red dashed lines indicate participants whose detection probabilities at minimum and maximum intensity levels fell outside the required margin of <10% and >90% (white background) and were thus excluded from the analyses. The red dotted line indicates 1 participant in the matching task that was excluded because of poor EEG data quality.

Each of these models captures a unique aspect of the processing stages expected to occur during the tasks, but not all of them are independent. Specifically, because target detection becomes more likely with increasing stimulus intensity, the intensity, detection probability, and detection models are positively correlated. This collinearity complicates classical GLM analysis since corresponding variance in the data cannot be uniquely assigned to any one of the regressors (e.g., the contrast between hits and misses would always be confounded by differences in stimulus intensity). Therefore, we used an alternative approach, Bayesian model selection (BMS) (Stephan et al., 2009), which can capitalize on variance that is explained by each of the models beyond their shared variance. Importantly, the intensity, detection probability, and detection models each make unique predictions: while the intensity and detection probability models both assume a gradual increase of activity with increasing intensity, the intensity model does so in a linear fashion whereas the detection probability model predicts a sigmoidal response profile, with slow changes at low and high intensity levels and a sharp increase near the threshold intensities. Within one intensity level, the detection probability model predicts the same level of activation for all trials of that intensity level, regardless of whether they were detected or not, whereas the detection model predicts categorically higher activity for detected than undetected stimuli, despite being presented at the same intensity level. Accordingly, the detection model assumes an all-or-none response for detected stimuli that is not captured by any of the other models.

To implement the BMS approach, the data from both experiments were analyzed using the same analysis pipeline: the seven GLMs were fitted to participant's trialwise EEG data using the Bayesian estimation scheme as implemented in SPM's spm_vb_glmar.m function. This function approximates the posterior distributions of regression coefficients using variational Bayes (Penny et al., 2003) and provides free energy approximations to the log model evidence (LME), which can be used for model comparison (Penny et al., 2007). To obtain time-resolved estimates of LMEs for each model, electrode, and participant, we fit our GLMs to each time point of each electrode individually (with the autoregressive model order set to zero, effectively reducing the error term to independent and identically distributed Gaussian errors and Gaussian priors for the regression coefficients with mean $w0 = 0$ and variance $\alpha^{-1} = 0.005$). All EEG data were *z*-scored across trials before model fitting to obtain data of comparable signal amplitudes.

To identify which model best explained the EEG data at every time point, the estimated LMEs were then used to perform time-resolved BMS (Stephan et al., 2009). BMS computes exceedance probabilities (EPs) for all models, quantifying the probability that a particular model explains the data better than any of the other models. In addition to enabling model comparison of non-nested models, this approach allows for comparison of models that share variance to different degrees. If models are correlated, their shared variance reduces the relative difference between their LMEs. Accordingly, if correlated and uncorrelated models were included in the comparison individually, the correlated models would be at a disadvantage because they would have to compete against very similar models. At the same time, by assigning equal prior probability to correlated and uncorrelated models, identical portions of variance would be assigned too much prior weight, again resulting in an unfair comparison. BMS offers a simple solution to this problem by presenting the possibility to combine similar models into model families and adjusting the models' prior probabilities accordingly (Penny et al., 2010). The combined models are then assessed on the family level, facilitating fair comparisons. In our case, we combined the intensity, detection probability, and detection models into a model family (which we termed +family because of their positive correlations) and performed BMS on the family level, comparing the +family with the uncertainty, match, cue, and null models. For time points that were best explained by the +family, we further determined which of the individual +family models best explained the data by running the model comparison on the +family models only and weighting the resulting EPs by the +family EP.

To identify time points of interest, we imposed two criteria: (1) the winning model family had to score an EP $\geq 99\%$ demonstrating a very high probability that the respective model family explained the data better than any of the other model families; and (2) across participants, the β estimates of the winning models' experimental regressors had to systematically deviate from zero. Since BMS does not take the directionality of effects across participants into account (LMEs can be high regardless of whether an effect is positive or negative), we added this criterion to ensure that only signals that systematically varied with any of our experimental regressors would be identified. To test this, we extracted β estimates of the winning models' experimental regressors and tested these for systematic deviation from zero using a Bayesian equivalent of the one-sample *t* test (Krekelberg, 2019). Thus, time points of interest were defined as those exceeding both the EP threshold and a β evidence threshold of $\mathrm{BF10} \geq 3$. The null model was exempt of this rule as it did not have an experimental regressor and thus was only required to exceed the EP threshold. When using BMS, it is usually not required to explicitly correct for multiple comparisons, since estimating posterior probabilities does not constitute a statistical test with a binary outcome that would result in false positives (Friston and Penny, 2003). However, when threshold criteria are applied to identify data segments of interest as done here, false positives become a possibility. In this context, it has been noted that thresholding posterior probabilities and labeling the threshold-crossing data segments as "active" is analogous to controlling the false discovery rate in classical inference (Friston and Penny, 2003; Marchini and Presanis, 2004). In our case, by thresholding EPs at 99%, we ensure that, among the data segments surpassing that threshold, at most 1% may be false positives. Moreover, by using the additional criterion of systematic β estimates, unsystematic variation across participants is further prevented from resulting in false positives, such that the true false discovery rate is expected to be even lower.

