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# Spatio-temporal localization and task specificity in the search for neural correlates of perceptual consciousness

PhD dissertation

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Health
Aarhus University
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# Preface

Why investigate the neural correlates of perceptual consciousness? Why just in the visual domain when the underlying question is: what is consciousness?

Let's take the story back about 10 years. I was about to begin my studies of philosophy here at Aarhus University where I now also submit my thesis for defence. It might seem as a weird choice to study philosophy given that I had received a diploma from my *gymnasium* for being the best mathematical student of the year, but the questions that attracted me were of a grander scale; the aforementioned: what is consciousness? or with more philosophical vocabulary: how do we solve the mind/body problem?, but also the linked questions: what is knowledge and how do we acquire it? Getting introduced to distinguished thinkers of the likes of René Descartes, David Hume and Immanuel Kant, their insights on these questions did nothing more than strengthen my aspirations towards understanding consciousness and the nature of knowledge. The first bigger project I was involved in during my studies of philosophy was about how the mind/body problem could be resolved, giving an explanation of how something mental and subjective, our minds, can exist in an otherwise material world.

To cut this story a little shorter, I will cut to the chase. Sure, we were introduced to interesting modern findings and anecdotes about the study and the complexities of the mind, such as chicken sexers, blindsight patients and invisible gorillas, but I grew tired of waiting around for the next cool experiment to show up. I wanted to do it myself. Therefore, I went to the Netherlands to get a Master of Science in Brain and Cognitive Sciences where I realized that the only feasible experimental way to study the grand, underlying question is by meticulous study of all the cogs and wheels of the brain. One such important cog is the study of perceptual consciousness understood as what processes of the brain allow us to enjoy subjective experiences of the sensory information that constantly impinge on our bodies. I am very happy about having this opportunity to submit my investigation of this important cog, namely the investigation into the realization of visual subjective experience, to a committee of specialists.

I try to answer a few but important questions that can be asked about perceptual consciousness, such as how perceptual consciousness should be measured and how brain states may be classified according to their level of perceptual consciousness, and whether there do exist unique neural spatio-temporal correlates of perceptual consciousness, or whether the cognitive context partly determines what neural spatio-temporal correlates we find.

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# Introduction – setting the stage

> “But what then am I? A thing that thinks. What is that? A thing that doubts, understands, affirms, denies, is willing, is unwilling, and also imagines and has sensory perceptions.” (Descartes, 1985, p. 19)

In this quotation, Descartes concludes that he is a thinking thing, *res cogitans*, that, crucially for this dissertation, among other things has sensory perceptions that ultimately owe their existence to material things, *res extensa*. It is clear, however, that *res cogitans* is not only a passive recipient of sensory input, but that it also is an active thing that doubts, understands, denies, is willing, is unwilling and imagines; processes that with more modern language can be called cognitive processes. Descartes (in)famously argued that *res cogitans* and *res extensa* are metaphysically two separate things, thus in effect separating mind and body wholly from one another. He was, however, never able to argue convincingly how they were able to interact, which everyone experiences that they do on a daily basis. How mind and body interact vexed many following great philosophers. Leibniz, Hume, Berkeley, Kant and many others all tried to *theoretically* bridge *res cogitans*, mind, and *res extensa*, body, and explain how they interact, but none gave a satisfying account.

It was not until the late 19th century and early 20th century that *experimental* psychology started flourishing, but the predominant experimental attitude was that of behaviourism wherein the mind was seen as a black box. What mattered were the dependencies between stimuli and responses. What happened in between could not be observed, and there was thus no need for a link between mind and body. Putative mental explanations of why an organism responded as it did were argued to be redundant, notably reflected in this quote by Skinner:

> “A single set of facts is described by the two statements: “He eats” and “He is hungry.” A single set of facts is described by the two statements: “He smokes a great deal” and “He has the smoking habit.” A single set of facts is described by the two statements: “He plays well” and “He has musical ability.”” (Skinner, 1965, p. 31)

This reduces the study of the mind to observable behaviour, which for all practical purposes reduces mind to body. Skinner was right to emphasize that many mental explanations were redundant, but what he could not foresee was how the advance of technology would make it possible to investigate in great detail what the black box consists of. This technology opens for the possibility to investigate *perception*, understood as occurring in between the sensation of a stimulus and the response made on that stimulus. Crucially, these advances allow one to investigate the processes behind perception and not just restate observable behaviour in mental terms, as Skinner rightfully objected to. The state-of-the-art technologies, among others, include magnetic resonance imaging (MRI: Lauterbur, 1973), with which changes in blood flow can be used to localize which brain regions are active and electro- and magnetoencephalography (EEG: Berger, 1929; MEG: Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993), with which electrical potentials and magnetic fields produced by neurons in the cortex can be measured on the scalp. The advent of these brain imaging and brain recording technologies not only made it possible to investigate the processes of the brain that mediate stimulus-response dependencies, but also potentially the processes that are associated with the presence and absence of conscious perception. This may provide a first step into understanding how mind and body can be bridged since consciousness is regarded as an archetypical mental phenomenon (Chalmers, 1997; Nagel, 1974).

A necessary first step is to define what I mean by consciousness and specifically what I mean by perceptual consciousness. Consciousness can be characterized as an umbrella term, a term that incorporates several meanings. An important distinction is between state consciousness and consciousness of content. Different bodily states are associated with differing levels of consciousness. Everyday examples are the differences between being asleep and awake or between being sober and intoxicated. More clinical examples of altered states of consciousness are those of being comatose or vegetative. These different states alter the repertoire of responses that an organism have available, and what cognitive operations it can undertake (Laureys, Owen, & Schiff, 2004). In the present dissertation, however, my emphasis will be on consciousness of content, and specifically content derived from the senses. I forthwith use “perceptual consciousness” to mean consciousness of content. When a stimulus impinges on the sensory modalities of an organism, the perceived content may differ even when the conscious state, as discussed above, is constant. It may differ between organisms; for example young humans can hear a wider spectrum of pitches than old humans can. Crucially, perceived content of otherwise identical stimuli may also differ between trials within a participant. In the simplest example, on some trials a participant may claim that he did not consciously perceive presented stimuli whereas on otherwise identical trials he may claim that he did consciously perceive the stimuli. If the physical circumstances are identical, and only the perceived content differs, then by contrasting brain activity from trials with conscious perception with brain activity from trials with no conscious perception it should in theory be possible to find the neural correlates of perceptual consciousness, or in other terms make the brain processes of perceptual consciousness available for investigation. It is important to recognize that seen from a Cartesian viewpoint, it is only a small sub-component of the mind, *res cogitans*, that one studies when one studies perceptual consciousness, namely that of sensory perception. The investigation of this sub-component, perceptual consciousness, may follow one of two courses, one where it is seen as *non-integrated* with other cognitive processes of the mind, and one where it is seen as *integrated* with other cognitive processes of the mind, what I will call the *cognitive context*. Both these proposals are very distinct from Descartes' suggested neural correlate of consciousness, the pineal gland. Activity in the pineal gland, from the Cartesian viewpoint, is seen as the *general* neural correlate of consciousness understood as correlating with any of the above processes, such as affirming, denying, imagining *et cetera*. Even when restricting ourselves to investigating *perceptual* consciousness understood as what is related to what Descartes called sensory perception, we in theory have, at least, 3 levels of neural correlates of *perceptual* consciousness that we could design experiments for unravelling. Firstly, a *general* neural correlate of perceptual consciousness that would encompass all sensory modalities, secondly, *specific* neural correlates of consciousness for each sensory modality and thirdly, *cognitive context dependent* neural correlates for each sensory modality (Figure 1).

## Deciding between levels of description

*A priori* there is no way one can determine which level matches reality the best, and because of the apparent hierarchical relationship between the levels, interpretations as to what different experimental results indicate will differ greatly. Compared to a given level, then from any level higher in the hierarchy, differences between sub-divisions at the given level of the hierarchy will be seen as sources of noise rather than sources of signal. For example, from the level that there exists a unique *general* neural correlate across sensory modalities, any *specific* differences between modalities will be seen as noise, and the emphasis will be on unravelling what is common across modality specific differences. Similarly, from the level that there exists a unique *specific*, say, visual neural correlate of consciousness, any *cognitive context dependent* differences will be seen as noise, and the emphasis will be on unravelling what is common about visual correlates across differences in cognitive context. Logically speaking, there is no final experiment that can decide at which level one should expect to find neural correlates of perceptual consciousness. Despite the differences one might find between specific sensory modalities, a proponent of a general neural correlate may always, with no logical fault, insist that one simply has not searched thoroughly enough for what is common across the sensory modalities. The same goes for a proponent of there existing specific neural correlates of consciousness for a given modality, who similarly, with no logical fault, can insist that any cognitive context dependent differences obscuring the common correlate for that modality is just a consequence of not having searched thoroughly enough. Conversely, seen from a lower level in the hierarchy, there is no logical reason that the higher levels should encompass anything common about the levels just below them. It is important to recognize that whatever level one believes that perceptual consciousness should be studied from carries a set of assumptions that determines how one will interpret the outcomes of experiments. To sum up, a modality dependent viewpoint, what I in this dissertation call a *non-integrated* viewpoint (Figure 1: middle level), thus has the theoretical consequence that there must exist unique neural correlates of perceptual consciousness, independent of changes in cognitive context, whereas a context dependent viewpoint, what I in this dissertation call an *integrated* view, has the theoretical consequence that neural correlates of perceptual consciousness may differ between different cognitive contexts (Figure 1: lower level).

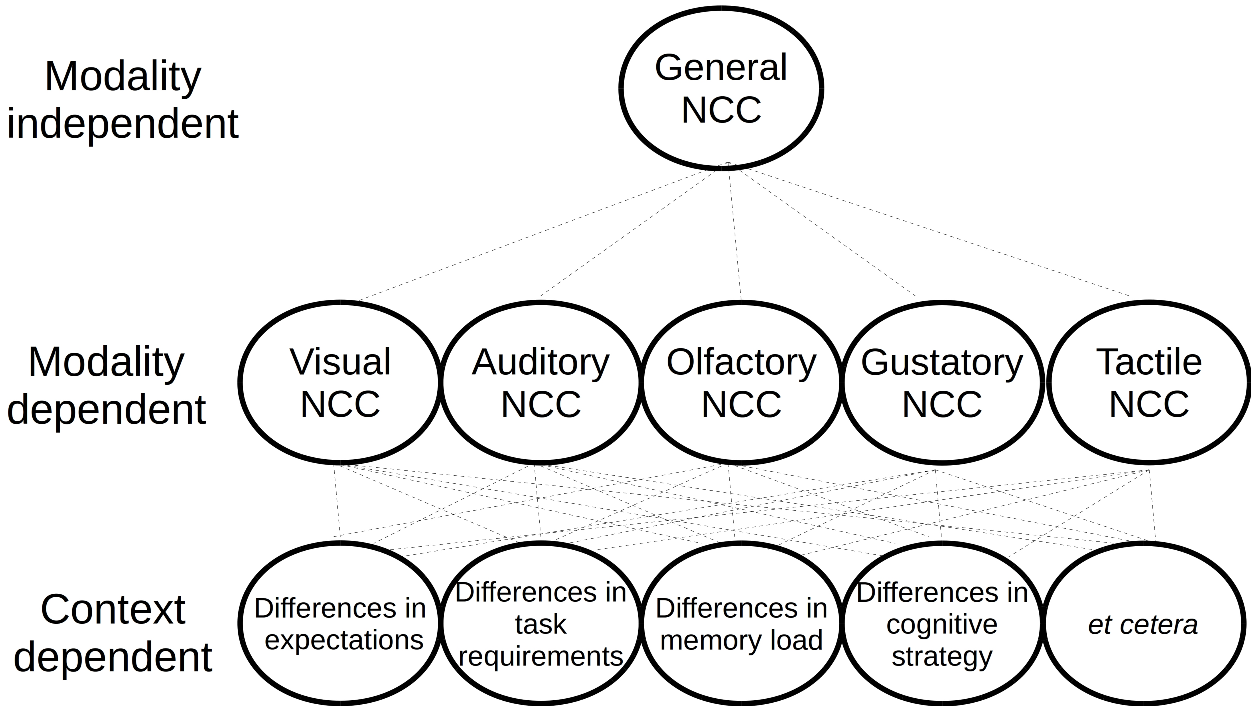


**Figure 1:** Different levels of neural correlates of perceptual consciousness: theoretically, there can be at least 3 levels of neural correlates of perceptual consciousness (NCC). A modality independent NCC, which is independent of sensory modality. A modality dependent NCC, which varies dependent on which sensory modality is investigated. Finally, NCC's can be dependent on cognitive context, thus for any sensory modality, one would expect that NCC's may differ across differences in context.

Before this distinction can be discussed in greater detail and in terms of experiments, an understanding of how perceptual consciousness can be behaviourally operationalized is necessary.

First, however, an outline of the remaining part of the dissertation will be presented.

## Outline of the dissertation

In this dissertation, I will review and discuss how perceptual consciousness best can be measured. This will be followed by a discussion of what EEG and MEG studies have revealed about brain activity correlating with changes in perceptual consciousness. An introduction into how one may expect differing results dependent on whether one sees perceptual consciousness as integrated with cognitive context or not follows. I will then present and summarize the 3 experimental studies that this dissertation is based on. A methodological paper that I co-authored is also included in the summary, which forms parts of the basis of 2 of the experiments. In the discussion, I will argue that these studies indicate how an integrative view of perceptual consciousness and cognitive context is preferable to a non-integrative view. These results make it possible to hone in on how the brain connects the seemingly two disparate kinds of things that Descartes envisioned were connected by the pineal gland.

# Background

## Perceptual consciousness

### Behavioural methods for separating conscious and non-conscious trials

A necessary step for elucidating the brain processes behind perceptual consciousness is designing behavioural experiments that can optimally separate conscious trials from non-conscious trials. 2 main strands, an *objective* and a *subjective*, are present in the literature. In the objective strand, trials are separated into conscious and non-conscious trials by performance. For example, if the proportion of correct responses for a simple detection task is not significantly different from chance-level performance, or alternatively that sensitivity (*d*') (Macmillan & Creelman, 2005) is not significantly different from zero, this is taken as absence of perceptual consciousness whereas above chance-level performance or above-zero sensitivity is taken as presence of perceptual consciousness (Hannula, Simons, & Cohen, 2005). Using signal detection analyses, it is also possible to separate sensitivity (*d*') from criterion (*c*), the bias a participant has towards a response, which is something that can be problematic for subjective approaches, as discussed below. A potential problem with objective approaches is that it seemingly assumes a dichotomous view of perceptual consciousness, either performance is different from chance or it is not. Furthermore, because it is only possible to measure performance as different from chance when trials are summarized over conditions, it is impossible to have physically identical conscious and non-conscious trials. This is a real problem because it results in physically induced differences in the electrophysiological components that may correlate with perceptual consciousness as shown by Fisch et al. (2009).

On the other hand, using subjective ratings of perceptual consciousness, it is possible to group single trials as participants indicate. This has the further consequence that one is not restricted to a dichotomous view of consciousness, but can ask participants to rate perceptual consciousness using however many rating points the experimenter please. For example, subjective scales with 21 points (Sergent & Dehaene, 2004), 7 points (Nieuwenhuis & de Kleijn, 2011), 4 points (Ramsøy & Overgaard, 2004) and 2 points (Lau & Passingham, 2006) have all been used. It is not only heavily debated how many points should be used, but also how participants should categorize their experiences according to the points available. There are at least three ways often used: either the participant is asked for how clearly he saw the stimulus (Ramsøy & Overgaard, 2004), how confident he is that he answered correctly (Rademaker, Tredway, & Tong, 2012) or how much he would bet on being correct (Persaud, McLeod, & Cowey, 2007). A potential problem with subjective scales is that there is no principled way of estimating the criterion of a participant (Hannula et al., 2005). One participant might use a liberal criterion; whenever he sees the slightest signal, he rates it as conscious. Another participant might use a conservative criterion; he only rates it as conscious whenever he sees a very clear signal. This problem is only multiplied when there are more than 2 points on a rating scale. For example, using a 7-point scale, said colloquially, one man's rating of 3 might be another man's rating of 5.

In the studies of this dissertation, we have used the Perceptual Awareness Scale (Ramsøy & Overgaard, 2004) to let participants quantify their experiences. In the section below, I will argue why this scale might be especially fit for revealing relevant brain processes underlying differences in perceptual consciousness.

## Perceptual Awareness Scale

An intuition that permeates this whole dissertation is that subjective reports of perceptual consciousness must be taken seriously. If doubts linger as to whether participants are using scales in differing manners, then experimenters should not blame the participants. They should rather blame themselves; experimenters need to make sure that participants are comfortable using the scales that they demand they use. To meet these demands, Ramsøy and Overgaard (2004) had participants perform a number of tasks on briefly presented stimuli. They had to indicate either the colour, shape or position of the stimulus. Subsequently participants were to describe, in their own words, their perceptual consciousness of the stimulus, and then throughout the experiment come up with categories that reflected the range of experiences they had. They were suggested that the end points could be *no experience* and *clear experience* respectively. Participants agreed on a 4-point scale with the following rating descriptions: 1: *No Experience*, 2: *Weak Glimpse*, 3: *Almost Clear Experience*, 4: *Clear Experience* (Table 1).

This scale is called the Perceptual Awareness Scale (PAS). What sets PAS apart from many other scales is that the rating points are categorical (Table 1), meaning that the rating points differ qualitatively from one another. Most other scales are purely ordinal such as the 21-point scale that Dehaene endorses (Dehaene, 2014; Sergent & Dehaene, 2004), meaning that the relations between rating points are only qualitative in terms of “more” and “less”. Only the end points are clearly defined, e.g. *zero visibility* and *full visibility.* This leaves a lot open for interpretation for the individual participant regarding where to set the criterion as discussed above (Hannula et al., 2005). PAS leaves less open for interpretation due to its categorical nature. The difference between *No Experience* and *Weak Glimpse* can be defined as whether there was an *experience* of anything at all. The difference between *Weak Glimpse* and *Almost Clear Experience* can be defined as whether there was an experience of *content*. The difference between *Almost Clear Experience* and *Clear Experience* can be defined as whether there was an *unambiguous* experience of content (Andersen, Pedersen, Sandberg, & Overgaard, 2015).

**Table 1:** The Perceptual Awareness Scale (PAS)

| **Label** | **Description (from Ramsøy and Overgaard 2004)** |
|---|---|
| (1) No Experience (NE) | No impression of the stimulus. All answers are seen as mere guesses |
| (2) Weak Glimpse (WG) | A feeling that something has been shown. Not characterized by any content, and this cannot be specified any further |
| (3) Almost Clear Experience (ACE) | Ambiguous experience of the stimulus. Some stimulus aspects are experienced more vividly than others. A feeling of almost being certain about one's answer |
| (4) Clear Experience (CE) | Non-ambiguous experience of the stimulus. No doubt in one's answer |

*Scale steps and their descriptions*

These categorical differences between ratings served as a guideline for instructing participants in the studies in this dissertation. The arguments above for the fitness of PAS to measure perceptual consciousness are all theoretical, and they need to be empirically grounded. Dienes (2007) has suggested two criteria by which perceptual consciousness scales can be judged. Firstly, the stronger the correlation is between ratings of perceptual consciousness and performance, the more *sensitive* the scale is in allowing the participant to rate his perceptual consciousness correctly. Secondly, assuming no unconscious processing, a scale that reveals performance not different from chance when participants claim no experience will be *exhaustive*. Testing *sensitivity* and *exhaustiveness* Sandberg et al. (2010) compared PAS with confidence ratings and post-decision wagering. They found that PAS showed a significantly stronger correlation between accuracy and perceptual consciousness than both the other types of ratings did, indicating that PAS is the most *sensitive* scale of the three. They also found that PAS attributed the least amount of unconscious processing to participants. Given two assumptions, this entails that PAS is the better of the 3 scales in *exhausting* the kinds of experiences participants may have. These two assumptions are: firstly, that the amount of unconscious processing should be independent of the scale used to rate one's experiences; and secondly, that above-chance performance when claiming no experience can partly be a consequence of the scale not being fully exhaustive.