To visualize the influence of the different task requirements on ERPs elicited by detected and undetected stimuli independent of differences in physical stimulus properties, we extracted subsamples of hit and miss trials that were matched for stimulus intensity. For each participant, we identified all intensity levels that resulted in both hits and misses and randomly sampled trials such that the number of hits and misses was identical within each intensity level (see Fig. 4*A*). The subsampled trials were then pooled across intensity levels (main experiment: 225.96 ± 43.32 trials per condition; control experiment: 211.23 ± 47.35 trials per condition [mean ± SD]) and grand-averaged hit and miss ERPs were plotted for electrodes of interest.

Code and data accessibility

MATLAB scripts, including all analysis code, are publicly available on Github at: https://github.com/PiaSchroeder/SomatosensoryTargetDetection_EEG. Preprocessed EEG data and log files holding all relevant trial information can be downloaded from: https://doi.org/10.6084/m9.figshare.13160381.

Results

Behavior

Participants detected 53.77 ± 9.49% of targets in the matching task and 55.84 ± 8.99% in the direct report task. Target detection was most variable on trials with intermediate stimulus intensity levels resulting in characteristic sigmoidal psychometric curves (Fig. 2). The two tasks resulted in similar psychometric curves, as indicated by a lack of evidence for differences in their characteristics (50% thresholds: matching task $\mathrm{T50} = 2.52 \pm 0.79$ mA, direct report task $\mathrm{T50} = 2.82 \pm 0.80$ mA, $\mathrm{BF10} = 0.58$; slopes: matching task slope = 7.53 ± 4.92, direct report task slope = 8.82 ± 3.82, $\mathrm{BF10} = 0.43$). Reaction times were slightly shorter for hits than misses (matching task: hits: 308.97 ± 32.25 ms, misses: 314.05 ± 36.52 ms, $\mathrm{BF10} = 9.27$; direct report task: hits: 313.62 ± 34.17 ms, misses: 333.89 ± 42.28 ms, $\mathrm{BF10} = 568.68$). The matching task successfully dissociated target detection from overt reports as suggested by Bayesian tests of association ($\mathrm{BF01} > 5$ for all participants).

EEG

Task dependence of early and late somatosensory ERPs

To test our hypotheses regarding the task dependence of the P50, N140, and P300, we inspected the BMS results in three electrodes of interest: CP4, C6, and CPz. These electrodes were selected based on previous research (Del Cul et al., 2007; Auksztulewicz et al., 2012; Pitts et al., 2014; Cohen et al., 2020), and we confirmed that they captured the components of interest by inspecting grand-averaged topographies of all hit trials across both experiments at relevant time points (P50: 50 ms, N140: 140 ms, P300: 350 ms; Fig. 3). The grand-averaged EEG signals plotted for each intensity level showed the largest deflections for stimuli of high intensity levels and the smallest deflections for stimuli of low intensity levels, suggesting correlation with the +family. This observation was confirmed by BMS: in the matching task, the P50 in contralateral electrode CP4 was best explained by the intensity model, indicating processing of physical stimulus properties at this latency (Fig. 3*A*; Table 1). The P50 was followed by a centroparietal P100, which was similarly modulated by stimulus intensity but showed a transition to reflect detection probability at ~120 ms. The N140 in electrode C6 was the first to show an effect of target detection at ~150 ms, but this effect was preceded by an effect of physical stimulus intensity, suggesting a transition from physical to perceptual processing stages at this latency. From ~250 ms onwards, the P300 in electrode CPz was best explained by the detection probability model (please note that this model assumes no differences between detected and undetected stimuli of the same intensity) and showed little evidence for a late effect of target detection (maximum EP reached by the detection model in this component compared against the intensity and detection probability models: $\mathrm{EP}_{\mathrm{det}} = 16.54\%$, compare Table 1). To get an impression of the spatial extent of this effect, we inspected effect topographies across the scalp for relevant time points and found that the centroparietal electrode cluster constituting the P300 did not show a homogeneous response

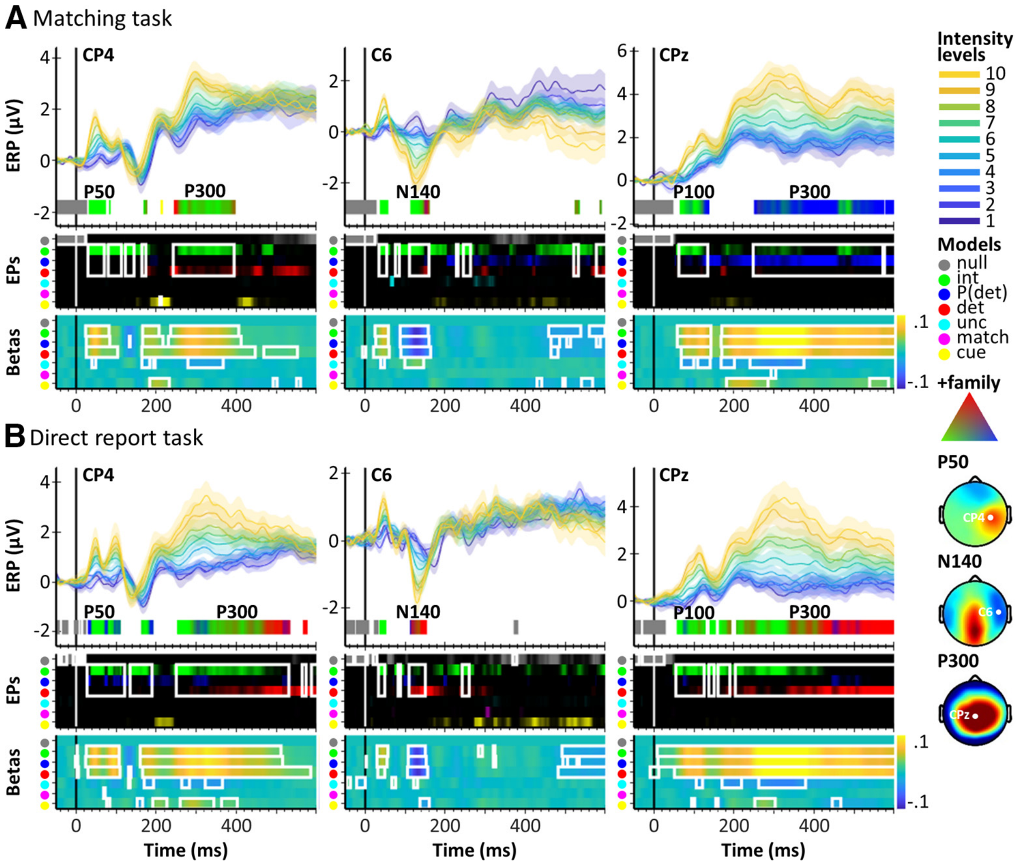

Figure 3. ERPs and BMS results for three electrodes of interest (CP4, C6, CPz, marked in grand-averaged Hit topographies on the right) in the matching task (***A***) and in the direct report task (***B***). For each electrode: Top, Stimulus-locked, grand-averaged ERPs (mean ± SE) for each intensity level (1-10). Below the ERPs, BMS results are plotted for time points of interest (EP$>=$99% and BF10$_{\text{beta}}$ $>=$3) as color bands representing the winning model families. For time points best modeled by the +family (intensity, P(detection), detection), the color represents an RGB value that is composed of the EPs of the three +family models (compare the RGB triangle: corners correspond to EP = 100%, signifying a clear winner of the model comparison within the +family, whereas intermixed colors represent similar EPs for the respective models). Corresponding peak +family model EPs are presented in Table 1. Middle, Unthresholded EP time courses for each model. Bottom, Time courses of group-averaged β estimates of each model's experimental regressor (warm colors represent positive β estimates; cold colors represent negative β estimates). White rectangles represent data segments that exceed the respective thresholds. The results suggest that the P50 was modulated by stimulus intensity in both tasks. The N140 showed a transition from stimulus intensity to target detection in the matching task and a pure effect of target detection in the direct report task. The P300 was strongly task-dependent, showing an effect of detection probability in the matching task and a transition from stimulus intensity to target detection in the direct report task.

Table 1. Peak EPs of +family models as displayed in Figure 3[a]

	Matching task			Direct report task		
	Intensity	P(detection)	Detection	Intensity	P(detection)	Detection
P50	100.00 (43)	0.00 —	0.00 —	100.00 (56)	1.26 (41)	0.00 —
P100	99.92 (102)	96.95 (135)	17.53 (119)	100.00 (66)	50.91 (76)	30.75 (111)
N140	99.97 (123)	34.12 (152)	71.96 (156)	34.61 (133)	78.73 (111)	99.87 (145)
P300	85.64 (482)	99.99 (393)	16.54 (262)	98.74 (307)	57.48 (453)	99.96 (578)

[a] The maximum model EPs within time points best explained by the +family in components of interest are presented for the matching task and the direct report task: P50 (40-60 ms, CP4), P100 (60-140 ms, CPz), N140 (100-160 ms, C6), and P300 (200-600 ms, CPz). Peak EPs are displayed along with the latency at which they occurred [% (ms)]. Where a maximum EP occurred repeatedly within a component, the earliest corresponding latency is noted.

across electrodes. Instead, it was dominated by the intensity model in contralateral electrodes and the detection probability model in midline and ipsilateral electrodes (see Fig. 5*A*).