It thus seems that PAS allows for more *sensitive* and *exhaustive* reporting of perceptual consciousness than confidence rating and post-decision wagering do. Committing to PAS, however, furthermore assumes to some degree that one believes that perceptual consciousness is graded. Whether this is so is a hotly debated issue. Classically, perceptual consciousness was operationalized as dichotomous, an all-or-none phenomenon. This was probably a consequence of using objective methods, where performance or sensitivity was either different from chance-level or not, as discussed above. In the very influential global neural workspace theory of Dehaene (2014), perceptual consciousness is argued to be realized in an all-or-none manner. I will now therefore discuss the evidence for and against a dichotomous view of perceptual consciousness.

## Dividing perceptual consciousness

As argued earlier, a dichotomous view of perceptual consciousness follows naturally from operationalizing perceptual consciousness based on objective performance criteria. Using subjective criteria, perceptual consciousness has also been thought of as dichotomous (Lau & Passingham, 2006; Weiskrantz, 1990). In global neural workspace theory (Dehaene, 2014; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006) perceptual consciousness is also seen as a dichotomous phenomenon, where stimuli are either *seen* or *not-seen*. In the experiments that Dehaene and his group use to provide evidence for the dichotomousness of perceptual consciousness, they mostly use a 21-point subjective visibility scale to let participants provide subjective ratings of the stimuli shown (Del Cul, Baillet, & Dehaene, 2007; Sergent, Baillet, & Dehaene, 2005; Sergent & Dehaene, 2004). An advantage of using this scale is that it does not assume that perceptual consciousness is dichotomous, but it might still reveal dichotomous responding. The endpoints of this scale are labelled *not seen* and *maximally visible* with steps of 5 % in between. Sergent and Dehaene (2004) found results on an attentional blink task that provided evidence for perceptual consciousness being dichotomous. The attentional blink (Raymond, Shapiro, & Arnell, 1992) is a phenomenon that occurs when two target stimuli, T1 and T2, are presented rapidly among a series of distractors. As long as one is only required to respond to one of the targets, one almost never misses that target. However, when responding is required to both targets, T2 is often not consciously perceived, presumably due to attention being directed towards T1. Using this task they found that subjective visibility responses clustered around 0 % and 100 % for T2 when participants had to respond to both targets. A concern about using a 21-point scale is that it may not be clear for participants how to use all the points, and criterion setting might differ substantially between participants. Nieuwenhuis & de Kleijn (2011) tested whether the number of points on the rating scale made a difference to the nature of the distribution of visibility ratings. They used a 7-point scale, but otherwise repeated the experiment of Sergent and Dehaene (2004). They found a more graded pattern with a substantial amount of ratings around 50 % visibility. Furthermore, in a subsequent experiment, they introduced a task requirement on T2. T2 was one of 8 digits and participants had to judge which was shown. In the original task, participants just had to judge the visibility of T2, but false alarms were controlled for by using blank T2's on a subset of trials. The task requirements changed the pattern of responses dramatically with participants using all 7 points of the scale for the visibility ratings. These 2 manipulations indicate that the cognitive context has an effect on the ratings of perceptual consciousness.

Furthermore, Sandberg et al. (2010) fitting psychometric curves for both performance and perceptual consciousness as functions of stimulus duration in a masking task found relationships that were significantly different from an all-or-none relationship. An ideal all-or-none relationship would be a step function, but their data heavily supported that perceptual consciousness is not all-or-none. Finally, Overgaard, Rote, Mouridsen and Ramsøy (2006) compared PAS with a dichotomous rating scale in a localization task. Interpreting their results according to the *sensitivity* and *exhaustiveness* criteria discussed earlier (Dienes, 2007; Sandberg et al., 2010), they found both greater *sensitivity*, a stronger correlation between performance and reported perceptual consciousness, and greater *exhaustiveness*, lower above-chance performance for reports of no experience, for PAS compared with a dichotomous scale. Thus, there is good behavioural evidence for PAS being a better fit than other tested scales.

### Informativeness of perceptual states

Another important aspect of this dissertation is an effort of how to best quantify the informativeness of subjective experiences. The informativeness of perceptual states can be construed as what kinds of actions and responses they allow for. I have already discussed that an ideal scale for rating perceptual consciousness should be *sensitive* and *exhaustive* (Dienes, 2007; Sandberg et al., 2010). For a scale to be exhaustive, it should allow participants enough scale points to rate all kinds of conscious experiences they may have, however faint they may be. That means that if there is no unconscious processing of stimuli on a task, participants should perform around chance level when they claim no conscious experience of the stimuli. I here propose that in the absence of unconscious processing, there is a third property, besides sensitivity and exhaustiveness, that is attractive for a scale to have. The informativeness of a state of no conscious experience for a subsequent response, assuming no unconscious processing, should show *cognitive independence* of external and internal differences in cognitive context, such as sensory saliency, top-down expectations, task settings *et cetera*. It is well known that differences in top-down expectations towards stimuli affect response times (Doherty, Rao, Mesulam, & Nobre, 2005), that differences in sensory saliency affect response times (Eriksen & Hoffman, 1972) and accuracy of responses (Sandberg et al., 2010) and that differences in task setting affect response times (Posner & Mitchell, 1967). I propose that if a scale truly is exhaustive, trials where participants report no conscious experience (NE: Table 1) should show *cognitive independence* of external and internal factors if there is no unconscious processing of stimuli. We investigated whether we could find evidence of *cognitive independence* on trials where participants claim to have no conscious experience in Study 3 (Andersen & Tong, in preparation), potentially further strengthening PAS as a scale fit for measuring perceptual consciousness.

With these considerations in mind, I will now focus on prior results based on contrastive analyses, argued to reveal neural correlates of perceptual consciousness and how studies done with PAS may inform the literature on neural correlates of perceptual consciousness even further. When discussing EEG and MEG components, I will discuss some further arguments pertaining to global neural workspace theory that may be taken to indicate that perceptual consciousness is all-or-none.

## Contrastive analyses

Baars (1988) proposed contrastive analyses as a method to elucidate the neural correlates of conscious experience. In terms of perceptual consciousness, the idea is that if objective stimuli are identical across trials while perceived content differs, then any differences in brain activity must be neural correlates of perceptual consciousness. This would, in principle, work for any modality, visual, auditory, olfactory, gustatory or tactile. Crick and Koch (1990), however, suggested that the visual modality would be the most conducive to study because, compared to the other modalities, much was already known about the basics of the visual system and cortex (Polyak, 1957). In this dissertation, I follow Crick and Koch's suggestion and study perceptual consciousness based on visual experimentation. This focus on the visual modality means that I will not consider any possible commonalities across sensory modalities (Figure 1). I will thus only consider possible commonalities across differences in cognitive context (Figure 2).

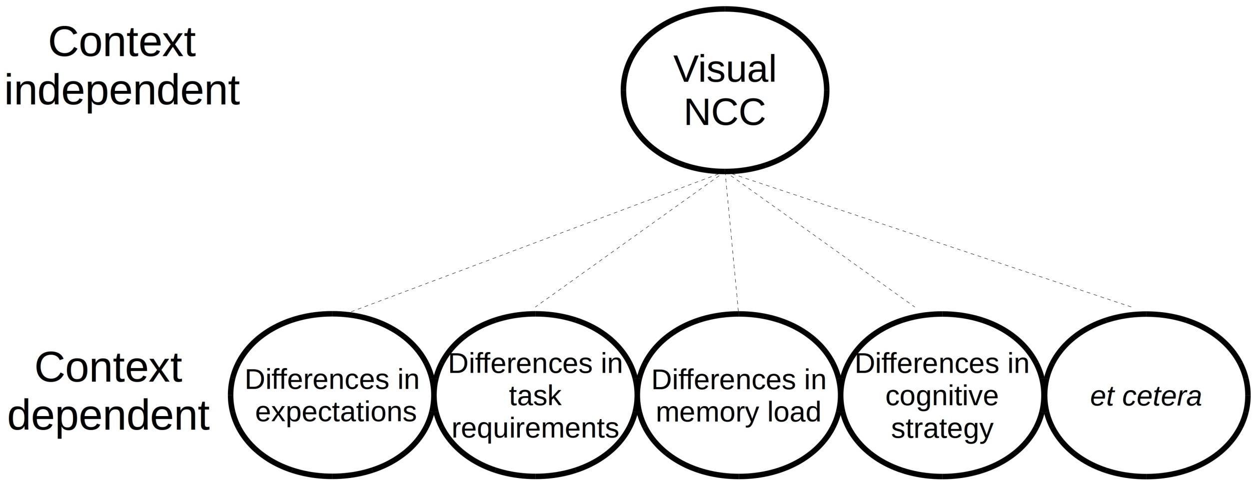


**Figure 2:** The 2 levels of neural correlates of perceptual consciousness (NCC) of main interest in this dissertation: a context independent NCC, which is invariant across differences in cognitive context, and cognitive context dependent NCC's, which vary differ across differences in context.

Examples of early studies of the neural correlates of perceptual consciousness are the studies of ffytche et al. (1998) and of Dehaene et al. (2001). Both studies used functional magnetic resonance imaging (fMRI), but they localized the neural correlates of perceptual consciousness to different ends of the brain, ffytche et al. to the occipital lobe and Dehaene et al. to the frontal lobe. The experimental procedures were very different, however, with ffytche et al. testing patients with the Charles Bonnet syndrome (de Morsier, 1936) and Dehaene et al. testing healthy volunteers.

Setting aside the vices and virtues of the two studies, they are telling of an ever-present debate regarding the neural correlates of perceptual consciousness. Put very roughly, it is a debate of whether the *proper* neural correlates of perceptual consciousness are early, < 300 ms, and occipito-temporally realized or whether they are late, > 300 ms, and fronto-parietally realized [for reviews see Koivisto and Revonsuo (2010) and Rees, Kreiman and Koch (2002)].

## Electro- and magnetoencephalographic studies of perceptual consciousness

In EEG and MEG studies of the neural correlates of perceptual consciousness, there are two usual suspects, N1-N2, < 300 ms, and P3a, > 300 ms, that seem to correlate with perceptual consciousness independently of whether the manipulation of perceptual consciousness was obtained through masking (Andersen et al., 2015; Koivisto et al., 2008), the attentional blink (Koivisto & Revonsuo, 2008; Sergent et al., 2005), change blindness (Koivisto & Revonsuo, 2003) or low contrast stimuli (Pins & Ffytche, 2003). Both N1-N2 (Koivisto & Revonsuo, 2010) and P3a (Dehaene, 2014) have been claimed to be the proper neural correlates of consciousness. For the sake of completeness, it should be mentioned that P1 has also been argued to be a neural correlate of perceptual consciousness (Pins & Ffytche, 2003; Veser, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008), but because it shows up much less consistently than N1-N2 and P3a [for a review, see (Koivisto & Revonsuo, 2010)], I focus on N1-N2, also called the Visual Awareness Negativity (VAN), and P3a in this dissertation (Figure 3A).

Source reconstructions of EEG data have localized the N1-N2 in the occipito-temporal lobes and the P3a to the fronto-parietal lobes (Koivisto & Revonsuo, 2010; Sergent et al., 2005). One position in the literature is that the early occipito-temporal activity is a proper neural correlate of perceptual consciousness, and that the late fronto-parietal activity is further processing of the perceived stimulus, such as loading it into working memory, preparing a motor response based upon it, internally attending to it *et cetera*. (Koivisto & Revonsuo, 2010; Lamme, 2006). Another position is that it is exactly this late fronto-parietal activity that is a proper neural correlate of perceptual consciousness whereas the early occipito-temporal activity reflects perceptual integration of the features of the stimuli (Dehaene, 2014; Sergent et al., 2005). Aru, Bachmann, Singer and Melloni (2012) introduced terminology that is helpful in characterizing this debate. They distinguished between neural *prerequisites* and *consequences* of perceptual consciousness and demarcate these from the *proper* neural correlates of perceptual consciousness. An example of, what in hindsight, can be termed a neural *prerequisite* of perceptual consciousness is the finding of Busch et al. (2009). They presented transient light flashes at participant threshold and categorized responses as hits and misses according to the signal detection framework. They found that hits and misses revealed different phase distributions in the alpha frequency bands *prior* to stimulus onset. They interpreted these differences in phase distributions as probably driven by stochastic fluctuations in neural excitability (G. H. Bishop, 1932). An example of what might be a neural *consequence* of perceptual consciousness is the preparation of a response based on the perceived stimulus (Pitts, Martínez, & Hillyard, 2012).

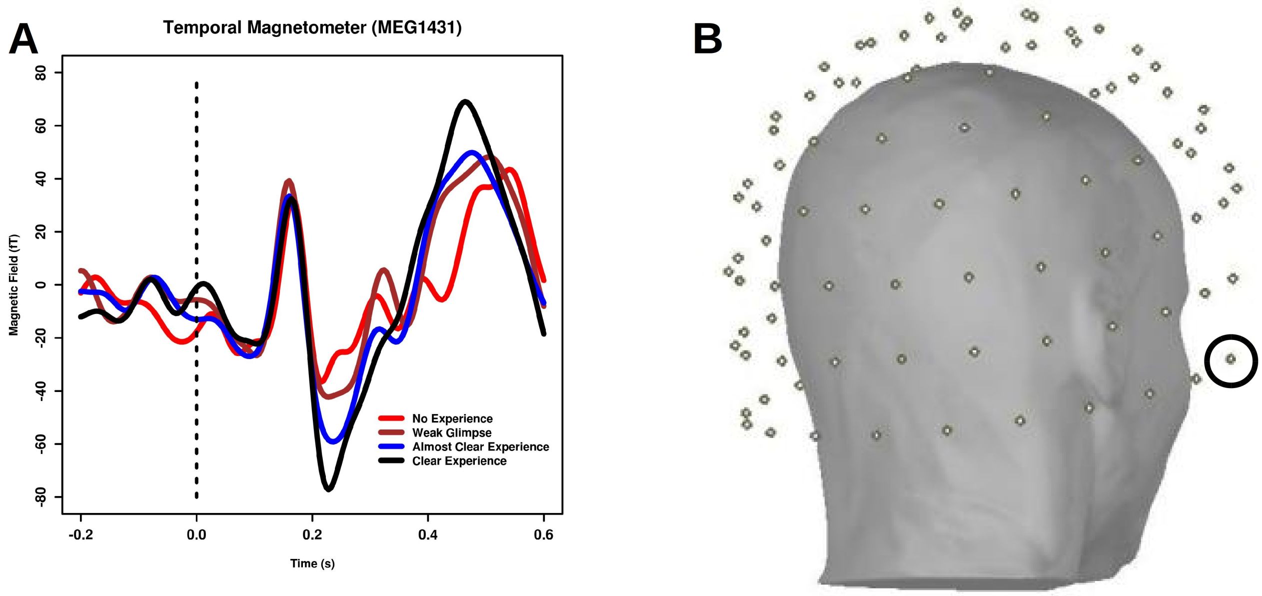


**Figure 3:** A) An example of an MEG response: grand average over 10 participants. Graded differences are visible in the Visual Awareness Negativity Range (130-320 ms), and a less graded difference is present around the P3a (~430 ms). From Study 2 below. B) The positions of magnetometers and gradiometers around the head of an example participant. Encircled is the magnetometer shown in A.

Using this terminology, the debate can be framed as one position (Dehaene, 2014) stating that the late fronto-parietal activity is the *proper* correlate and that the early occipito-temporal activity is a neural *prerequisite* of perceptual consciousness, specifically integration of the perceptual features. The other position states that the early occipito-temporal activity is the *proper* correlate, and that the late fronto-parietal activity is a neural *consequence* of perceptual consciousness.

Integral to global neural workspace theory is that perceptual consciousness is a dichotomous concept and what separates conscious from unconscious processing is a non-linear transition where, through the involvement of fronto-parietal areas, perceptual information is either made globally available, reaching consciousness, or fails to be made globally available, not reaching consciousness. Proponents of global neural workspace theory argue that P3a, the late fronto-parietal component, is the only component that shows the same bimodal character (Del Cul et al., 2007) that, they claim (Sergent & Dehaene, 2004), perceptual consciousness does. I have supplied arguments in an earlier section for why this is probably only the case for very specific paradigms, e.g. the attentional blink but not masking (Sergent & Dehaene, 2004), and even so only when the task related to the blinked target is not too demanding (Nieuwenhuis & de Kleijn, 2011). Instead of trying to resolve the debate as to which component reflects the proper neural correlate of perceptual consciousness by comparing the characteristics of EEG and MEG components and relating them to considerations about how perceptual consciousness can be sliced up, I opted for another way of providing evidence to the debate. Classically, in EEG experiments when one wants to make the argument that component *A*, and not component *B*, is the one that is related to process *P*, one aims at creating an experimental situation where component *B* is dissociated from process *P* while component *A* still shows evidence of association with process *P*. This approach of dissociating components may be infeasible, however, if neural consequences of perceptual consciousness always or mostly follow neural correlates of perceptual consciousness (Sandberg, Andersen, & Overgaard, 2014). Instead of following this road, (but see (Pitts et al., 2012; Pitts, Metzler, & Hillyard, 2014) for a successful attempt of dissociating P3a from perceptual consciousness), I chose to compare the predictive powers of the two components using multivariate analysis (Opinion: Sandberg et al., 2014) on source reconstructed data from MEG recordings (Study 1: Andersen et al., 2015). I argue below in the summary of articles that this makes it possible to find evidence which of the 2 proposed correlates correlates the best with perceptual consciousness. At this point, it should be noticed that the studies of perceptual consciousness that I have discussed so far view perceptual consciousness and cognitive context as non-integrated processes. This is also present in the distinctions Aru et al. (2012) make between proper correlates of perceptual consciousness and consequences of perceptual consciousness, which assume that there are *proper* neural correlates of perceptual consciousness that can be found independently of differences in cognitive context such as differences in task requirements. These *proper* correlates are theorized to correlate only with conscious experiences as such (Aru et al., 2012; Block, 2005) and not with context (Figure 2: upper level).

## The potential influence of cognitive context

I will supply a very general operationalization of what one should expect to differ between non-integrative and integrative viewpoints. A non-integrative viewpoint has as its most important theoretical consequence that there is a definite neural *where and when* that correlates with differences in perceptual consciousness. Oppositely, a weak formulation of an integrative viewpoint has the theoretical consequence that there is no reason to expect a definite *where and when*, while a strong formulation has the theoretical consequence that there is no definite *where and when*. In the REFCON model (Overgaard & Mogensen, 2014), for example, what correlates the best with differences in perceptual consciousness is neural information relevant to the cognitive context, e.g.

task, at hand. A theoretical consequence of this is that perception may be restricted to the extraction of only the necessary features in relation to the task at hand when perceptual circumstances are less than optimal. This means that we should not necessarily expect that we will find the same neural correlates of perceptual consciousness across all tasks and paradigms, but that they will differ according to cognitive context. Especially for the graded ratings, one could expect to find differences across tasks since this is where cognitive strategies may differ the most, due to which strategies are available. For perfectly clear and crisp experiences, we thus expect less differences, due to the expected availability of all potential cognitive strategies. For absent experiences, we also expect less differences because there are no cognitive strategies to apply, thus there should be no differences between tasks. This of course assumes that we have a scale that has a rating that shows *cognitive independence*, which I discussed earlier.

# Aims

The general aim of this dissertation is to inform the debate about what constitutes neural correlates of perceptual consciousness and how perceptual consciousness should be measured.