The control experiment using a direct report task showed similar effects in the early components but marked differences in the late components (Fig. 3*B*; Table 1). As in the matching task, the P50 and P100 were modulated by stimulus intensity and the N140 showed an effect of target detection. Interestingly, in the direct report task, the detection effect in the N140 dominated the entire component, without a preceding effect of stimulus intensity. However, the most striking difference was seen in the P300 component. While the early phase of the P300, starting at ~200 ms, was best explained by the intensity model, its later phase, starting at ~350 ms, showed a sustained effect of target detection with an EP as high as EP$_{\text{det}}$ = 99.96% (compare Table 1). Previous studies have shown that the P300 can be subdivided into an earlier, frontocentral P3a and a later, centroparietal P3b (Yamaguchi and Knight, 1991; Polich, 2007). In visual awareness, these subcomponents are assigned different roles: while the P3a is considered an automatic response that can occur nonconsciously, the P3b is commonly discussed as a candidate marker of awareness (Muller-Gass et al., 2007; Dehaene and Changeux, 2011; Boncompte and Cosmelli, 2018). The transition from physical to perceptual processing stages observed here is, in principle, compatible with this distinction, showing that detection effects occur in the later phase of the P300 (>350 ms, P3b). However, the corresponding effect topographies suggest that the transition from intensity to detection effects occurred similarly across the P300 electrode cluster, with no clear shift from frontocentral to centroparietal electrodes, leaving it somewhat unclear whether the observed effects truly reflect P3a and P3b, respectively (see Fig. 5*B*).

To further inspect the different detection effects in the two tasks, we plotted grand-averaged subsamples of hit and miss trials that were matched for intensity levels (for details, see Fig. 4*A*).