I argue that the debate about neural correlates of perceptual consciousness can be greatly informed by the application of multivariate analyses to source reconstructed magnetoencephalographic data. The theoretical arguments for this is given in the included Opinion, and applications of multivariate analyses are in Studies 1 & 2.

In Study 1 we applied multivariate analyses to a simple perceptual task with a *constant* task requirement. We specifically tested whether occipital sources or frontal sources were most predictive of perceptual consciousness. Seen in isolation this study can only reveal something about perceptual consciousness given the assumptions of a non-integrative view (Figure 2: upper level).

In Study 2 we also manipulated the task requirements to test whether cognitive context had an effect on what neural activity was found to correlate with perceptual consciousness, thus investigating whether these results could be understood from an integrative view (Figure 2: lower level).

In Study 3 we further investigated how perceptual consciousness and cognitive context interact. I designed a behavioural study where we investigated how top-down expectations affect perceptual consciousness. This also allowed for assessing whether the Perceptual Awareness Scale fulfils the suggested criterion of *cognitive independence*.

The specific aims of the 4 manuscripts included in this dissertation were:

## Opinion: Using multivariate decoding to go beyond contrastive analyses in consciousness research:

The aim of this opinion article was to argue for the use of multivariate decoding analyses in detecting the neural correlates of perceptual consciousness. We argue that because multivariate decoding analyses are most sensitive to patterns of neural activity that are consistently present on the single trial level they are especially fit for revealing the neural correlates of perceptual consciousness.

## Study 1: Occipital MEG activity in the early time range (< 300 ms) predicts graded changes in perceptual consciousness

The aim of this study was to investigate whether early occipital activity (< 300 ms) or late frontal activity (> 300 ms) was the best predictor of perceptual consciousness in a simple perceptual task. For this analysis, we used multivariate statistics, as argued in the Opinion paper (Sandberg et al., 2014), based on source reconstructions of magnetoencephalographic recordings.

## Study 2: Task differences induce differences in magnetoencephalographic correlates of consciousness

The aim of this study was to compare 2 tasks with minimal differences in stimuli. From a non-integrative view of perceptual consciousness and cognitive context, one would expect that there would be one unique spatio-temporal proper neural correlate of perceptual consciousness. From an integrative view (Overgaard & Mogensen, 2014) of perceptual consciousness and cognitive context, where task requirements partly determine the neural correlates of perceptual consciousness, one would expect spatio-temporal differences in what spatio-temporal activity that correlated with perceptual consciousness dependent on task requirements. We investigated whether a non-integrative or an integrative approach to perceptual consciousness and cognitive context would make most sense of the data.

## Study 3: Top-down expectations affect the gradedness of perception and the evidence weighting of informative levels of perceptions:

Nieuwenhuis & de Kleijn (2011) found that differences in task difficulty and the rating scale used affected in how graded a manner participants rated perceptual consciousness, which can be interpreted as evidence of perceptual consciousness and cognitive context interacting. We conducted this study to investigate how top-down expectations, a manipulation of cognitive context, towards prospective stimuli affected ratings of perceptual consciousness and expected that the vaguer one's expectations were, the more graded perceptual consciousness participants would report. We also investigated how this change in cognitive context affected accuracy and response times across different levels of perceptual consciousness, and specifically whether the “No Experience” rating (Table 1) showed evidence of *cognitive independence*.

# Summary of articles

## Opinion article

### Univariate approach for detecting neural correlates of perceptual consciousness

In a traditional univariate analysis, each participant's epoched data is summarized by averaging over all the epochs for each of the relevant experimental conditions. In turn, these individual averages can be summarized as grand averages, which are averages of all participant averages for each of the relevant experimental conditions. These grand averages for the experimentally relevant conditions can then be compared to one another, and summary statistics can, in principle, be done for each of the time points. If one were to do a univariate test for each time point, however, one would face the “multiple comparisons problem” (Shaffer, 1995). This problem is that as the number of statistical tests one performs increases, so does the number of false positives, null hypotheses rejected due to chance and not because of a real difference between 2 conditions. Due to the dependencies between data points, one cannot use a classical correction such as the Bonferroni-correction because this assumes that the tests performed are independent of one another, which is evidently false. A classical way to reduce the number of tests and thus to mitigate the multiple comparisons problem is to only compare peak amplitudes of predefined components (Luck, 2014). Comparisons of peak amplitudes for different levels of perceptual consciousness have been exploited to generate great amounts of knowledge about potential neural correlates of perceptual consciousness (Koivisto & Revonsuo, 2010; Rees et al., 2002; Sergent et al., 2005). As discussed earlier, especially 2 components have been proposed as neural correlates of perceptual consciousness, the N1-N2, ~130-320 ms, and the P3a, ~320-510 ms, (Koivisto & Revonsuo, 2010). One limitation of the univariate method is that there is no way to compare which components correlate the best with perceptual consciousness. Naïvely, one might think that one could simply compare the amplitude sizes of components, but such comparisons do not reveal anything about differences in the underlying sources (Luck, 2014). One could try and dissociate components from perceptual consciousness, but these attempts are made more difficult by the insight (Aru et al., 2012) that contrastive analyses may not only elicit the neural correlates of perceptual consciousness, but also prerequisites and consequences of perceptual consciousness. Aru et al. suggested that experimenters design studies where it is possible to dissociate neural consequences and prerequisites from proper neural correlates of consciousness. I will argue here that multivariate analyses can provide a way to find evidence for which component correlates the best with perceptual consciousness without making a design that dissociates neural consequences and prerequisites of perceptual consciousness. Note that differences in activity for estimated sources for different levels of perceptual consciousness are seldom statistically compared, but mostly used for visualization of the probable underlying sources (Koivisto & Revonsuo, 2010; Sergent et al., 2005). This is probably due to the multiple comparisons problem exploding when being brought to the source space, and also due to components being less well-defined in the source space. In theory, this should not pose a problem for multivariate analyses.

## Proposed multivariate approach for detecting neural correlates of perceptual consciousness

In multivariate analyses, one can use the full richness of the data (C. M. Bishop, 2006) to model the level of perceptual consciousness. Multivariate models exploit the information inherent in the co-dependencies between sources across time points and the co-dependencies between time points across sources. At this point, it is necessary to introduce some terminology. Take an MEG data set for a participant that has $x$ epochs of label $A$ (e.g. Weak Glimpse) and $x$ epochs of label $B$ (e.g. Almost Clear Experience). Each data point of each epoch, whether it be at the source or the sensor level, is called a *feature*. With $n$ sources and $t$ time points, one will thus have $n \times t$ features for each epoch. To get a metric of how much information about the labels $A$ and $B$ there is in the epochs of a given participant, one can divide his epochs into 2 sets, a training set (~80-90 % of the epochs) and a test set (~10-20 % of the epochs). A model is fitted to the training set. The simplest model, which we have also used in the studies in this dissertation, is a logistic model. A logistic model assigns a weight to each feature, which dependent on its sign raises the posterior probability of a given epoch of belonging to label $A$ or label $B$. The training set is now used to predict the labels of the test set. For each epoch in the test set, its feature weights, based on the fitted model, are summed together. The predicted label for a given epoch is then the label that has the higher posterior probability. A classification accuracy can be calculated as the probability of correctly predicted labels in the test set. Whether the classification accuracy can be generalized can be tested by cross-validation, that is: letting the training and test sets consist of different epochs (Figure 4).

In contrast to amplitude sizes in univariate testing, classification accuracies can be compared between components and between conditions. They may thus allow one to assess which component best predicts perceptual consciousness. Some precautions must be taken, however, when doing multivariate analyses. Among other things, one must control the number of spatial (sources) and temporal (samples) features in the comparisons one make (Sandberg et al., 2014), and the differences in the components that one tries to classify on should be of comparable size on the level of the evoked response (Sandberg et al., 2014; Smith, Kosillo, & Williams, 2011).

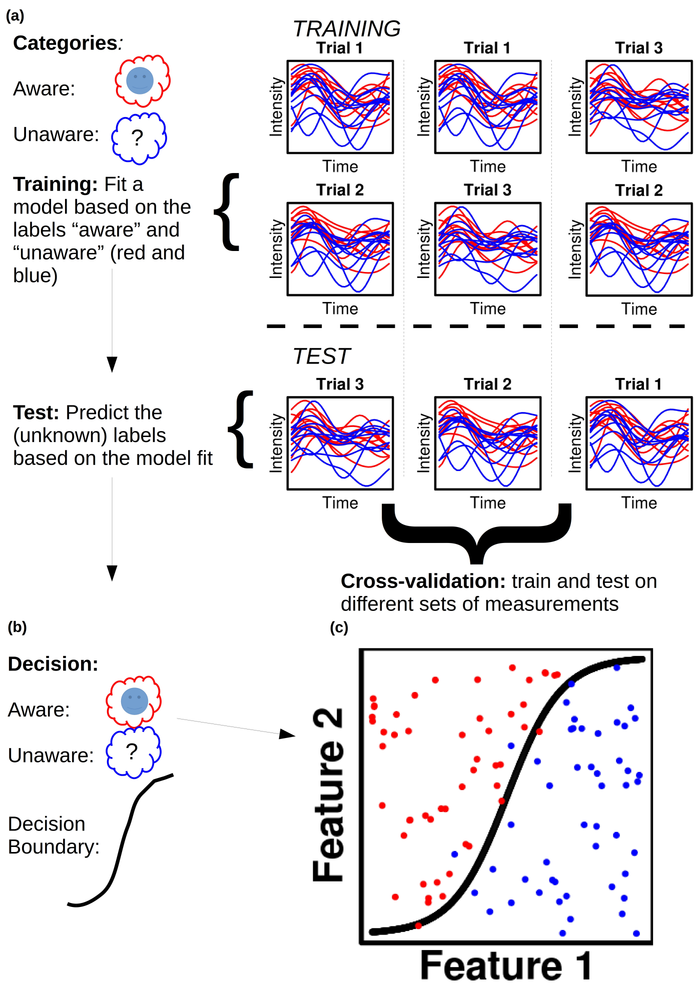


**Figure 4:** Illustration of a hypothetical classification analysis and the steps involved. (a) The classifier is to distinguish between two categories: "Aware" (red) and "Unaware" (blue). Trials are separated into training and test sets in three different ways to ensure cross-validation. The plots show hypothetical activity developing over time courses for 3 trials of aware and unaware respectively. (b) The decisions reached based on the model fit in the training set. (c) Classification is performed for 100 trials (50 aware and 50 unaware) with a non-linear decision boundary. Adapted from (Sandberg et al., 2014).

## Consistency and amplitude size

An intuition that drives why we have chosen multivariate analyses over univariate analyses in the studies in this dissertation is that the best neural correlate of perceptual consciousness must be the one that correlates the best on the trial level and not just on the summary statistic level. It is possible for a component to be less *consistent* on the trial level than another component, while showing a greater *amplitude size* when trials are averaged (Sandberg et al., 2014) (Figure 5).The *consistency* of a component on the trial level, thus, does not necessarily correlate with *amplitude size* on the summarized level. The test statistic of a univariate analysis is based on *amplitude size* and only indirectly on *consistency* whereas the test statistic of a multivariate analysis is based on the *consistency* of the component *and* the *amplitude size*, on the single-trial level. The intuition can thus be restated as: *consistency* matters more than *amplitude size*. This intuition drove our interpretations of the results of Studies 1 & 2.

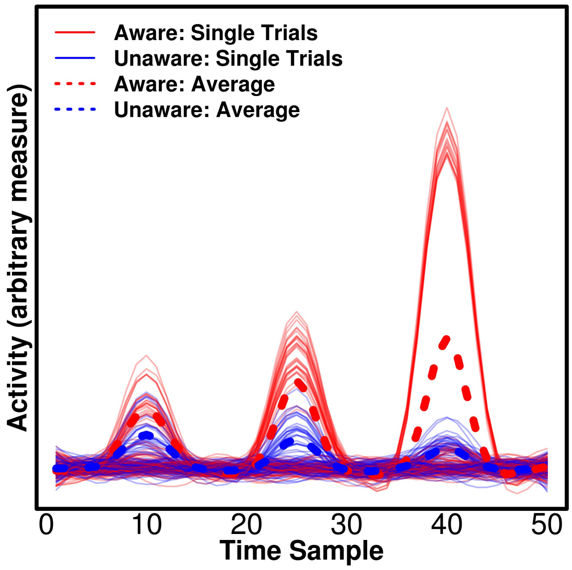


**Figure 5:** Consistency of the NCC. Three simulated, hypothetical signals of differing consistency and strength are plotted. All could be candidate neural correlates of consciousness (NCC), thus reflecting differences between trials classified as "aware" and "unaware" by a participant. For the first component, there is a small average difference, but the component is not consistently larger for "aware" trials, making it unlikely that the component reflects awareness. The component could reflect a prerequisite for consciousness as it has to be present for awareness, but it does not guarantee awareness. For the second component, there is a medium average difference, and the component is consistently larger for "aware" trials. On the single trial level, the component thus reflects awareness and it may thus be an actual NCC. Finally, for the third component, there is a large average difference, but the component is only found on a subset of "aware" trials, and it does thus not consistently reflect awareness. The component could thus reflect processes that are consequences of awareness, which occur exclusively for "aware" trials, but may not occur on every single aware trial. Note that traditional univariate statistics based on averaged participant-specific averages would erroneously find more evidence for the last component being the NCC proper in this example. Adapted from (Sandberg et al., 2014).

## Common procedures for MEG data in Studies 1 & 2

To understand why Studies 1 & 2 can be informative about the spatial and temporal aspects of the neural signal that correlates with perceptual consciousness, the origins of the magnetoencephalographic signal is outlined below.

## Magnetoencephalography (MEG)

Magnetoencephalography is the recording of minuscule magnetic fields and gradients at the scalp picked up by magnetometers and gradiometers. These magnetic fields are primarily produced by the post-synaptic currents flowing in dendrites of pyramidal cells in the cortex. For a magnetometer, at any given time point, the magnetic field measured is proportional to the net effect of the post-synaptic currents of the sources that generated it. Because the pyramidal cells of the cortex are ordered in a parallel manner perpendicular to the cortical surface, it is thus possible to pick up a measurable magnetic field. Even so, the strengths of such fields are minuscule, compared to ambient noise, about 8 orders smaller. Therefore, MEG is recorded in a magnetically shielded room. Furthermore, the magnetometers are cooled down by liquid helium such that the wire becomes superconducting and current can be induced. If there were any resistance, the magnetic field would be too weak to induce current. Finally, this current is amplified by superconductive quantum interference devices (SQUIDS) such that voltage finally can be recorded (Papanicolaou, 2009).

The Elekta Neuromag Triux system that I had access to has 102 magnetometers and 204 gradiometers. Gradiometers are two magnetometers placed in close proximity to one another and wound in such a way that what is measured is the magnetic gradient and not the magnetic flux. The gradient is the difference in flux over the two magnetometers making up the gradiometer. This means that gradiometers are more sensitive to proximate sources than to distal sources, because the difference in flux will be much less for a distal source compared to a proximate source. In contrast, magnetometers are sensitive to both proximal and distal sources, but will also be sensitive to distally originated noise. The magnetometers and gradiometers are placed such that they cover the whole head (Figure 3B).

There are two “spaces” in which data can be analysed: the sensor space and the source space. I will now explicate the differences between these.

### The sensor space

In the sensor space, data can be represented by the 306 sensors and the positions of those on a head model based on the individual participant. These can, roughly, be divided into occipital, temporal, parietal and frontal sensors. It may, however, be very misleading to think of these sensors as localizing relevant activity. Due to the fact that the magnetic signal is spreading in a sphere-like manner from its origin and that what is measured at any given sensor will be the *net* effect of signal present at that moment in time, inferences about origin of the signal are extremely capricious in nature. On the other hand, though, it is possible to speak of components, event-related fields (ERFs), that are associated with certain cognitive operations or phenomena. These are often characterized by appearing during similar time intervals and on similar sensors even between individual participants. P3a and N1-N2 are examples of such components that show up in both EEG and MEG experiments. To gain more knowledge about the origin of such signals and components, one may turn to the source space.

## The source space

In a sense, it is misleading to speak of there being two spaces where data can be analysed. Where data in the sensor space are what is recorded and picked up by the respective sensors, there is no real data in the source space. Rather the source space is a *model* of the origin of the recorded signal from the sensor space data. A first reasonable assumption is that the origin is somewhere within the participant's head. With that assumption one does not get very far since there is literally an infinite number of combinations of sources that would give rise to the signal recorded by the MEG sensors. With a precise anatomical image obtained in a magnetic resonance scanner the head can be separated into scalp, skull and brain and the brain into grey and white matter and cerebro-spinal fluid. On the basis of this anatomical image a forward model can be created. In brief, the forward model constrains the number of possible solutions and makes it possible to find the best one (Hämäläinen & Ilmoniemi, 1994). A forward model consists of three components: 1) a model of where in the head the sources are situated, 2) how the currents of these sources spread and 3) with what sensitivity the signal associated with the current (flux/gradient) can be picked up by the different sensors.

In my modelling of the source space, I used the minimum norm estimate (MNE) algorithm (Hämäläinen et al., 1993), an algorithm that assumes minimal prior information, namely only that the modelled sources are spatially restricted to the cortex. In simple terms, it aims to explain what is observed in the sensor space, by allocating the minimal amount of total current across all sources.

A source space model based on the MNE algorithm contains a number of inferred sources, typically ~8000 cortical sources, that each have a time course, based on the durations of epochs, of estimated current.

Such a source space model can thus be used to assess which spatio-temporal patterns of estimated neural activity correlate the best with differences in perceptual consciousness (Studies 1 & 2).

## Preprocessing

The described preprocessing procedures apply to both Studies 1 & 2.

The head shapes of participants were digitized and together with an anatomical magnetic resonance image they were used for creating a unique forward model for each participant.

The recorded magnetic fluxes and gradients in the sensor space make up a very rich data set. With a sample frequency of 1000 Hz, one gets 306,000 data points per second. A Maxwell filter was used to apply spatio-temporal signal space separation (tSSS), which separates the brain signal from the external disturbances outside the sensor array, leaving only the brain signal. After applying tSSS, movement compensation was applied based on continuous head position measurements. tSSS and movement compensation were both performed using MaxFilter, version 2.2 (Elekta). A bandpass filter (0.5-15 Hz, Butterworth) was applied to the data. To reduce the size of the data set to a more manageable size, we downsampled the data to 250 Hz and epoched the data into smaller time series around the presentation of the target stimulus, -200 ms to 600 ms. Components related to eye movements and blinks were removed with independent component analysis (Hyvärinen & Oja, 2000). The same was the case for heart beat components (only Study 2). FreeSurfer (Dale, Fischl, & Sereno, 1999) was used to model individual cortical reconstructions and volumetric segmentations, and the activity of ~8000 modelled sources were distributed across the cortical surface. Dynamic statistical parametric mapping was used to overcome the superficial bias of MNE (Dale et al., 2000). Even with a data set reduced in size by epoching and downsampling, the source reconstructed data were still enormously rich and full of spatio-temporal co-dependencies and therefore multivariate analyses were appropriate (Opinion: Sandberg et al., 2014).

# Study 1

## Methods

19 participants were administered a masking task where they were to identify a briefly presented target stimulus followed by a mask (Stimulus Onset Asynchrony = 33.3 ms) (Figure 6). The target was one of 2 simple figures. After identification, participants were to rate perceptual consciousness using the Perceptual Awareness Scale (Table 1). The contrast of the target stimuli were thresholded throughout the experiment to get a sufficient amount of each rating from the Perceptual Awareness Scale. 8 participants were excluded from the study (for specific reasons, see: Andersen et al., 2015).