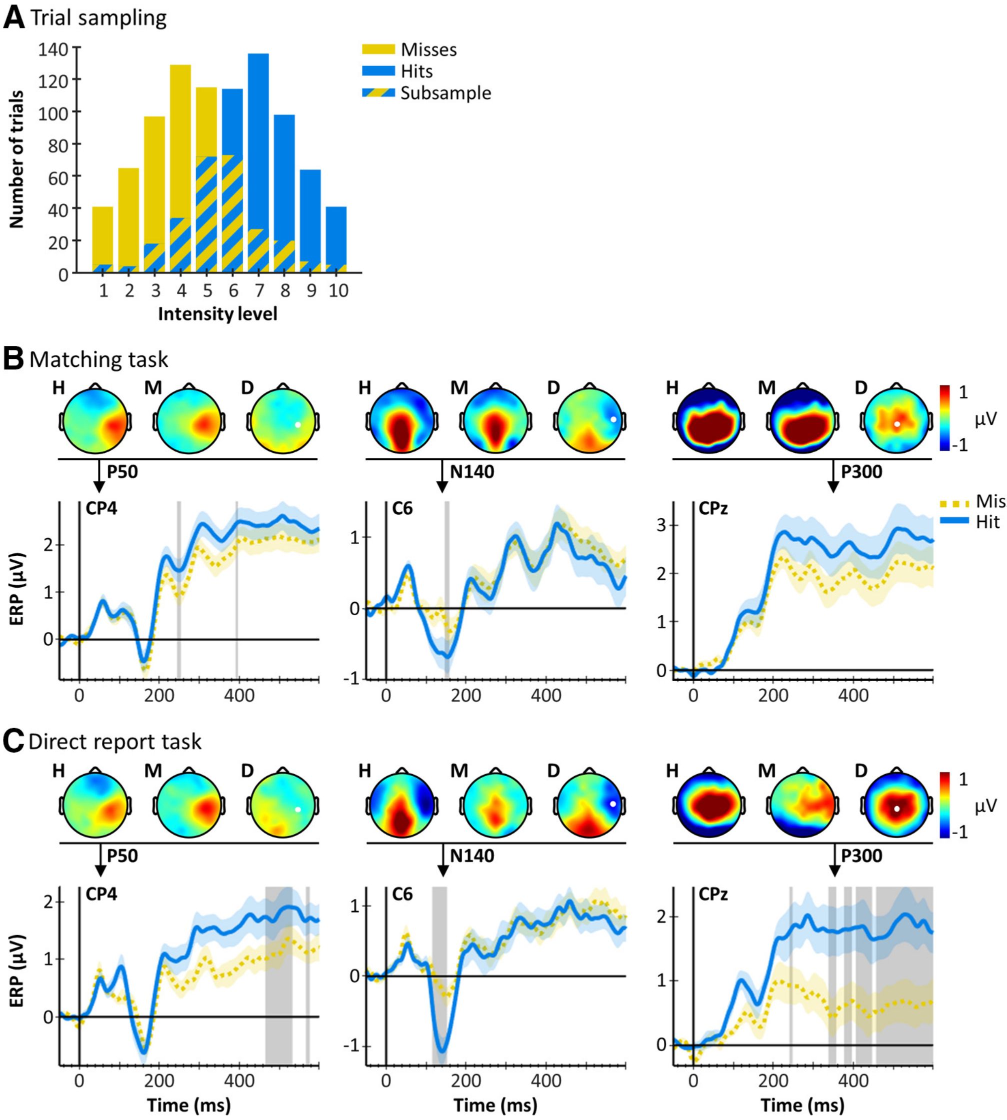

Figure 4. Intensity-matched hit and miss ERPs. ***A***, Trial distributions are shown for one exemplary participant. Lower-intensity levels resulted in more miss trials (yellow), whereas higher-intensity levels resulted in more hit trials (blue). To obtain intensity-matched subsamples of hit and miss trials, for each intensity level, we determined the number of trials obtained per condition and sampled as many trials from the condition with more trials as available for the condition with fewer trials. The subsampled trials (overlap) were then pooled across intensity levels to obtain a hit and a miss pool with identical intensity distributions. ***B***, Hit and miss ERPs (mean ± SE) in the matching task and (***C***) in the direct report task. Topographies for hits (H), misses (M), and their difference (D) are displayed for time points of interest (indicated by black arrows). Gray shaded areas represent time points that were best explained by the detection model. The P50 was not modulated by target detection in either task, whereas the N140 exhibits larger amplitudes for hits compared with misses in both tasks. The P300 shows a large difference between hits and misses in the direct report task but not in the matching task.

The resulting ERPs and corresponding scalp topographies showed no difference between hits and misses in the P50 component, further confirming that early EEG signals reflect processing of physical stimulus properties (Fig. 4*B*,*C*). The N140, on the other hand, showed a clear amplitude enhancement for hits compared with misses; and this effect was apparent in both experiments, although in the matching task, the detection model only dominated the model comparison in a later time window. In contrast, the P300 clearly reflected the different BMS results in late time windows. In the matching task, hits and misses elicited similar P300 amplitudes, whereas in the direct report task, hits elicited much larger P300 amplitudes than misses, resembling the commonly reported P300 detection effect. Please note that these results represent only a small subset of trials that was largely dominated by near-threshold stimuli (which are susceptible to near-threshold confounds, e.g., the focus of attention and general alertness). For this reason (and to avoid circular analysis), we did not perform any further statistical tests on these data. Nonetheless, this way of looking at the results helps to better understand the evolution of detection effects observed in the BMS results. For example, looking at the intensity-matched hit and miss ERPs in electrode CPz, the late detection effect in the direct report task appears to emerge as early as 200 ms (compare Fig. 4*C*). However, the BMS results indicate that the detection effect only started at ∼350 ms, whereas earlier time points were explained by stimulus intensity. This suggests that, although target detection in near-threshold trials seems to have had some effect on the signal already at 200 ms, the intensity model still did a better job at explaining the data at this point and only later, at ∼350 ms, did the detection model become the most dominant. Similar conclusions may be drawn for the early phase of the N140.

Effects across time and space

To obtain a more global impression of the spatiotemporal evolution of model probabilities, we determined the overall model performances across time as defined by the proportion of electrodes

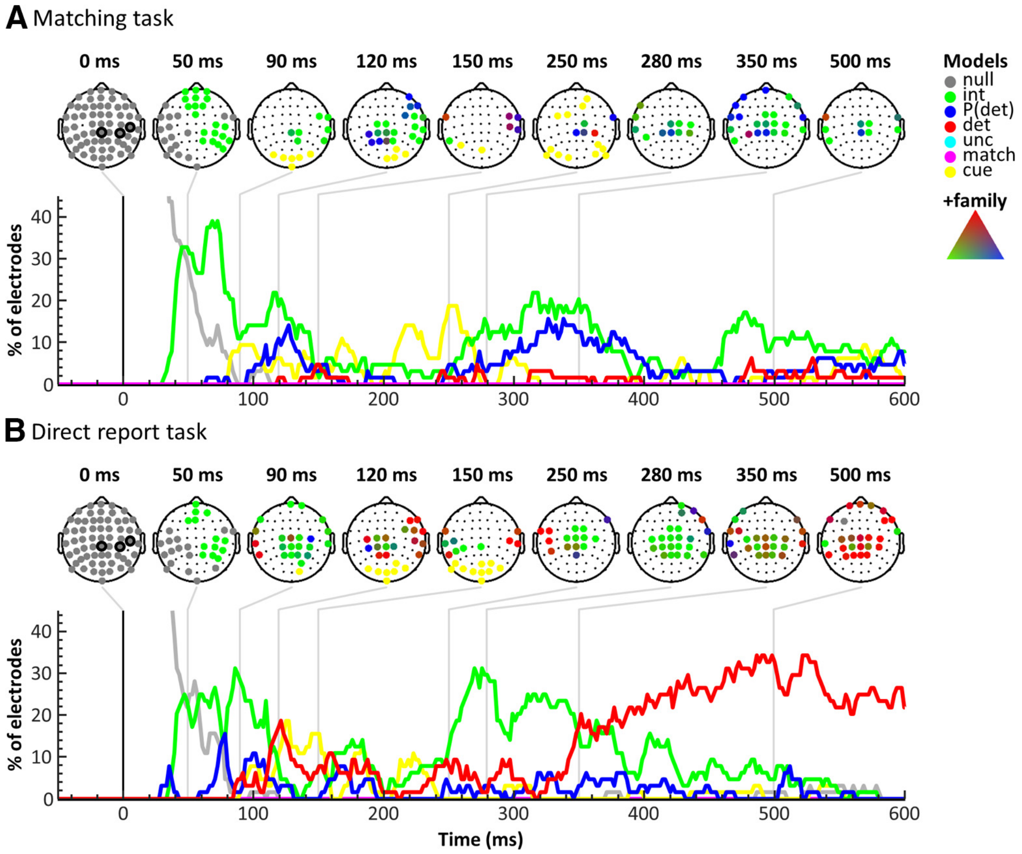

Figure 5. BMS results across electrodes in the matching task (***A***) and the direct report task (***B***). For each task, scalp topographies for time points of interest (top) and model time courses across electrodes (bottom) are displayed. The scalp topographies indicate winning models in electrodes surpassing the threshold criteria using colors as in Figure 3. The circled electrodes at 0 ms represent electrodes CP4, C6, and CPz. Model time courses are plotted as the proportion of electrodes showing above-threshold effects over time. The results suggest a striking reduction of target detection effects (red) in the matching task compared with the direct report task, especially in late time windows >350 ms.

showing above-threshold effects for each model (Fig. 5). As expected, activity in the baseline period was best explained by the null model, validating the specificity of our analysis approach. The intensity model showed similar effects in both tasks: the first clear evidence of somatosensory stimulus processing emerged at ~50 ms, consistent with the P50 response. The BMS topographies at this time point showed a widespread intensity effect in contralateral somatosensory and frontal electrodes, which rotated slightly throughout the following ~100 ms to include more centroparietal electrodes. Then, starting at ~250 ms, a second strong intensity effect occurred, encompassing primarily centroparietal electrodes. The detection probability model first explained the data in the matching task at ~120 ms and showed an additional late effect starting at ~250 ms that paralleled the late intensity effect. Both of these effects showed a centroparietal topography, but the intensity effect occurred primarily in contralateral electrodes, whereas the detection probability effect was mostly found in slightly more posterior midline and ipsilateral electrodes. In the direct report task, the detection probability model showed several smaller peaks with similar topographies as the early intensity effect, but across time and electrodes the detection probability model did not explain the data well in this experiment. The detection model showed the most striking difference between the two experiments. In the matching task, the earliest effect of target detection was observed at the N140 latency, and this effect was confined to only two electrodes (C6 and FC6) and a brief period of time. Likewise, detection effects in later time windows were sparse with only very brief effects in isolated electrodes. In contrast, in the direct report task, the earliest detection effect occurred at ~90 ms in ipsilateral temporal electrodes, followed by a more widespread detection effect in contralateral central and frontal electrodes at ~120 ms (including the N140) and yet another effect at ~250 ms in ipsilateral central electrodes. Finally, from ~350 ms onwards, a large centroparietal electrode cluster reflected target detection throughout the rest of the time window. These results suggest a striking difference between the two tasks, with a widespread centroparietal detection effect at ~350 ms in the direct report task that was virtually absent in the matching task. Surprisingly, neither the uncertainty nor the match model scored high EPs in either task, and this lack of effects was unaltered by inspecting later time points or data segments that had not passed the threshold criteria. However, we found effects of the matching cue in both tasks, starting at ~90 ms in occipital electrodes. In the matching task, this effect lasted slightly longer (until ~300 ms) and encompassed frontal and parietal electrodes. This difference was unsurprising given that further processing of the matching cue was vital to the matching task but not to the direct report task.

Discussion

In this study, we scrutinized the relevance of early and late ERP components as markers of somatosensory awareness. Both in a revised detection task that used a matching procedure to control for report requirements and a control experiment with direct reports, the somatosensory P50 component was modulated by physical stimulus intensity, confirming Hypothesis 1. The N140 was modulated by target detection in both tasks, although in the matching task, this modulation occurred later and was preceded by an effect of stimulus intensity, such that Hypothesis 2 was only partly confirmed. The P300 was clearly task-dependent, showing a widespread detection effect in the direct report task that was largely absent in the matching task, when report requirements were controlled for. These results confirmed Hypothesis 3 and suggest that the P300 is not a reliable marker of somatosensory awareness but reflects postperceptual processing.

The intensity effect observed in the P50 component replicates a recent ERP study that has similarly shown scaling of the P50 amplitude with stimulus strength (Forschack et al., 2020). More generally, our finding concurs with research showing that early stimulus processing in primary somatosensory cortex does not differentiate between detected and undetected stimuli but reflects physical stimulus properties in both humans (Schröder et al., 2019) and macaques (de Lafuente and Romo, 2005, 2006). We thus add to the growing consensus that very early sensory potentials index preconscious processing (Railo et al., 2011; Wühle et al., 2011; Rutiku et al., 2016; Forschack et al., 2020) and support the notion that initial feedforward processing in early sensory regions is not sufficient for conscious perception (Lamme, 2006).