The estimated source data were divided into 2 time ranges the N1-N2 range, ~130-320 ms, (VAN range), and the P3a time range, ~320-510 ms, and into 4 lobes, occipital, frontal, temporal and parietal. Occipital and frontal lobes were of greatest interest to compare (Koivisto & Revonsuo, 2010), but temporal and parietal lobes and the whole brain were included for exploratory reasons. Multivariate analyses were then run on the 10 different spatio-temporal combinations for each of the 3 neighbouring PAS comparisons, No Experience versus Weak Glimpse, Weak Glimpse versus Almost Clear Experience and Almost Clear Experience versus Clear Experience (Table 1). These analyses thus included $n \times t$ features, where $n$ is the number of sources in a lobe and $t$ is the number of time samples in a time range.

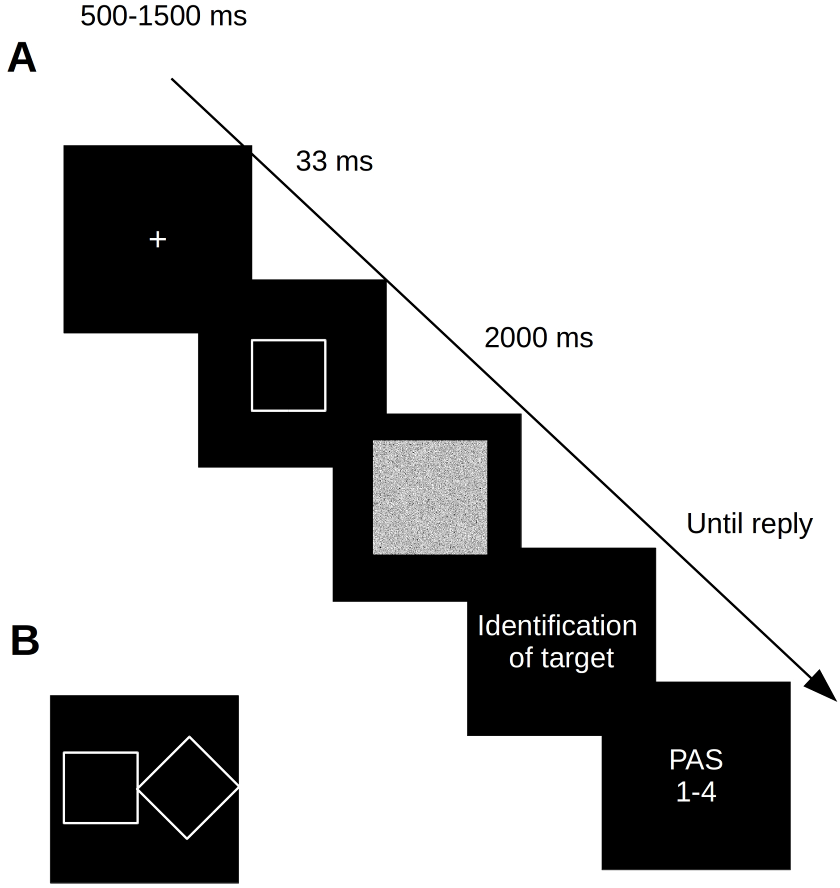


**Figure 6:** Paradigm and stimuli: A) First a fixation cross was presented for either 500, 1000, or 1500 ms. Following that, the target (one of two figures, rectangle or rotated rectangle) was presented for 33.3 ms. This was immediately followed by a static noise mask presented for 2000 ms. During these 2000 ms, participants reported the identity of the target by a button press with one hand. Finally, they indicated the clarity of their experience using the Perceptual Awareness Scale (PAS) (Table 1). A contrast staircase, a modified 2-up-1-down, was used throughout the experiment. B) the two target stimuli used throughout the experiment.

A second analysis was run to estimate how classification accuracy evolved over time. A multivariate analysis was done on each time sample included in the epochs. The analyses were done in a cumulative manner, such that each analysis included all the time samples leading up to the one being added. This was done for the frontal and occipital lobes and for each of the 3 aforementioned PAS comparisons.

## Results

The first analysis revealed that sources in the occipital lobe more accurately predicted perceptual consciousness than sources of any of the other lobes (Figure 7).

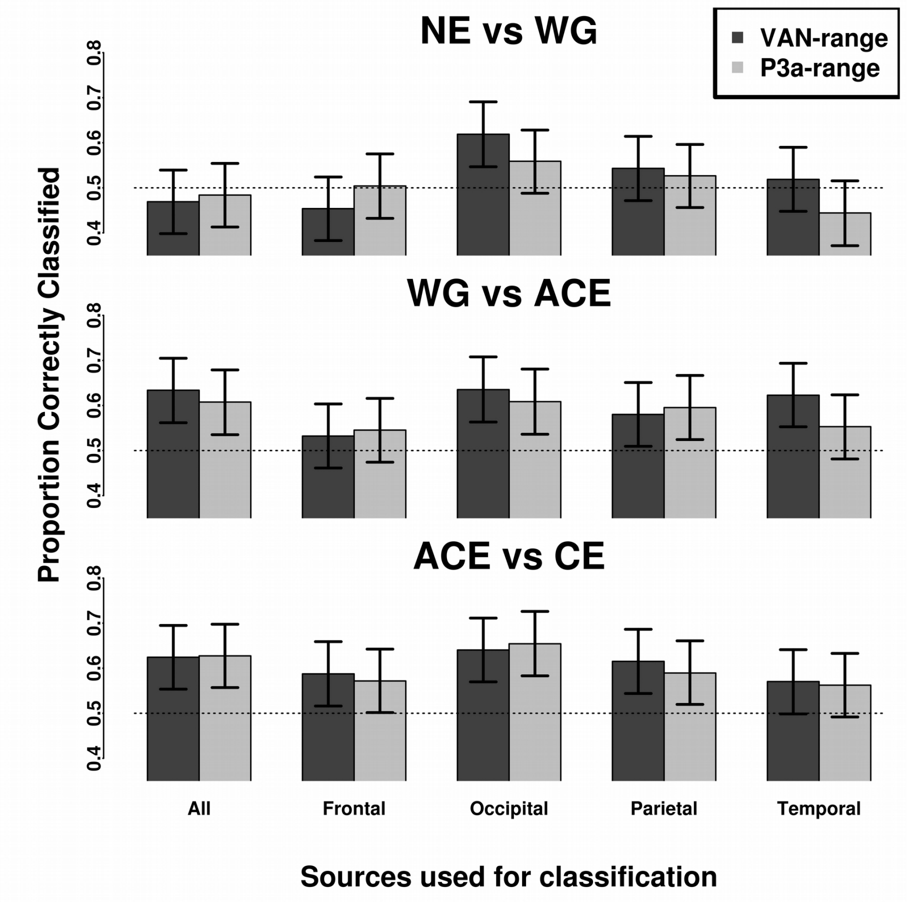


**Figure 7:** Mean classification accuracies for each of the five lobes tested for the three PAS comparisons for each of the two ranges: the VAN range (132-320 ms) and the P3a time range (324-512 ms). NE vs WG is the difference of a subjective experience as such. WG vs ACE is the experiential difference of content. ACE vs CE is the experiential difference of unambiguity. Of special importance is it that occipital sources can be used to classify all PAS comparisons significantly above chance. The error bars are 95 % confidence intervals tested against chance, bootstrapped using 10000 simulations, from a mixed model having Time Range (2) and PAS comparison (3), and Lobe (5) as fixed effects including all possible interactions. Participants (11) were modelled with individual intercepts (random effect). Adapted from (Andersen et al., 2015).

The second analysis revealed a steep increase in classification accuracy for occipital sources during the N1-N2 (VAN) time range, ~130-320 ms (Figure 8).

After this time range, classification accuracy was not increased further by including more time points (Figure 8A). Classification accuracy for frontal sources did not seem to be associated with either the N1-N2 time range or the P3a time range (Figure 8B).

## Conclusions

We found that participants used the Perceptual Awareness Scale to report perceptual consciousness in a graded manner, and that spatio-temporal information in the occipital lobe during the N1-N2 time range was critical for distinguishing these graded differences in perceptual consciousness. This supports that the neural activity that most *consistently* correlates with graded differences in perceptual consciousness is early (< 300 ms) and occipitally realized. In the general discussion, I will discuss what this has of consequences for neural theories of perceptual consciousness such as Lamme's theory of recurrent processing (Lamme, 2006) and Dehaene's global neural workspace theory (Dehaene, 2014).

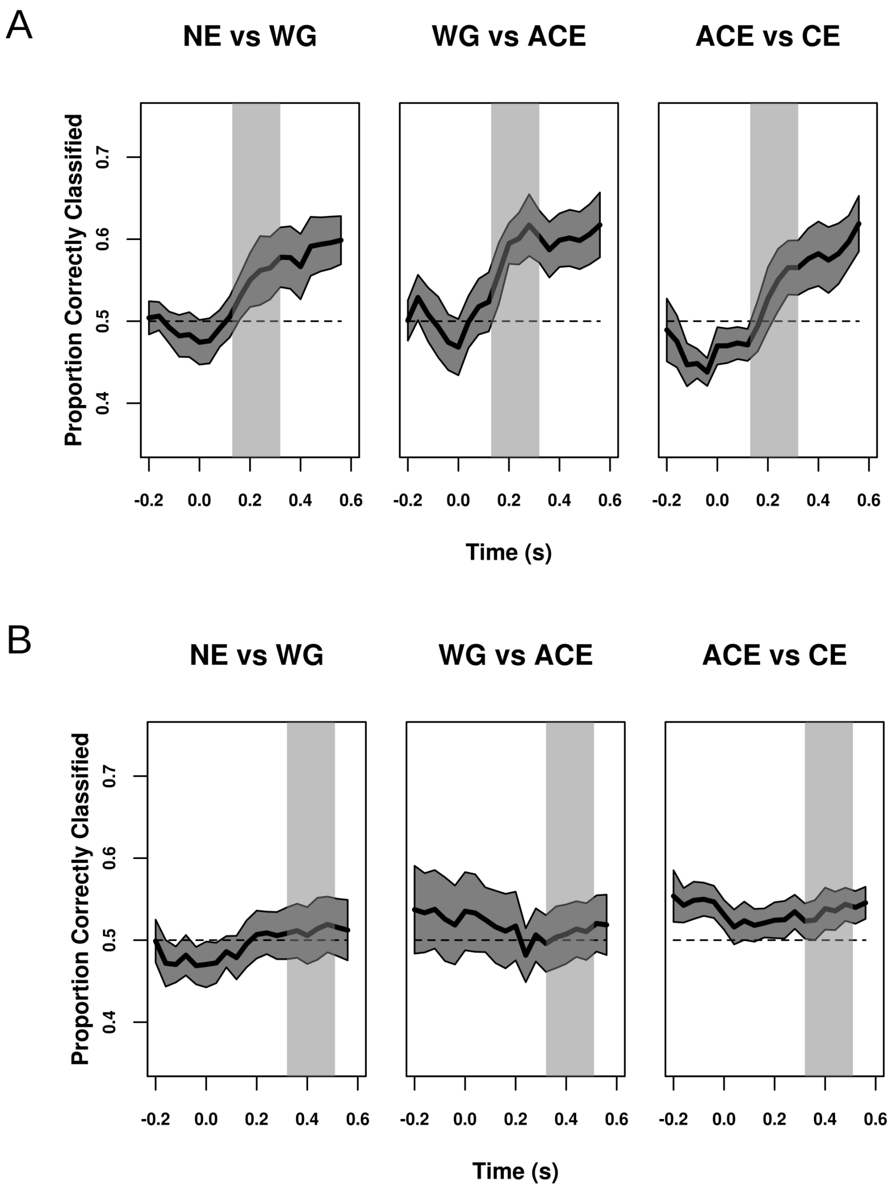


**Figure 8:** Mean cumulative time point classification accuracies A) for the occipital lobe and B) for the frontal lobe tested for the 3 PAS comparisons. The light grey indicates the VAN time range A) and the P3a time range B), respectively. Note that the largest increase in decoding accuracy occurred during the VAN at occipital sources. The darker grey area indicates one standard error of the mean. Curves have been smoothed by only plotting every tenth point. These points are based on the mean of the nine samples that came before them. The standard error of the mean is calculated over ten points as well. Adapted from (Andersen et al., 2015).

## Study 2

### Methods

40 participants were administered a masking task where they had to indicate whether 2 letters presented alongside one another were “same” or “different” (Posner & Mitchell, 1967). Participants participated in one of two tasks, either a *perceptual* or a *conceptual* task. Participants in the perceptual task were to respond “same” if the 2 letters were identical and “different” if not. Participants in the conceptual task were to respond “same” if the 2 letters were of the same type in terms of vowel- and consonanthood and “different” if not (Figure 9). Participants were to use the Perceptual Awareness Scale to rate the clarity of their experiences.

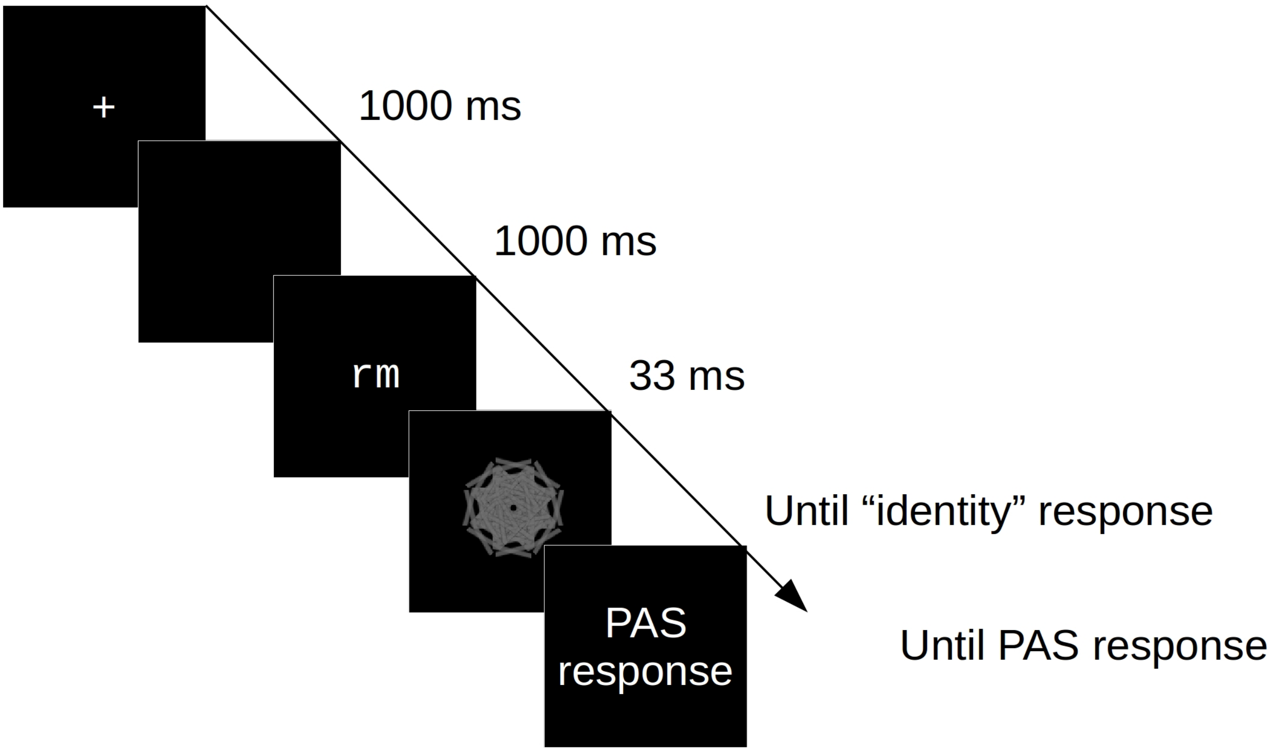


**Figure 9:** Paradigm: A fixation cross was presented for 1000 ms, followed by a delay of 1000 ms, to prevent forward masking of the target stimulus. A pair of letters was then presented for 33 ms immediately followed by a mask that remained on until the participant indicated whether the 2 letters were “same” or “different”. In the *perceptual* task the target letters were defined as “same” if they were identical, e.g. “rr”, and “different” in all other cases. For the *conceptual* task, the target letters were defined as “same” if they were of the same type according to whether they were consonants or vowels, e.g. “eu” or “sv”, and “different” if they were of opposite types, e.g. “ev”. After that participants had to indicate perceptual consciousness by one of 4 ratings, No Experience, Weak Glimpse, Almost Clear Experience or Clear Experience.

We used multivariate analyses to test whether task, *perceptual* or *conceptual*, influenced how predictive of differences in perceptual consciousness occipital, frontal, temporal and parietal lobes were during the N1-N2 and P3a time ranges. We used a stochastic approximation staircase aiming at an accuracy level of 75 % (Faes et al., 2007), such that we for each participant would get a good distribution of all 4 PAS ratings. Note that lobes and time ranges were defined in the same manner as in Study 1.

2 types of multivariate analyses were done. First, we performed a multinomial analysis where all 4 ratings were tested against one another, done for each time sample throughout the epoch duration. This analysis could reveal when information was present for predicting differences in perceptual consciousness across lobes and tasks. Second, we performed a multinomial analysis again, but where all 4 ratings were tested against one another using all samples from either the N1-N2 time range or all samples from the P3a time range. This analysis was different from the sample-by-sample analysis in that it could also model temporal co-dependencies during the 2 predefined time ranges tested. Due to a conservative criterion where participants needed at least 30 trials of each PAS rating, only 10 participants could be included in the analyses, 6 from the perceptual task and 4 from the conceptual task. The aim, to reiterate, was to investigate whether a non-integrative or an integrative approach to perceptual consciousness and cognitive context would make most sense of the data.

## Results

The sample-by-sample analyses revealed some interesting patterns that were hard to incorporate into a view of perceptual consciousness where it and cognitive context are not integrated. In the perceptual task for the occipital sources, we found results that closely matched the sample-by-sample analysis from Study 1, which also can be categorized as a perceptual task. All ratings seemed discernible from one another around ~170-270 ms (Figures 10E-H). The conceptual task, however, resulted in a different pattern where the graded ratings, Weak Glimpses and Almost Clear Experiences, seemingly could not be classified in the N1-N2 time range for the conceptual task (Figures 10B-C), while Almost Clear Experiences increased a little and was sustained in accuracy in the P3a time range for the conceptual task (Figures 10C).

In general, the conceptual task showed some evidence of sustained classification accuracy through the P3a time range compared to the perceptual task.

Surprisingly, frontal sources could also classify perceptual consciousness in a graded manner for the perceptual task, peaking around 300 ms (Figures 11E-H). This probably reflects the N3 component reported by Sergent et al. (2005), but which they report to be bimodal. In the conceptual task, frontal sources were more bimodal in their classification accuracy, being able to classify only No Experiences and Clear Experiences. Sergent et al. (2005) also used a conceptual task thus the present results indicated that the bimodality of N3 might depend on task requirements. The sample-by-sample analyses (Figures 10 & 11) revealed the information present at each individual time point, and can thus only model the spatial dependencies between sources.

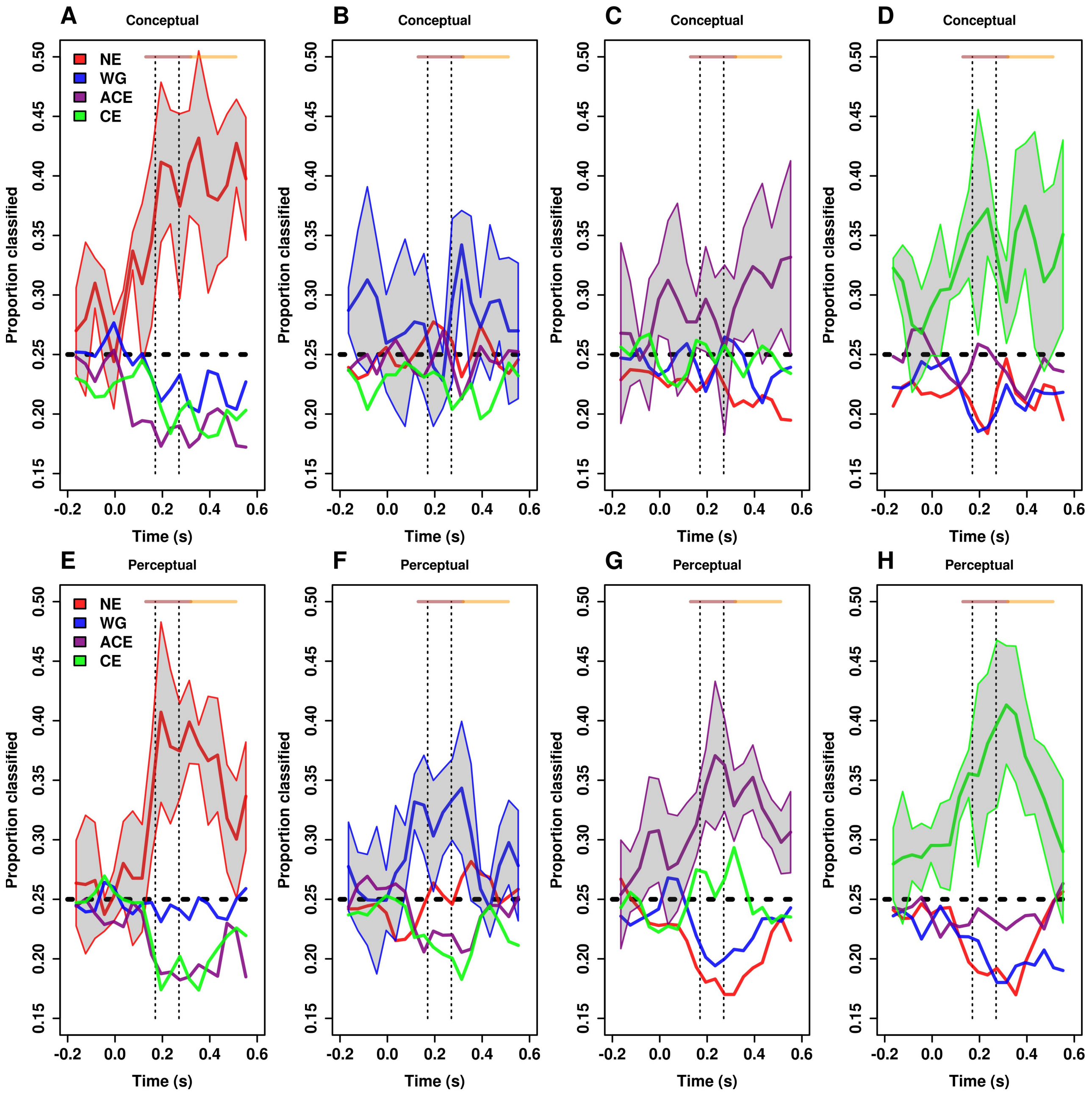


**Figure 10:** Sample-by-sample analyses for occipital sources: the upper row of panels (A-D) shows conceptual sources classification for No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) respectively. The lower row of panels (E-H) shows the same for the perceptual task. Mean classification accuracies across participants, smoothed by taking every 10$^{th}$ sample and taking the mean across that sample and the 10 samples on each side, are shown for all classifications. Shaded regions are standard errors of the mean smoothed the same way. The 2 bars at the top indicate the width of the 2 time ranges tested in other analyses. Vertical lines indicate 170 ms and 270 ms respectively.

The final planned multinomial analyses tested whether temporal dependencies played a role in predicting perceptual consciousness.

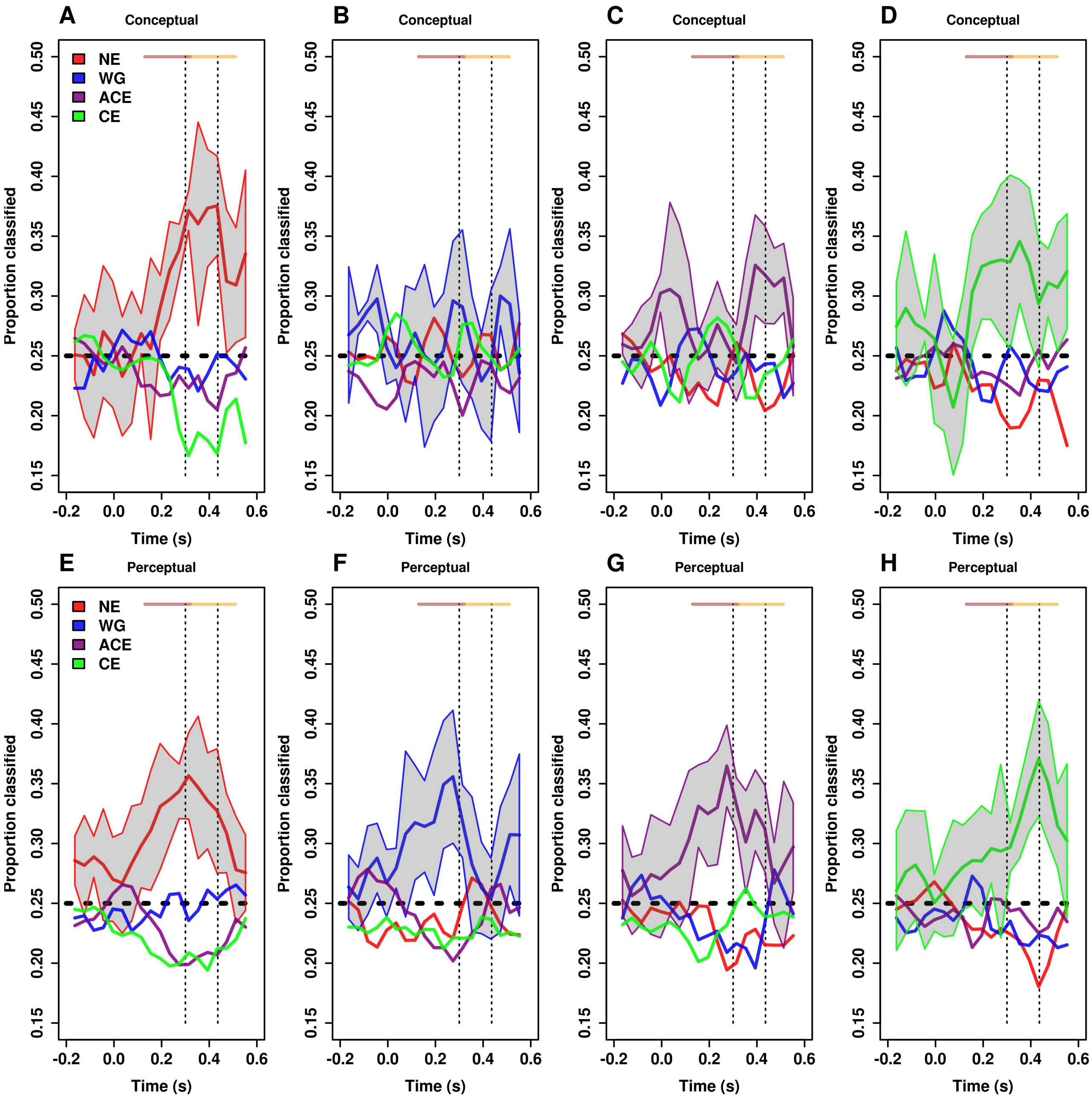


**Figure 11:** Sample-by-sample analyses for frontal sources: the upper row of panels (A-D) shows conceptual sources classification for No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) respectively. The lower row of panels (E-H) shows the same for the perceptual task. Mean classification accuracies across participants, smoothed by taking every 10th sample and taking the mean across that sample and the 10 samples on each side, are shown for all classifications. Shaded regions are standard errors of the mean smoothed the same way. The 2 bars at the top indicate the width of the 2 time ranges tested in other analyses. Vertical lines indicate 300 ms and 436 ms respectively.

The accuracy of classification for each PAS rating was found to significantly interact with which lobe was used for classification (Figure 12A). Furthermore, the accuracy of classification for each PAS rating was also found to significantly interact with the interaction of what task participants were doing and the time range during which classification was done (Figure 12B).

In many ways, the results mirrored the sample-by-sample analyses revealing the timing difference between the 2 tasks in when graded differences in perceptual consciousness could be classified. The N1-N2 time range was significantly better for classifying the graded ratings, Weak Glimpses and Almost Clear Experiences, in the perceptual task compared to the conceptual task (Figure 12B). For classification of graded ratings the conceptual task fared better in the P3a time range with significantly better classification of Almost Clear Experiences than in the N1-N2 time range (Figure 12B). This corroborates that effects on neural correlates of consciousness between tasks is greatest for the graded ratings.

We also found that occipital sources classified perceptual consciousness significantly better than frontal sources for the extreme ratings, No Experiences and Clear Experiences, where we expected the smallest differences between tasks. This fits well with the finding from Study 1 that occipital sources classified perceptual consciousness better than frontal sources.

Interestingly, the ability to classify the graded ratings in the perceptual task was not dependent on which lobe was used for classification. The sample-by-sample analyses suggested that the capability of frontal sources to discern Weak Glimpses and Almost Clear Experiences during the N1-N2 time range was based on a peak around 300 ms, presumably the N3 (Figures 10E-H). This classification peak was absent for the conceptual task, where the classification was more bimodal (Figures 10A-D). A bimodal pattern for the N3 was also reported by Sergent et al. (2005). Their task was also conceptual in nature; participants had to indicate visibility of numbers spelt out as words. Whether N3 is bimodal or graded may thus depend on task requirements. It has been argued that N3 reflects object processing and early categorization, but not the semantics associated with letters (Eddy, Schmid, & Holcomb, 2006; Hamm, Johnson, & Kirk, 2002; McPherson & Holcomb, 1999). Interestingly, classification accuracy for Clear Experiences did not peak until around 436 ms, the classical P3a peak (Sergent et al., 2005).

A potential explanation of this can be supplied by REFCON (Overgaard & Mogensen, 2014). With a fully crisp and clear experience, conscious access to all features of the stimuli should be available, and the task may be solved by comparing whether the letters were the same, that is, where they were seen as *letters*. This full access may correspond to Dehaene's global workspace (2014). Thus, according to an integrative viewpoint, it is possible that broadcasting to a global workspace is necessary for seeing the letters as *letters*, but importantly cognitive strategies for graded perceptions do not, and maybe cannot, depend on such a broadcasting. With less clear experiences however, the task may be solved by relying on whatever features are available, that is, the early categorization of shape supplied by the N3. REFCON can explain this result in a cohesive way since it exactly predicts that the activity that will correlate the best with differences in perceptual consciousness is dependent on what cognitive strategies are available. Given that No Experiences are used to report about a *cognitively independent* state, the finding that No Experiences reach peak classification at comparable times between tasks: occipital sources: ~170 ms (Figures 9A & E), frontal sources: ~300 ms (Figures 10A & E), temporal sources: ~ 300 ms (not shown here) and parietal sources: ~ 170 ms (not shown here) is unsurprising. The cognition behind responding randomly when not having any information, No Experience, should be similar across tasks if No Experiences are independent of the cognitive context. In the general discussion, I will further discuss the implication of these results in connection with the results of Study 3.

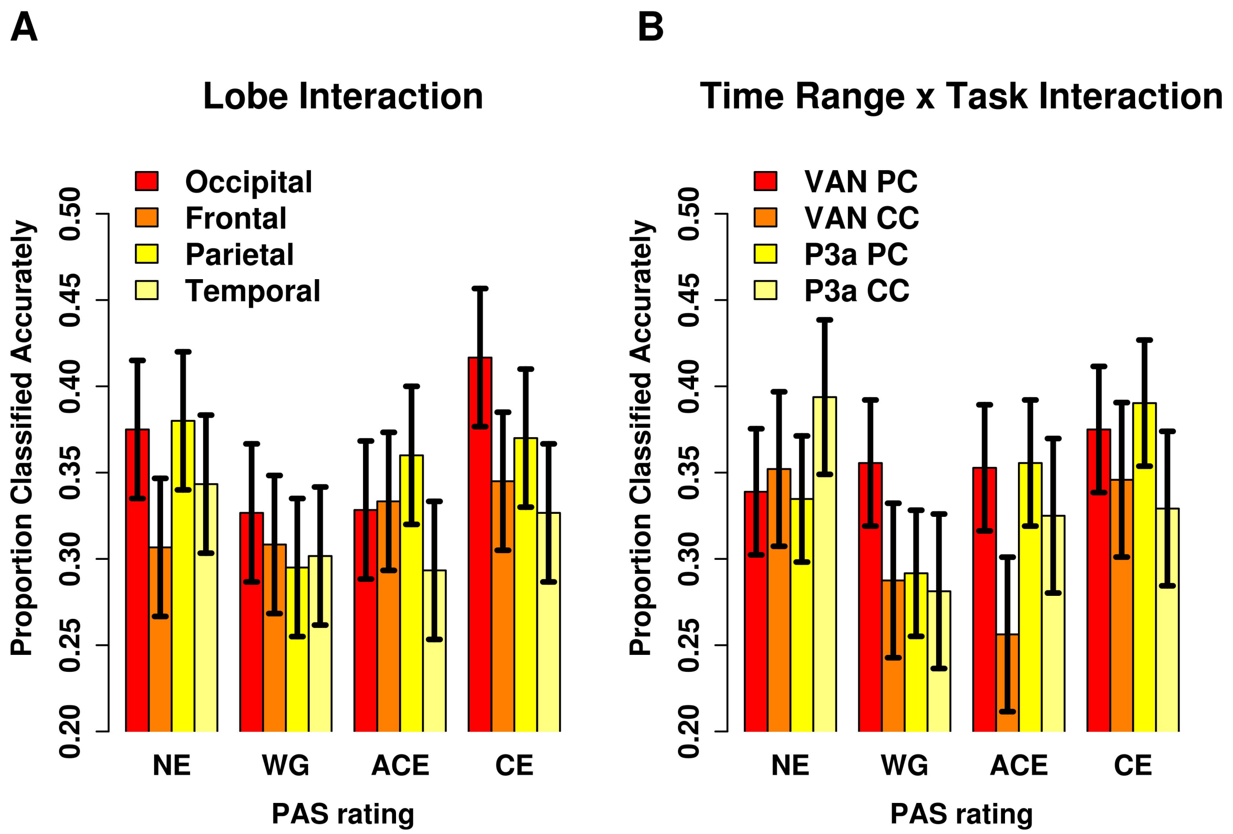


**Figure 12:** Illustration of the effects that Lobe and the Time Range × Task interaction had on classification accuracy. For extreme ratings, NE and CE, occipital sources were found to be significantly more accurate than frontal sources, whereas the interaction between time range and task was driven by graded ratings, WG and ACE, being affected differently by the 2 tasks (PC = perceptual; CC = conceptual) administered. Error bars are 95 % confidence intervals.

The current results do not fit with a non-integrative view where there is one unique spatio-temporal neural correlate of perceptual processing across tasks, e.g. occipital processing in the N1-N2 time range as Study 1 suggested. Interestingly, in the present study, the N1-N2 time range revealed a stable level of classification accuracy across PAS ratings, but only in the perceptual task, similar to that found in Study 1, corroborating the stability of this effect (Figure 12B: VAN PC). An integrative view, e.g. REFCON (Overgaard & Mogensen, 2014), where task requirements partly determine what will correlate with differences in perceptual consciousness, can make more sense of these data, as I will discuss in the general discussion.

### Conclusions

The classification analyses revealed results that are difficult to incorporate into a non-integrative view of perceptual consciousness and cognitive context. Perceptual consciousness could be predicted in a graded manner during the N1-N2 time range, replicating Study 1 (Andersen et al., 2015). For the conceptual task, the P3a time range showed a more graded pattern, but was less able to classify Weak Glimpses compared to the perceptual task (Figures 9C & 11B). Also the frontal sources showed differences in prediction of perceptual consciousness across tasks. In the perceptual task, the N3 could classify graded ratings of perceptual consciousness during the N1-N2 time range whereas this was not possible in the conceptual task. Thus there does not seem to be evidence of one unique spatial-temporal neural correlate of perceptual consciousness. An integrative view of perceptual consciousness and cognitive context may be better able to accommodate these differences as I will discuss in the general discussion.

A general finding though was that occipital sources were better in predicting perceptual consciousness than frontal sources were and that the greatest differences between tasks were found in the graded ratings, Weak Glimpses and Almost Clear Experiences.

## Study 3

### Methods

We manipulated cognitive context by manipulating participants' top-down expectations towards what would be shown in subsequent trials by cueing what stimuli could be shown. Stimuli were the digits from 2-9. Participants had to indicate the parity of the masked digit shown. We aimed to estimate psychometric curves of perceptual consciousness and accuracy by presenting target stimuli and masks at different stimulus onset asynchronies (SOA). Participants had to rate the clarity of their experience of the digit using the Perceptual Awareness Scale (PAS) (Table 1) (Figure 13).

Either 2, 4 or 8 digits, an equal number of even and odd digits, were shown in the cue, thus varying how distinct their expectations towards the prospective stimuli were.

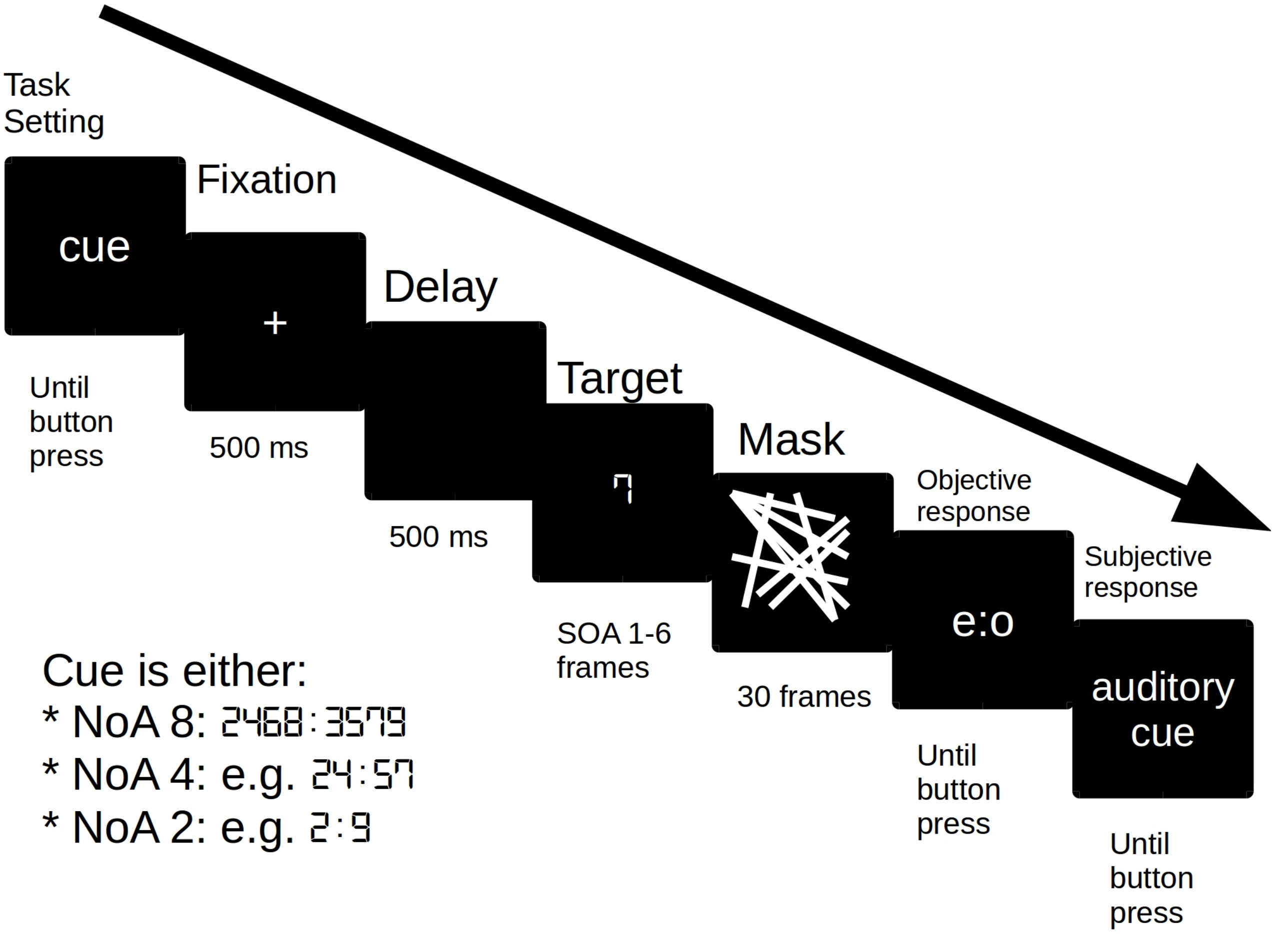


**Figure 13:** Experimental paradigm. A cue was presented, creating a top-down expectation as to which digits could be presented. The Number of Alternatives was one of 3 levels (2, 4 or 8 alternatives). A cue was repeated for 12 trials and was then changed. A high-pitched sound alerted participants whenever the cue changed. A fixation cross (500 ms) was followed by a delay, to avoid forward masking. A target digit (in a digital font) was then presented between 1 and 6 frames (1 frame = 11.8 ms), which was followed by a backward mask made of random lines presented for 30 frames. An objective response was prompted as to whether the presented digit was even, *e*, or odd, *o.* Finally, following an auditory cue, signalling that the objective response had been made, participants reported perceptual consciousness of the target by pressing one of the buttons 1-4.