The degree to which early negativities are task-dependent is not well understood. Here, the somatosensory N140 component was modulated by target detection even when postperceptual requirements were controlled for, corroborating its relevance for somatosensory awareness (Schubert et al., 2006; Zhang and Ding, 2010; Auksztulewicz et al., 2012; Auksztulewicz and Blankenburg, 2013; Al et al., 2020; Forschack et al., 2020). However, the BMS analysis revealed that, in the matching task, the N140 was first modulated by stimulus intensity before transitioning to an effect of target detection. Conversely, the N140 in the direct report task was exclusively modulated by target detection, suggesting that the different task demands had a considerable influence on the component's timing and distribution. Indeed, the N140 has previously been reported to be modulated by exogenous attention (Mena et al., 2020). The matching task enforced a reduction of poststimulus attentional engagement compared with the direct report task, which may have resulted in the reduced detection effect. This finding could have important implications for the interpretation of awareness-related negativities in general. Similar to the visual awareness negativity (Koivisto and Grassini, 2016) and auditory awareness negativity (Giani et al., 2015), the N140 has been suggested to result from recurrent interactions between sensory cortices (Auksztulewicz et al., 2012). Accordingly, these potentials have been taken as evidence for the Recurrent Processing Theory of conscious perception, which assumes that perceptual awareness emerges as soon as initial feedforward activity in sensory cortices is consolidated by re-entrant feedback (Lamme, 2006). Indeed, a number of studies have demonstrated detection-related feedback signals from secondary to primary somatosensory cortex in humans (Jones et al., 2007; Auksztulewicz et al., 2012; Auksztulewicz and Blankenburg, 2013), mice (Kwon et al., 2016; Yang et al., 2016), and macaques (Cauller and Kulics, 1991), supporting the role of local recurrent processing for somatosensory awareness. Our results are in principle compatible with Recurrent Processing Theory, but they also suggest that at least part of the awareness effects routinely reported at the N140 latency may be due to uncontrolled processes; and more direct manipulations of attentional allocation are necessary to elucidate this issue.

The P300 has previously been demonstrated to depend on report requirements in visual tasks (Pitts et al., 2014; Cohen et al., 2020; Schlossmacher et al., 2020), and we show that the same is true in the somatosensory modality. In opposition to early negativities, the P300 has been taken as evidence in support of the Global Neuronal Workspace Theory. Global Neuronal Workspace Theory assumes that any conscious percept presupposes a nonlinear "ignition" of global workspace neurons that are distributed across a network of brain regions, primarily in frontal and parietal cortices (Dehaene and Naccache, 2001). Given that several studies have now shown that the P300, often considered a hallmark of ignition (Dehaene and Changeux, 2011), vanishes in no-report paradigms, some researchers have suggested that early activity may reflect general "information accessibility," whereas late activity reflects proper "conscious access," which might be lacking when perception is not reported (Mashour et al., 2020). However, this explanation is not compatible with our results, since we show that a P300 can be elicited regardless of conscious access, further corroborating its postperceptual nature. Alternatively, one might argue that, because attentional resources had to be divided between the somatosensory and visual inputs in the matching task, the attention allocated to the electrical stimuli was not sufficient for them to truly become conscious, such that they remained "preconscious" (Dehaene et al., 2006). However, both the somatosensory and visual stimuli were highly relevant to the task, making it unlikely that attention was withdrawn to the point that the electrical pulses were prevented from becoming conscious. Moreover, we did not find any differences in psychometric functions between the experiments, which one might expect if they differed in their levels of conscious processing. Thus, although we cannot entirely exclude the possibility that there were subtle differences in perceptual experience between the two tasks, the task requirements and behavioral data lead us to believe that the electrical targets were indeed consciously perceived in both tasks, especially given that many of them were presented at superthreshold intensities. Our findings concur with results from fMRI studies showing that frontoparietal network activity does not correlate with conscious access when reports are controlled for (Frässle et al., 2014; Farooqui and Manly, 2018; Schröder et al., 2019). The apparent absence of any sign of ignition in these studies seems to suggest that such widespread, nonlinear activity may not be as relevant for conscious perception as postulated by Global Neuronal Workspace Theory. However, we must note that such findings do not necessarily invalidate the role of frontal or parietal regions for conscious perception, since univariate EEG and fMRI analyses are limited to studying the collective activity of large populations of neurons. It may well be that smaller assemblies or patterns of neurons in these regions correlate with awareness even when task demands are controlled for (see e.g., Kapoor et al., 2020). Nonetheless, research such as ours certainly suggests that the correlates of perceptual awareness are much more subtle than often claimed and that findings from studies showing large signal divergences for conscious stimuli without properly controlling for task demands cannot unreservedly be taken as evidence for any theory of conscious perception (Pitts et al., 2014; Tsuchiya et al., 2015).