We investigated how response times, accuracy and distributions of PAS ratings varied dependent on the distinctness of expectations and sensory saliency (duration presented). For response times and accuracy we also investigated their dependency on perceptual consciousness (PAS). We expected that the vaguer one's expectations were, the more graded perceptual consciousness participants would report. We defined graded ratings as Weak Glimpses and Almost Clear Experiences. This would also allow us to assess whether No Experiences were *cognitively independent* from the context. *Cognitive independence* would imply that response times and accuracy for No Experiences would be of equal magnitudes across any differences in cognitive context, such as sensory saliency and expectations.

## Results

The psychometric curves for perceptual consciousness and accuracy did not show any significant differences between expectations in terms of the steepness of the curve, the estimated threshold or the upper or lower asymptotes. The difference between the estimated threshold for accuracy and perceptual consciousness can be interpreted as the amount of unconscious processing (Koch & Preuschoff, 2007). We found no such difference in our task.

Based on the psychometric curves, we estimated a common threshold around 3 frames (~35.3 ms) and further investigated the distribution of PAS ratings below, at and above threshold. We found that perceptual ratings around threshold became more graded the more vague top-down expectations were (Figure 14). We thus extended the finding of Nieuwenhuis & de Kleijn (2011) that cognitive context interacts with perceptual consciousness. They found evidence in terms of task difficulty, and we in terms of top-down expectations.

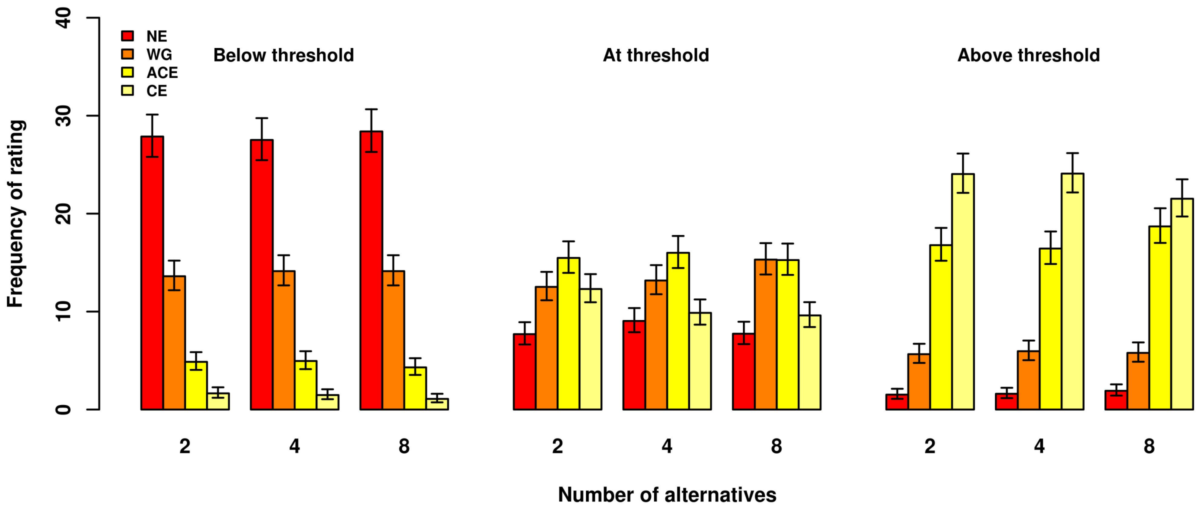


**Figure 14:** Mean number of times each rating on the Perceptual Awareness Scale (Table 1) was used below threshold, at threshold, 3 frames, and above threshold for each of the 3 conditions of top-down expectations (Number of alternatives). Error bars are 95 % confidence intervals. Model comparisons and statistical testing revealed that 8 alternatives was associated with fewer Clear Experiences (CE) and more Weak Glimpses (WG) than 2 alternatives. Below threshold, participants rated most trials as No Experiences (NE) or Weak Glimpses, while above threshold this shifted to them rating most trials as Almost Clear Experiences (ACE) or Clear Experiences. At threshold, participants used all gradations of the scale.

We also found that response times interacted both with top-down expectations and sensory saliency in a very interesting manner. In general, participants responded faster the more distinct expectations were, the more salient target stimuli were and the more clear experiences were, as one might expect. This was only true, however, for Weak Glimpses, Almost Clear Experiences and Clear Experiences

(Table 1), thus not for No Experiences. Response times for No Experiences were of equal duration, as Bayesian analyses supplied evidence for, independently of differences in top-down expectations and sensory saliency (Figure 15). No Experiences were furthermore characterized by chance accuracy for all combinations of top-down expectations and sensory saliency. Similarly to how Weak Glimpses, Almost Clear Experiences and Clear Experiences were associated with faster response times the more salient stimuli were, they were also associated with higher accuracy the more salient stimuli were. These results thus supply evidence for the *cognitive independence* of No Experiences to differences in cognitive context.

No significant differences in accuracy was found between expectations of differing distinctness.

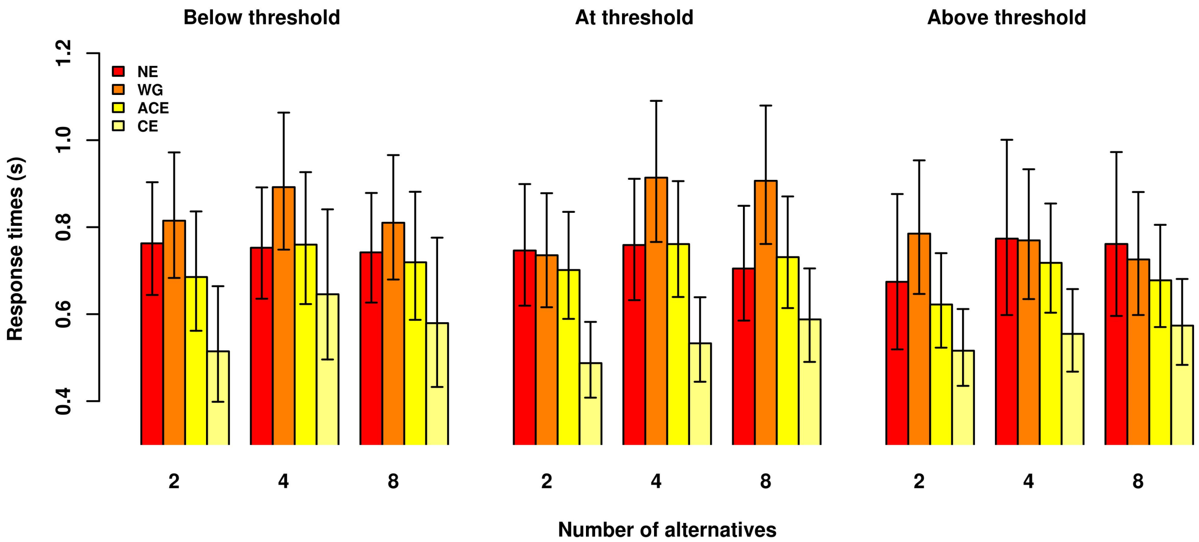


**Figure 15:** Mean response times for each rating on the Perceptual Awareness Scale (Table 1) shown below threshold, at threshold, 3 frames, and above threshold for each of the 3 conditions of top-down expectations (Number of alternatives). Error bars are 95 % confidence intervals. Model comparisons and statistical testing revealed that response times for Weak Glimpses (WG), Almost Clear Experiences (ACE) and Clear Experiences (CE) interacted both with objective differences in stimuli, i.e. whether the stimulus was presented below, at or above threshold and differences in top-down expectations (Number of alternatives). No Experiences (NE) did not interact however and was not significantly different from chance as judged by the confidence intervals.

## Conclusions

Based on these results, I propose that a distinction is made between uninformative and informative states of perceptual consciousness. In terms of the Perceptual Awareness Scale, I propose that this maps onto No Experience as being uninformative and Weak Glimpse, Almost Clear Experience and Clear Experience as being informative (Table 1). From this study, there is evidence that informative states are affected both by circumstances external and internal to the participant, that is the cognitive context. Internal differences in expectations reduce response times, and external differences in sensory saliency both reduce response times and increase accuracy. Uninformative states, on the other hand, are *cognitively independent* of external and internal circumstances. This study also supported the robustness of the Perceptual Awareness Scale in terms of exhaustiveness. Despite differences in top-down expectations and sensory saliency, participants could accurately report when they did not experience the stimuli, and thus also when they did not have any information as to the appropriate response.

This claim that there exist uninformative states that are *cognitively independent* from both external and internal circumstances, that is the cognitive context, of course needs to be substantiated by investigating other phenomena and task settings, such as for example priming (Tulving & Schacter, 1990) and differences in working memory load (Lavie, Beck, & Konstantinou, 2014).

In the general discussion, I will discuss whether different levels of informativeness may be reflected in the neural responses that are associated with perceptual consciousness.

# General discussion

## Occipital sources and perceptual consciousness

Everyone agrees on the almost self-evident fact that the visual cortex plays a vital role in realizing perceptual consciousness. There is great disagreement, however, as to what neural activity correlates with becoming conscious of a stimulus. In the influential global neural workspace theory, for example, (Dehaene, 2014), it is acknowledged that occipital activity correlates with graded reports of subjective visibility, but not with the possibility of subjective report (Del Cul et al., 2007; Sergent et al., 2005). Instead, it is argued that fronto-parietal activity P3a, which is claimed to be non-linearly increasing from unconscious to conscious states, correlates with subjective report and is thus the proper neural correlate of perceptual consciousness. Another influential proposal is that reentrant processing in the occipital cortex is the proper neural correlate of perceptual consciousness (Lamme, 2006). According to Lamme, fronto-parietal activity does not correlate with perceptual consciousness since frontal control processes can be activated even in the absence of perceptual consciousness (Lamme, 2010). The division of perceptual consciousness into 2 kinds, *phenomenal* and *access*, can be used to supply some common ground for these 2 seemingly diametrically opposite theories on perceptual consciousness. Block (2005) defines phenomenal consciousness as there being a subjective experience, using Nagel's (1974) expression that for subjective experiences there is something “it is like” to experience, say, the colour of a rotten tomato. Access consciousness on the other hand, he defines, as those contents of the subjective experience that can be used to control reasoning and behaviour. Both theories discussed here agree that access consciousness is a real thing, and that frontal activity reflects becoming access-conscious of stimuli. Where they disagree is whether there is such a thing as phenomenal consciousness at all. Lamme (2006) argued that phenomenal consciousness is a real thing because participants often report seeing more than they explicitly can report (Sperling, 1960), and that the subjective experience is realized by reentrant processing in the occipital cortex. Dehaene et al. (2006), on the other hand, argued that this amounts to an illusion of seeing, where for example change blindness paradigms (Simons & Levin, 1997) provide evidence that participants do not see more than they report, since otherwise it would be inexplicable why they would not notice very noticeable changes going on outside the scope of attention. Whether phenomenal consciousness exists is a thorny issue and is also discussed heavily in philosophical circles (Chalmers, 1997; Dennett, 1993). Instead of entering into this debate, I, in this dissertation, have mainly sidestepped the issue. Instead of arguing that one kind of consciousness is more proper than the other, I have argued that whether phenomenal consciousness exists or not, the neural activity most predictive of subjective ratings of perceptual consciousness should be regarded as the best neural correlate of perceptual consciousness. I argued that multivariate analyses were fit for assessing the predictive capabilities of different spatio-temporal patterns of activity. This was based on the argument that the outcome of a multivariate analysis, the classification accuracy, reflects how consistently a spatio-temporal pattern correlates with differences in perceptual consciousness. Univariate analyses, on the other hand, typically indicate mean differences in amplitude that only indirectly reflect consistency. The intuition followed is that consistency matters more than amplitude. Using that approach we found evidence of occipital sources predicting differences in perceptual consciousness (Study 1: Andersen et al., 2015) more accurately and thus more consistently than frontal sources did (Figure 7). The finding that this was primarily based on the N1-N2 time range (Figure 8) may be argued to be evidence for the validity for the concept of phenomenal consciousness. It is compatible with the view of Lamme (2006) that reentrant processing is what determines whether one will become perceptually conscious or not. On the other hand, the results seem less compatible with global neural workspace theory due to the inferiority of frontal sources relative to occipital sources and the poor predictive capabilities of frontal sources in general (Figures 7 & 8). Thus one might take occipital activity during the N1-N2 time range to be the *proper* neural correlate of perceptual consciousness (Aru et al., 2012). I will now discuss why this may too simple an account, and why one should not necessarily expect these findings to generalize across different tasks.

## Non-integrative and integrative views of perceptual consciousness and cognitive context

A general observation about both the viewpoints of Dehaene (2014) and of Lamme (2006, 2010) discussed above is that they seem to envisage perceptual consciousness and cognitive context as independent of one another (Figure 2). A perception is formed, whether there be phenomenal consciousness or not, and its contents are accessed allowing for appropriate responding. This implies that perception is a process where all content is equally accessible, if need be, for cognitive control and behavioural responding. REFCON (Overgaard & Mogensen, 2014) is an example of a model where perceptual consciousness is dependent on the cognitive context. According to this model, one should not expect a uniquely localizable spatio-temporal neural correlate of perceptual consciousness. More specifically, REFCON proposes that 2 factors may change *where* and *when* one will find correlates. One is the quality of the subjective experience, as can be measured with PAS, and the other is which cognitive strategy is used to solve the task. If the subjective experience is crisp and clear, all cognitive strategies may be available since all features can be accessed. However, if subjective experience is more graded, only a subset of cognitive strategies may be available due to limited access to features. More specifically, REFCON proposes that what correlates with perceptual consciousness is the information that is used to solve the task at hand, thus the interplay of differences in perceptual consciousness and differences in task requirements may cause the best correlate to manifest differently spatio-temporally seen. If perceptual consciousness and cognitive context did not integrate, it would be hard to explain why we found evidence of task requirements influencing how well the 4 PAS ratings could be classified (Figures 10, 11 & 12). One possible explanation is based on the proposal that low-level visual experience, roughly corresponding to our perceptual task, is graded, and that high-level visual experience, roughly corresponding to our conceptual task, is all-or-none (Windey & Cleeremans, 2015). This may explain why we find that the N1-N2 time range could successfully classify all 4 PAS ratings for the perceptual task, but only the dichotomous ratings for the conceptual task. This explanation is unsatisfactory, however, when the bigger picture is considered. It seems to be incompatible with the finding that one of the graded ratings, Almost Clear Experiences, can be classified significantly better during the P3a time range than during the N1-N2 time range in the conceptual task. REFCON is more compatible with these findings, but it is also still an account at a very general level of description. However, the difference in predictive capabilities of N3 between tasks may be an instructive example of the potential usefulness of REFCON, and so may the differences observed between time ranges. It must be emphasized that these explanations below of when specific ratings were best classified were not based on strict hypotheses, but we believe they are instructive in elucidating why cognitive context matters and may form the basis for more specific hypotheses in the future. Our analyses (Figures 10 & 11) indicated that N3 could classify graded states of perceptual consciousness, Weak Glimpses and Almost Clear Experiences, significantly better in the perceptual task compared to the conceptual task. There is evidence that N3 reflects object processing and categorization but not the semantics associated with letters whereas later activity has been associated with the extraction of semantics (Eddy et al., 2006; Hamm et al., 2002; McPherson & Holcomb, 1999). The information processing reflected by N3 may be sufficient for performing the perceptual task above chance, which requires only shape comparison. Therefore, according to REFCON, it is not surprising to see N3 correlating with differences in perceptual consciousness since this activity is directly relevant to behavioural goals in terms of task requirements. In contrast, the N3 activity will not be sufficient for performing the conceptual task above chance since the semantics, vowelhood and consonanthood, needs to be extracted.

Thus REFCON is compatible with the changes in classification found between the time ranges. To understand these differences more generally, it is fruitful to see the differences in PAS ratings as involving differences in informativeness, and what cognitive strategies they allow for. First, I will discuss why this distinction makes sense in terms of the behavioural results from Study 3 (Andersen & Tong, in preparation), and second I will discuss how the distinction between informative and uninformative states can be used to explain some of the results obtained in Study 2 (Andersen, Vinding, Sandberg, & Overgaard, in preparation), and what novel predictions it might lead to.

## Informative and uninformative states

In the domain of perception and responses, a definition of uninformative perceptual states may be that uninformative states are states where neither differences external to the organism nor differences internal to the organism influence its responses, what I earlier have called *cognitive independence*. The data from Study 3 (Andersen & Tong, in preparation) were evidence that participants can use the No Experience rating (Table 1) to accurately indicate when they are in an uninformative state even across different cognitive contexts, such as internal differences in top-down expectations and external differences in sensory saliency. These differences neither influenced accuracy nor response times, and Bayesian analyses provided evidence they were of equal magnitude. A definition of informative perceptual states may conversely be that informative states are states where cognitive context does influence the responses of the organism. The data from Study 3 would thus count as evidence that participants can use the Weak Glimpse, Almost Clear Experience and Clear Experience ratings to indicate that they are in an informative state in that differences in top-down expectations and sensory saliency decreased response times for these 3 ratings selectively. Furthermore despite the influence of top-down expectations and sensory saliency, participants were capable of discerning different gradations of informativeness as accuracy and response times were better the clearer a perception participants reported.

Study 3 in itself could not be used to say anything about the quality of the information associated with an informative state. Differences in quality of information may become apparent, however, if task requirements were manipulated. A strategy may be generally defined as the usage of information in a specific manner. Thus, if different tasks require different cognitive strategies, and if what cognitive strategies are available depends heavily on the quality of the information, then we might expect that different gradations of informativeness will have both behavioural and neural consequences. An example of such a neural difference might exactly be what we found in Study 2. The spatio-temporal differences in when graded perceptual consciousness, Weak Glimpse and Almost Clear Experience, could be classified across tasks (Figures 10 & 11 & 12) may plausibly be a consequence of differences in what cognitive strategies can be applied to solve the task at hand.

The finding that No Experiences can be used by participants to assess that they are in an uninformative state elegantly explains why exactly this rating showed almost no variation in peak classification time across task requirements in Study 2 (Figures 10 & 11). If they are truly *cognitively independent* as Study 3 suggests that they are, activity relevant for classification should be independent of task requirements. The cognitive strategy would be similar across tasks: 1) ascertain the lack of information for the task at hand, 2) carry out a random response (as participants were instructed to in all studies of this dissertation). The aforementioned predictive capabilities of N3 in the perceptual task, which are absent in the conceptual task, may be examples of differences in cognitive strategy that manifest as different spatio-temporal correlates of perceptual consciousness. When all cognitive strategies are available, such as they are theorized to be during Clear Experiences, the optimal cognitive strategy may be to integrate all information before committing to a response. The delayed peaking of Clear Experiences, relative to all other ratings (Figure 11 E-H), around the P3a peak (~ 430-440 ms) may reflect such as integration and broadcasting of all information, such as theorized in the global neural workspace theory (Dehaene, 2014), which would allow for comparison of them being the same type of *letter* and not merely the same shape, which is what Weak Glimpses and Almost Clear Experiences may allow for. If *only* Clear Experiences are associated with seeing stimuli as *letters*, this would explain why the conceptual task cannot discern the graded ratings based on the N3 in the conceptual task; in terms of REFCON the N3 is not related to a useful cognitive strategy for solving the conceptual task. In this sense, our findings are compatible with a theory of a global neural workspace, but importantly such a theory would only be able to explain a subset of the phenomena observed, namely those for Clear Experiences, which are the only ones that show the P3a peak, but not for what we observed for the graded ratings. Proponents of such a theory could bite the bullet and insist that only Clear Experiences are truly conscious and thus maintain a dichotomous view of perceptual consciousness. This would, however, mean that the dividing point between a conscious and an unconscious experience would be whether or not stimuli were *unambiguously* seen, not whether or not there was an experience of *content* (Table 1), which does not seem to be what most people have in mind when discussing perceptual consciousness (Chalmers, 1997; Dehaene, 2014; Lamme, 2006). I must stress that these specific explanations were not predicted by *a priori* hypotheses, but should rather be seen as potential explanations that may motivate further studies into how task requirements may influence the search for neural correlates of perceptual consciousness. However, the more general finding that the greatest differences between tasks would be in the graded ratings was directly motivated by predictions of REFCON.

These explanations should thus motivate researchers to look beyond the possibility of a unifying spatio-temporal "*proper*" (Figure 2: upper level) correlate across all gradations of perceptual consciousness, tasks requirements, cognitive strategies *et cetera*. Thus, I propose, that the data motivate further investigation into an integrated account of perceptual consciousness and cognitive context (Figure 2: lower level).

## Limitations – a philosophical afterthought

It is important here in closing to re-emphasize that there is no final experiment that will enable us to choose between integrative and non-integrative accounts. Proponents of non-integrative accounts insisting that there is one uniquely definable spatio-temporal neural correlate of perceptual consciousness can keep on insisting that without committing any logical fallacies. They may after all insist that we have not eliminated all confounds yet, and that we, if we just search pertinently enough, will find the minimal neural conditions sufficient for perceptual consciousness. The interpretation that I am suggesting especially of the data from Study 2 is not strictly incompatible with a non-integrative account. Study 2 may be taken as a what-if-question, namely: what if we assumed that perceptual consciousness and cognitive context were integrated? How then would we make sense of the data that we observe? Thus my proposal of interpreting brain responses elicited by stimuli in different cognitive contexts from the viewpoint of an integrative account may be understood as a proposal that this is a fruitful way to conceptualize how the brain realizes perceptual consciousness that will generate new predictions and incorporate results in a cohesive manner. Those are the hallmarks of a good theory (Kuhn, 2012).

## Concluding remarks

Descartes (in)famously conjectured that the pineal gland was where the interaction between the mental and the material world occurred. One might liken the search for the (visual) neural correlates of perceptual consciousness to a search for a metaphorical pineal gland. The pineal gland has the attribute of being a relatively stable structure both spatially and temporally during the lifetime of an organism. This dissertation casts doubt on whether the same can be said of the neural correlates of perceptual consciousness. We did find that occipital sources are generally better at predicting differences in perceptual consciousness than frontal sources, and we found evidence of the N1-N2 time range in general being very sensitive to differences in perceptual consciousness, so it might be tempting to conclude that *that* spatio-temporally isolated neural activity is the pineal gland we have been looking for. According to this dissertation, that may be a premature decision. Differences across task requirements provided evidence that *when* and *where* we find neural correlates of perceptual consciousness is dependent on differences in cognitive strategy and differences in the informativeness of perceptual states. Committing to a theoretical approach where perceptual consciousness and cognitive strategy are seen as integrated can explain these differences and may once make us able to make precise predictions as to where and when neural correlates of perceptual consciousness using contrastive analyses will be found. Although, we will never be able to strictly prove that an integrative account is better than a non-integrative account, integrative accounts can show their pragmatic usefulness by generating context-dependent predictions that can be validated. Precisely that pragmatic usefulness is what we should strive after as good scientists.

## Future studies

Behavioural evidence showed that differences both external and internal to the organism affected informative and uninformative states differently. It would be interesting to test how well this finding generalizes to other external and internal differences, such as differences in priming and load of working memory.

Given that cognitive context affects informative and uninformative states differently, it is expected that this would result in effects on the usual event-related components such as the P3a. Furthermore, it might do so qualitatively different in terms of the cognitive strategies the task at hand requires.

The next generation of magnetoencephalographic sensors that can be brought 3 centimetres closer to the head, which potentially increases the signal by a factor of 27, may help to make more precise source estimates of the occipital activity that seems so crucial for realizing the subjective experience of perceptual consciousness we all know so well.

The areas of the brain that were used for classification in this dissertation were coarsely defined. With more nice and specific distinctions, one may be able to look at for example V1 or V2. This would require some functional demarcation as well, which might be possible with the next generation of sensors.

The generality of spatio-temporal patterns can also be tested by applying between-participants analyses, where one participant's signal is used to predict another participant's perceptual consciousness.

# Acknowledgements

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# References

Andersen, L. M., Pedersen, M. N., Sandberg, K., & Overgaard, M. (2015). Occipital MEG Activity in the Early Time Range (<300 ms) Predicts Graded Changes in Perceptual Consciousness. *Cerebral Cortex*, bhv108. http://doi.org/10.1093/cercor/bhv108

Andersen, L. M., & Tong, F. (in preparation). Top-down perceptual expectations affect the gradedness of perception and the evidence weighting of informative levels of perceptions.

Andersen, L. M., Vinding, M. C., Sandberg, K., & Overgaard, M. (in preparation). Task differences induce differences in magnetoencephalographic correlates of consciousness.

Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews*, *36*(2), 737–746. http://doi.org/10.1016/j.neubiorev.2011.12.003

Baars, B. J. (1988). *A Cognitive Theory of Consciousness*. NY, USA: Cambridge University Press.

Berger, P. D. H. (1929). Über das Elektrenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, *87*(1), 527–570. http://doi.org/10.1007/BF01797193

Bishop, C. M. (2006). *Pattern recognition and machine learning*. Cambridge, UK: Springer, USA.

Bishop, G. H. (1932). Cyclic Changes in Excitability of the Optic Pathway of the Rabbit. *American Journal of Physiology -- Legacy Content*, *103*(1), 213–224.

Block, N. (2005). Two neural correlates of consciousness. *Trends in Cognitive Sciences*, *9*(2), 46–52. http://doi.org/10.1016/j.tics.2004.12.006

Busch, N. A., Dubois, J., & VanRullen, R. (2009). The Phase of Ongoing EEG Oscillations Predicts Visual Perception. *The Journal of Neuroscience*, *29*(24), 7869–7876. http://doi.org/10.1523/JNEUROSCI.0113-09.2009

Chalmers, D. J. (1997). *The Conscious Mind: In Search of a Fundamental Theory*. Oxford University Press USA.

Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, *2*, 263–275.

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage*, *9*(2), 179–94.

http://doi.org/10.1006/nimg.1998.0395

Dale, A. M., Liu, A. K., Fischl, B. R., Buckner, R. L., Belliveau, J. W., Lewine, J. D., & Halgren, E. (2000). Dynamic Statistical Parametric Mapping: Combining fMRI and MEG for High-Resolution Imaging of Cortical Activity. *Neuron, 26*(1), 55–67. http://doi.org/10.1016/S0896-6273(00)81138-1

Dehaene, S. (2014). *Consciousness and the Brain: Deciphering How the Brain Codes Our Thoughts*. NY, USA: Penguin.

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–11. http://doi.org/10.1016/j.tics.2006.03.007

Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J.-F., Poline, J.-B., & Rivière, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, *4*(7), 752–758. http://doi.org/10.1038/89551

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology, 5*(10), e260. http://doi.org/10.1371/journal.pbio.0050260

de Morsier, G. (1936). Les automatismes visuels (Hallucinations visuelles rétrochiasmatiques). *Schweizer Medizinische Wochenschrift*, *66*, 700–708.

Dennett, D. C. (1993). *Consciousness Explained*. UK: Penguin.

Descartes, R. (1985). *Meditationes de Prima Philosophia*. (J. Cottingham, Trans.). Cambridge University Press.

Dienes, Z. (2007). Subjective measures of unconscious knowledge. In R. B. and B. K. Chakrabarti (Ed.), *Progress in Brain Research* (Vol. 168, pp. 49–269). Elsevier. Retrieved from http://www.sciencedirect.com/science/article/pii/S0079612307680054

Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic Effect of Combined Temporal and Spatial Expectations on Visual Attention. *The Journal of Neuroscience*, *25*(36), 8259–8266. http://doi.org/10.1523/JNEUROSCI.1821-05.2005

Eddy, M., Schmid, A., & Holcomb, P. J. (2006). Masked repetition priming and event-related brain potentials: A new approach for tracking the time-course of object perception.

*Psychophysiology*, *43*(6), 564–568. http://doi.org/10.1111/j.1469-8986.2006.00455.x

Eriksen, C. W., & Hoffman, J. E. (1972). Temporal and spatial characteristics of selective encoding from visual displays. *Perception & Psychophysics*, *12*(2), 201–204. http://doi.org/10.3758/BF03212870

Faes, L., Nollo, G., Ravelli, F., Ricci, L., Vescovi, M., Turatto, M., … Antolini, R. (2007). Small-sample characterization of stochastic approximation staircases in forced-choice adaptive threshold estimation. *Perception & Psychophysics*, *69*(2), 254–262. http://doi.org/10.3758/BF03193747

ffytche, D. H., Howard, R. J., Brammer, M. J., David, A., Woodruff, P., & Williams, S. (1998). The anatomy of conscious vision: an fMRI study of visual hallucinations. *Nature Neuroscience*, *1*(8), 738–742. http://doi.org/10.1038/3738

Fisch, L., Privman, E., Ramot, M., Harel, M., Nir, Y., Kipervasser, S., … Malach, R. (2009). Neural “Ignition”: Enhanced Activation Linked to Perceptual Awareness in Human Ventral Stream Visual Cortex. *Neuron*, *64*(4), 562–574.

Hämäläinen, M. S., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, *65*(2), 413–497. http://doi.org/10.1103/RevModPhys.65.413

Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: minimum norm estimates. *Medical & Biological Engineering & Computing*, *32*(1), 35–42. http://doi.org/10.1007/BF02512476

Hamm, J. P., Johnson, B. W., & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology*, *113*(8), 1339–1350. http://doi.org/10.1016/S1388-2457(02)00161-X

Hannula, D. E., Simons, D. J., & Cohen, N. J. (2005). Imaging implicit perception: promise and pitfalls. *Nature Reviews Neuroscience*, *6*(3), 247–55. http://doi.org/10.1038/nrn1630

Hyvärinen, A., & Oja, E. (2000). Independent component analysis: algorithms and applications. *Neural Networks*, *13*(4), 411–430.

Koch, C., & Preuschoff, K. (2007). Betting the house on consciousness. *Nature Neuroscience*, *10*(2), 140–141. http://doi.org/10.1038/nn0207-140

Koivisto, M., Lähteenmäki, M., Sørensen, T. A., Vangkilde, S., Overgaard, M., & Revonsuo, A. (2008). The earliest electrophysiological correlate of visual awareness? *Brain and Cognition*, *66*(1), 91–103. http://doi.org/10.1016/j.bandc.2007.05.010

Koivisto, M., & Revonsuo, A. (2003). An ERP study of change detection, change blindness, and visual awareness. *Psychophysiology*, *40*(3), 423–9.

Koivisto, M., & Revonsuo, A. (2008). Comparison of event-related potentials in attentional blink and repetition blindness. *Brain Research*, *1189*, 115–126. http://doi.org/10.1016/j.brainres.2007.10.082

Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience and Biobehavioral Reviews*, *34*(6), 922–34. http://doi.org/10.1016/j.neubiorev.2009.12.002

Kuhn, T. S. (2012). *The Structure of Scientific Revolutions: 50th Anniversary Edition*. University of Chicago Press.

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501. http://doi.org/10.1016/j.tics.2006.09.001

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, *1*(3), 204–220. http://doi.org/10.1080/17588921003731586

Lau, H. C., & Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proceedings of the National Academy of Sciences*, *103*(49), 18763–18768. http://doi.org/10.1073/pnas.0607716103

Laureys, S., Owen, A. M., & Schiff, N. D. (2004). Brain function in coma, vegetative state, and related disorders. *The Lancet Neurology*, *3*(9), 537–546. http://doi.org/10.1016/S1474-4422(04)00852-X

Lauterbur, P. C. (1973). Image Formation by Induced Local Interactions: Examples Employing Nuclear Magnetic Resonance. *Nature*, *242*(5394), 190–191. http://doi.org/10.1038/242190a0

Lavie, N., Beck, D. M., & Konstantinou, N. (2014). Blinded by the load: attention, awareness and the role of perceptual load. *Philosophical Transactions of the Royal Society B: Biological*

*Sciences*, *369*(1641), 20130205. http://doi.org/10.1098/rstb.2013.0205

Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique*. MIT Press.

Macmillan, N. A., & Creelman, C. D. (2005). *Detection theory: a user's guide*. Mahwah, NJ: Erlbaum.

McPherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, *36*(1), 53–65. http://doi.org/10.1017/S0048577299971196

Nagel, T. (1974). What Is It Like to Be a Bat? *The Philosophical Review*, *83*(4), 435–450. http://doi.org/10.2307/2183914

Nieuwenhuis, S., & de Kleijn, R. (2011). Consciousness of targets during the attentional blink: a gradual or all-or-none dimension? *Attention, Perception & Psychophysics*, *73*(2), 364–73. http://doi.org/10.3758/s13414-010-0026-1

Overgaard, M., & Mogensen, J. (2014). Visual perception from the perspective of a representational, non-reductionistic, level-dependent account of perception and conscious awareness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130209. http://doi.org/10.1098/rstb.2013.0209

Overgaard, M., Rote, J., Mouridsen, K., & Ramsøy, T. Z. (2006). Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task. *Consciousness and Cognition*, *15*(4), 700–708. http://doi.org/10.1016/j.concog.2006.04.002

Papanicolaou, A. C. (2009). *Clinical Magnetoencephalography and Magnetic Source Imaging*. UK: Cambridge University Press. Retrieved from http://www.cambridge.org/us/academic/subjects/medicine/neurology-and-clinical-neuroscience/clinical-magnetoencephalography-and-magnetic-source-imaging?format=HB

Persaud, N., McLeod, P., & Cowey, A. (2007). Post-decision wagering objectively measures awareness. *Nature Neuroscience*, *10*(2), 257–61. http://doi.org/10.1038/nn1840

Pins, D., & Ffytche, D. (2003). The neural correlates of conscious vision. *Cerebral Cortex*, *13*(5), 461–74.

Pitts, M. A., Martínez, A., & Hillyard, S. A. (2012). Visual processing of contour patterns under conditions of inattentional blindness. *Journal of Cognitive Neuroscience*, *24*(2), 287–303.

http://doi.org/10.1162/jocn_a_00111

Pitts, M. A., Metzler, S., & Hillyard, S. A. (2014). Isolating neural correlates of conscious perception from neural correlates of reporting one's perception. *Consciousness Research*, *5*, 1078. http://doi.org/10.3389/fpsyg.2014.01078

Polyak, S. (1957). *The Vertebrate Visual System*. (H. Klüver, Ed.). USA: The University of Chicago Press.

Posner, M. I., & Mitchell, R. F. (1967). Chronometric Analysis of Classification. *Psychological Review*, *74*(5), 392–409. http://doi.org/http://dx.doi.org/10.1037/h0024913

Rademaker, R. L., Tredway, C. H., & Tong, F. (2012). Introspective judgments predict the precision and likelihood of successful maintenance of visual working memory. *Journal of Vision*, *12*(13), 21. http://doi.org/10.1167/12.13.21

Ramsøy, T. Z., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, *3*(1), 1–23. http://doi.org/10.1023/B:PHEN.0000041900.30172.e8

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*(3), 849–860. http://doi.org/10.1037/0096-1523.18.3.849

Rees, G., Kreiman, G., & Koch, C. (2002). Neural correlates of consciousness in humans. *Nature Reviews Neuroscience*, *3*(4), 261–270. http://doi.org/10.1038/nrn783

Sandberg, K., Andersen, L. M., & Overgaard, M. (2014). Using multivariate decoding to go beyond contrastive analyses in consciousness research. *Frontiers in Psychology*, *5*, 1250. http://doi.org/10.3389/fpsyg.2014.01250

Sandberg, K., Timmermans, B., Overgaard, M., & Cleeremans, A. (2010). Measuring consciousness: Is one measure better than the other? *Consciousness and Cognition*, *19*(4), 1069–1078. http://doi.org/10.1016/j.concog.2009.12.013

Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, *8*(10), 1391–400. http://doi.org/10.1038/nn1549

Sergent, C., & Dehaene, S. (2004). Is Consciousness a Gradual Phenomenon? Evidence for an All-or-None Bifurcation During the Attentional Blink. *Psychological Science*, *15*(11), 720–728. http://doi.org/10.1111/j.0956-7976.2004.00748.x

Shaffer, J. P. (1995). Multiple Hypothesis Testing. *Annual Review of Psychology*, *46*(1), 561–584. http://doi.org/10.1146/annurev.ps.46.020195.003021

Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, *1*(7), 261–267. http://doi.org/10.1016/S1364-6613(97)01080-2

Skinner, B. F. (1965). *Science And Human Behavior*. Simon and Schuster.

Smith, A. T., Kosillo, P., & Williams, A. L. (2011). The confounding effect of response amplitude on MVPA performance measures. *NeuroImage*, *56*(2), 525–530. http://doi.org/10.1016/j.neuroimage.2010.05.079

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*(11), 1–29. http://doi.org/10.1037/h0093759

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science*, *247*(4940), 301–306. http://doi.org/10.1126/science.2296719

Veser, S., O’Shea, R. P., Schröger, E., Trujillo-Barreto, N. J., & Roeber, U. (2008). Early correlates of visual awareness following orientation and colour rivalry. *Vision Research*, *48*(22), 2359–2369. http://doi.org/10.1016/j.visres.2008.07.024

Weiskrantz, L. (1990). *Blindsight: a case study and implications*. Oxford: Oxford University Press.