Given the ubiquity of the P300 in studies on perceptual awareness, it is worth considering which cognitive variables are its most likely generators and should therefore be most rigorously controlled. In a recent review, Verleger (2020) argues that stimulus-response-link reactivation, memory storage, and closure of cognitive epochs are the most relevant candidates. In both our tasks, timing cues indicated the exact moment of a potential stimulus delivery and, thus, controlled for closure of cognitive epochs. However, the two tasks clearly differed in their control of stimulus-response-link reactivation and memory storage, which may have caused the different results. In the series of no-report experiments conducted by Pitts and colleagues (Pitts et al., 2014; Cohen et al., 2020; Schlossmacher et al., 2020), the stimuli of interest were not relevant to the task, such that none of the processes in question were initiated upon stimulus perception and no P300 was elicited. In contrast, Sanchez et al. (2020) used a go/no-go paradigm with response reversals and were able to decode target detection from late MEG activity. However, because of unpredictable stimulus timing and a response delay, their task was not controlled for closure or working memory effects, which may have caused the late effects. Koivisto et al. (2016) used a similar task but incorporated timing cues and speeded responses, leading to better control of closure and memory effects, and they found a modulation of the P300 by reports. However, the same task in the auditory modality did not reveal any effect of reports on the P300 (Eklund et al., 2019). Whether this discrepancy reflects genuine differences between modalities or results from residual task confounds remains to be tested.

Although the P300 in our study was clearly affected by report requirements, it did not correlate with reports in the matching task. Indeed, the match and uncertainty models did not explain any segments of the EEG data in either task. Possibly, the anatomic locations of regions previously found to show such effects (on the medial wall inside the longitudinal fissure or folded deeply into the cortex) (Schröder et al., 2019) prevented strong influences on the overall EEG signal, leading the respective effects to go unnoticed or, alternatively, signals related to uncertainty and matching reports may not have been time-locked to the stimuli. Whatever the reason, since both perceptual uncertainty and overt reports were controlled for in the matching task, the observed detection effects were free of these confounds (for a more extensive discussion of this point, see Schröder et al., 2019). Instead of reflecting overt reports, the P300 in the matching task was best explained by the intensity and detection probability models, potentially suggesting that neither of these models perfectly accounted for the trial-to-trial response variations in this component. A potential interpretation may be that these models captured variability related to the perceptual quality of the stimuli, which is expected to covary with stimulus intensity, at least for detected targets. The goal of our study prohibited subjective awareness ratings, but a previous study has indeed demonstrated that the N140 and P300 amplitudes correlate with graded awareness levels (Auksztulewicz and Blankenburg, 2013). Assuming a graded nature of awareness (Overgaard et al., 2006) might also explain why the effects of categorical target detection were so limited in the matching task. Interestingly, in our fMRI study using the same task (Schröder et al., 2019), effects of stimulus intensity and detection probability were limited to areas in primary and secondary somatosensory cortex. Whether the late signals observed here also originate from these regions remains to be established.

In conclusion, our study demonstrates that conscious access of somatosensory information is not reflected in widespread cortical activation as indexed by the P300 but instead seems to manifest in earlier, locally restricted activity over somatosensory regions. The generally sparse effects of categorical target detection in our study speak against global, nonlinear effects of conscious somatosensory perception. Indeed, focusing on large signal divergences for perceived versus unperceived stimuli may be misleading as they seem to emphasize postperceptual processing rather than perceptual awareness. Our study further stresses the need for carefully controlled experimental paradigms to be able to unequivocally attribute observed effects to stimulus awareness and effectively further our understanding of the neural processes supporting the emergence of conscious perception.

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Author contributions

Declaration pursuant to Sec. 7 (3), fourth sentence, of the Doctoral Study Regulations regarding my own share of the submitted scientific or scholarly work that has been published or is intended for publication within the scope of my publication-based work

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III. Explanation of own share of these works:

Regarding II. 1.: Study conceptualisation and design (vast majority), programming of task (all), data collection (vast majority), data analysis (all), discussion of results (vast majority), writing/revising the manuscript (vast majority)

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Eidesstattliche Erklärung

Hiermit versichere ich,

- dass ich die vorliegende Arbeit eigenständig und ohne unerlaubte Hilfe verfasst habe,
- dass Ideen und Gedanken aus Arbeiten anderer entsprechend gekennzeichnet wurden,
- dass ich mich nicht bereits anderwärtig um einen Doktorgrad beworben habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze, sowie
- dass ich die zugrundeliegende Promotionsordnung vom 08.08.2016 anerkenne.

Berlin, 02. Mai 2021

Pia Schröder

Curriculum Vitae

For reasons of data protection, the Curriculum Vitae is not included in the public version of this thesis.