Windey, B., & Cleeremans, A. (2015). Consciousness as a graded and an all-or-none phenomenon: A conceptual analysis. *Consciousness and Cognition*, *35*, 185–191. http://doi.org/10.1016/j.concog.2015.03.002

# English summary

What consciousness is is one of the perennial questions that have vexed human beings throughout known history. In this dissertation, I have used magnetoencephalographic recordings to investigate what happens in the brain when one becomes conscious of a visual stimulus. I have also investigated how one can manipulate when and how one becomes conscious. It might seem self-evident that occipital activity is what makes us become conscious of visual stimuli, but many theories regard frontal activity as crucial for becoming conscious of stimuli. Based on 3 experiments and an opinion article, I found that occipital activity best explained the differences in perceived clarity that participants reported. My analysis of the magnetoencephalographic data was based on multivariate analyses since, as we argue in the opinion article, they are more sensitive than traditional univariate analyses are to how consistently spatio-temporal patterns of neural activity correlate with changes in perceptual consciousness. In experiment 1, I found that perceived differences in perceptual consciousness were best explained by occipital activity during an early range (~130-300 ms). This might lead one to believe that exactly this spatio-temporal activity could by itself explain the becoming conscious of visual stimulation. Experiment 2, however, showed that one's theory must be more nuanced, and that task requirements and cognitive strategies influence the timing of activity and which activity that can explain differences in perceptual consciousness. Experiment 3 showed that top-down expectations and sensory saliency changed how informative different levels of perceptual consciousness were, and that participants have insight into when they are in an informative state or not, no matter how minuscule the amount of information is.

Altogether, I have found evidence that the occipital lobe is the most important area for realizing visual perceptual consciousness, but that the exact timing and the involvement of other brain areas depend on the availability of cognitive strategies and how informative one's perceptual state is.

# Dansk resumé

Hvad bevidsthed er, er et af de tilsyneladende evige spørgsmål, som menneskeheden har måttes brydes med igennem historien. Måske vi nu er i en tidsperiode, hvor vi har muligheden for at begynde at svare på det. I denne afhandling har jeg undersøgt, hvordan man ved hjælp af magnetoencefalografi kan afgøre, hvilke dele af hjernens aktivitet der stemmer overens med det at blive bevidst om visuelle indtryk, og hvordan man kan påvirke og forandre denne bliven bevidst. Det kunne virke selvindlysende, at om man bliver bevidst om visuelle sanseindtryk, må afhænge af occipitallappen, siden det er her den tidlige visuelle processering finder sted, men i mange teorier ses aktivitet i frontallappen som afgørende for, om man kan blive bevidst. Baseret på 3 eksperimenter fandt jeg, at generelt set forklarede neural aktivitet i occipitallappen bedst de forskelle i klarheden af visuelle indtryk, som man kan fremprovokere ved hjælp af velkontrollerede eksperimentelle opstillinger. I min analyse af det magnetoencefalografiske data, brugte jeg multivariate analyser, som er følsomme over for, hvor konsistent et bestemt mønster af neural aktivitet sammenfalder med det at blive bevidst om sanseindtryk. I eksperiment 1 fandt jeg, at tidlig aktivitet i occipitallappen (~130-300 ms) konsistent faldt sammen med det at blive bevidst om sanseindtryk. Dette kunne foranledige en til at antage, at præcis denne rum-tidslige aktivitet forklarer bevidsthed i den visuelle sans. Eksperiment 2 viste dog, at billedet måtte være nuanceret, og at man må tage højde for, hvilke mål man har og kognitive strategier man bruger, når man skal afgøre, hvilken aktivitet der sammenfalder med det at blive bevidst. Eksperiment 3 viste, at forventninger til, hvad der ville blive vist, ændrede, hvor informative forskellige bevidsthedstilstande var, og at forsøgspersoner har selvindsigt i, hvornår de er i en informativ tilstand eller ej, hvor lille den mængde information end måtte være.

Alt i alt har jeg fundet evidens for, at aktivitet i occipitallappen er det vigtigste område for at realisere visuel bevidsthed, men at tidspunktet og involvering af andre hjerneområder for denne realisering afhænger af kognitiv strategi og hvor informativ en perceptuel tilstand, man er i.

# Appendices

Appendix I

Paper 1: Using multivariate decoding to go beyond contrastive analyses in consciousness research

Appendix II

Paper 2: Occipital MEG activity in the early time range (< 300 ms) predicts graded changes in perceptual consciousness

Appendix III

Paper 3: Task differences induce differences in magnetoencephalographic correlates of consciousness

Appendix IV

Paper 4: Top-down expectations affect the gradedness of perception and the evidence weighting of informative levels of perceptions

Appendix V

Co-authorship declarations

# Appendix I

frontiers in
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# Using multivariate decoding to go beyond contrastive analyses in consciousness research

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Contrasting conditions with and without awareness has been the preferred method for investigating the neural correlates of consciousness (NCC) for decades, yet recently it has been suggested that further insights can be made by moving beyond this method, specifically by meticulously controlling that potential precursors and consequences of the NCC are not mistaken for an NCC. Here, we briefly review the advantages and potential pitfalls of existing paradigms going beyond the contrastive method, and we propose multivariate decoding of neural activity patterns as a supplement to other methods. Specifically, we emphasize the ability of multivariate decoding to detect which patterns of neural activity are consistently predictive of conscious experiences at the single trial level. This is relevant as the "NCC proper" is expected to be consistently predictive whereas processes that are consequences of consciousness may not occur on every trial (making them less predictive) and prerequisites of consciousness may be present on some trials without conscious experience (making them less predictive).

**Keywords: consciousness, multivariate decoding, multivariate pattern analysis, contrastive analyses, MEG, fMRI**

## THE EVOLUTION OF CONTRASTIVE ANALYSIS

In early outlines of contrastive analyses in consciousness research, emphasis was placed on comparing pairs of psychological phenomena of which one was conscious and the other was not (e.g., Baars, 1994). Behavioral characteristics and neural activity could thus be compared between the conscious and unconscious cases. In the case of vision, for instance, neural activity related to masked and unmasked stimulus presentations (Dehaene et al., 2001) or to stimuli presented at various durations (Kjaer et al., 2001) has been investigated. Over the last two decades, methods have evolved so rapidly that it is now difficult to determine what is a natural extension of the contrastive analysis method and what is an alternative method. In this article, we discuss some of the recent developments, and we consider how multivariate decoding, as an extension of or in combination with contrastive analysis, can contribute to identifying neural correlates of consciousness (NCC).

Many recent paradigms were developed in order to avoid confounds present in the original proposals and experiments. For instance, if stimulus duration is varied, the two conditions no longer differ exclusively in terms of the subjective experience of the participant, but also in terms of an important stimulus characteristic, which could be expected to have an impact on conscious as well as unconscious processing (Overgaard, 2004). For this reason, some scientists have preferred paradigms where the physical parameters remain stable, but only the conscious experience varies. This has been done, for instance, using masked stimuli by contrasting trials based on reports of awareness (e.g., Babiloni et al., 2010). Furthermore, in some relatively early studies participants primarily performed objective tasks, and to the extent that awareness reports were used, they were used to confirm that conditions could be treated as subliminal/supraliminal (Dehaene et al., 2001; Kjaer et al., 2001; Silvanto et al., 2005). In contrast, in some later studies, scientists have more often preferred to base analyses on trial-by-trial reports of awareness (or confidence) even when multiple physical stimulus conditions are used (Christensen et al., 2006; Koivisto, Mäntylä et al., 2010). The use of awareness reports can be seen as a necessary consequence of the wish to control for physical parameters. Methodologically speaking, these reports separate conditions when trials no longer differ in terms of objective characteristics. But their use is also partly a consequence of theoretical arguments in favor of the crucial role of awareness ratings as a key measure of validity in consciousness research (Overgaard, 2006, 2010). Some scientists even prefer to keep accuracy stable so that *only* the level of awareness varies between conditions (Lau and Passingham, 2006; Lau, 2008) or to examine the correlates of accuracy and awareness separately while ensuring that mask and stimulus have very different neural signatures (Hesselmann et al., 2011).

Common to most recent studies is that the need to control for potential confounds has resulted in a shift from the examination of complete unawareness versus complete awareness to the examination of smaller differences in graded awareness ratings or changes in the probability of obtaining reports of awareness. As the change between conscious and unconscious perception occurs more suddenly across stimulus intensity for the attentional blink (than for masking), this paradigm has sometimes been preferred (e.g., Sergent et al., 2005) although others are reluctant to use the paradigm as they suspect it reflects failure to attend (possibly conscious) perception (e.g., Lamme, 2006). Bistable perception provides another method for ensuring both conscious and unconscious perception under equal stimulation conditions. Many earlier studies using ambiguous perception examined differences in neural activity related to ambiguity/non-ambiguity (Lumer et al., 1998) or reversals of perception (Kornmeier and Bach, 2004), but some have also compared neural activity related to one perceptual state versus another (Andrews et al., 2002; Sterzer and Rees, 2008; Sandberg et al., 2013).

## RECENT DEVELOPMENTS

Recently, it has been argued that it is possible that studies using contrastive analyses cannot distinguish between a NCC and its prerequisites (NCC-pr) and consequences (NCC-co; Aru et al., 2012). An NCC-pr is neural activity associated with task specific initial processing (which predicts later conscious experiences) whereas an NCC-co is neural activity related to a process that occurs for conscious stimuli only, for instance encoding in working memory. Aru et al. (2012) have argued that by manipulating stimulus processing in various ways, NCC-pr and NCC-co should change, but the NCC should remain stable. In one experiment, Melloni et al. (2011) manipulated the stimulus expectation across conditions and found that an early EEG component (around 100 ms) only reflected differences between seen and unseen stimuli when there was no expectation of the stimulus, and similarly a later component (the P300) only correlated with awareness when stimuli had to be encoded in working memory, but not when a representation was already present. In contrast, a component between the two, at around 200–300 ms, correlated with conscious perception independently of condition. This indicated that the first component was an NCC-pr, the middle component at 200–300 ms a likely NCC candidate, and the P300 an NCC-co.

Although this method for moving beyond contrastive analysis is certainly novel and useful, it assumes one can evoke the same experience by means of multiple, very different manipulations. However, there is no guarantee that the experience is identical even if the same proportion of awareness responses is obtained across conditions. Ratings of awareness can be viewed as a decision process in which evidence is gathered for a particular response (e.g., Lau, 2008), for example "seen," but when different manipulations are made, the decision axis is no longer shared, and thus it is unknown if the NCC can be expected to remain unchanged (Jannati and Di Lollo, 2012). A potential solution to this could be the use of more detailed awareness ratings, but it may also be possible to improve the paradigm in general using decoding approaches as we will return to later.

Accordingly, we still have no paradigm to investigate NCCs without potential systematic confounds. Newer paradigms, to some degree, have solved problems in previous paradigms, yet have introduced new ones. For this reason, we argue that converging evidence across multiple paradigms is essential in the search for the "NCC proper" (Overgaard, 2011).

## MULTIVARIATE DECODING

Here, we use the term multivariate decoding [also sometimes referred to as multivariate/multi-voxel pattern analysis, pattern classification, "brain reading," or simply decoding (Haynes and Rees, 2006; Norman et al., 2006; Haynes, 2009)] as an umbrella term for a group of analysis techniques for which the goal, in this context, is to decode the conscious experience of a participant based on large amounts of brain data. We will exemplify the general logic behind multivariate decoding by example of a within-subject decoding.

Take an MEG dataset (**Figure 1**), for instance, of a subject with $x$ epochs of class **A** (e.g., "aware") and $x$ epochs of class **B** (e.g., "no awareness"): each data point of each epoch is called a feature. For a given dataset with $n$ sensors/sources and $t$ time points, one will thus have $n$ X $t$ features for each epoch. The dataset is then divided into two parts, a training set (often 90% of the data) and a test set (the remaining 10%; **Figure 1A**). A model is fitted to the training set and each feature is assigned a weight. Dependent on the sign of a given weight, it raises the posterior probability of a given epoch to belong to class **A** or **B**, respectively. The fitted training set, with its feature weights, is then used to predict the class of each epoch for the test set (**Figure 1B**). The predicted class label for a given epoch is the class label that has the highest posterior probability assigned to it when the feature weights for that epoch are summed together. One can then obtain a classification score, which is the percentage of correctly classified epochs. **Figure 1C** shows an example of this. To test the generality of the classification score, one can cross-validate the score by dividing the data set into training and test sets in different ways.

We believe that multivariate decoding has a role in neuroscientific consciousness research for several reasons and in the following we will go through these. We will, however, first emphasize that decoding results should be interpreted with care: although a given mental state can be decoded above chance from particular neural activity, this does not in itself imply a causal relationship. In this sense, multivariate decoding shares some of the limitations of correlation studies. Multivariate decoding, nevertheless, opens up new possibilities that have not previously been available.

## INCREASED SENSITIVITY OF MULTIVARIATE DECODING

One main advantage of multivariate decoding is the greater sensitivity than that of traditional mass-univariate approaches typically used in contrastive analyses (i.e., the testing of single variables one at a time; Haynes and Rees, 2006; Norman et al., 2006). Multivariate decoding is more sensitive that univariate testing due to pooling of information and the informativeness of the co-variance of the features (Haynes and Rees, 2006). Furthermore, univariate tests typically test for linear relationships whereas the nature of the relationship does not need to be specified to achieve successful decoding (Haynes, 2009). The advantage of multivariate decoding in consciousness research has been shown for fMRI where Haynes and Rees (2005) showed that decoding based on V1–V3 voxels combined was more predictive of perception during binocular rivalry than decoding based on the combined mean of the same voxels. Similarly, using MEG Sandberg et al. (2013) showed that perception during binocular rivalry can be decoded at an accuracy just a few percent below peak decoding accuracy (around 75%) using just 10 occipital sensors, which were individually at chance (below 51.5%).

At its core, all univariate testing regards data points as independent of one another, which is evidently false for both MEEG and

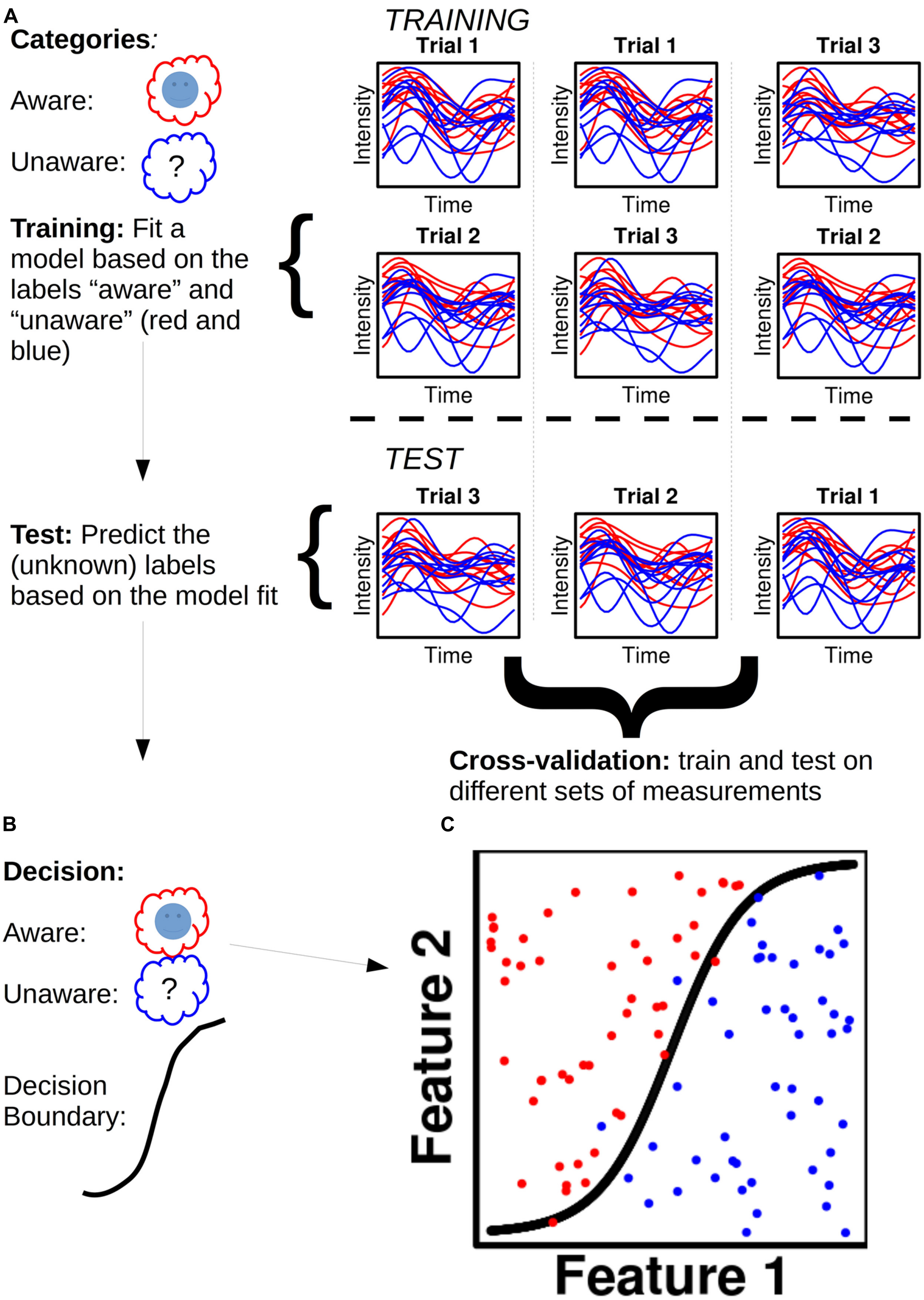


**FIGURE 1 | Illustration of a hypothetical classification analysis and the steps involved. (A)** The classifier is to distinguish between two categories: "Aware" (red) and "Unaware" (blue). Trials are separated into training and test sets in three different ways to ensure cross-validation. The plots show hypothetical activity developing over time courses for ten trials of aware and unaware respectively. **(B)** The decisions reached based on the model fit in the training set. **(C)** Classification is performed for 100 trials (50 aware and 50 unaware) with a non-linear decision boundary.

fMRI data. It is precisely the heavy spatial and temporal correlations of neuroimaging data that make them fit for multivariate analyses. In contrast to univariate tests, multivariate tests can facilitate the information contained in the temporal and spatial dependencies between data points in both sensor and source space (MEEG) and in voxel space (fMRI) in a single test.

## FINDING CONSISTENT CORRELATES USING MULTIVARIATE DECODING

Multivariate tests are more sensitive to differences between conditions that are present during *all* epochs, and that they are less sensitive to differences between conditions that are only present during *some* of the epochs. Indeed, Haynes (2009) emphasized that a core NCC (or "NCC proper") should in principle be able to predict a conscious state perfectly. From this it follows that higher decoding accuracy is generally a sign of greater representational accuracy although it must be emphasized that care should be taken when comparing decoding accuracies across different brain areas, and there are several aspects to consider. For instance, Kamitani and Tong (2006) found that perceived motion direction was only decoded as well from MT+ as from earlier visual areas V1–V4 when the same number of voxels was used. Indeed, a later article by Smith et al. (2011) mention that when comparing fMRI decoding accuracies across conditions, participants, or brain regions, it is important that several factors are controlled for including the number of voxels and stimulus repetitions (and we might add that not only the number of spatial, but also the number of temporal, features should be controlled for). Additionally, they specifically emphasize the importance of controlling for or taking into account the mean amplitude of the component of interest as they show that decoding accuracy increases as a function of mean amplitude even if specificity is not increased. The function with which classifier accuracy increases as a function of response amplitude (measured as percent signal change for fMRI) can nevertheless be estimated and compared across areas for a more valid comparison of decoding accuracy. A simpler, but not always feasible solution is to compare components of equal amplitude.

A note of caution is necessary, however: even when mean amplitude is controlled for, the obtainable signal from two components may differ in their signal-to-noise ratios (for instance, if the angle of the neurons prevents a good signal in MEEG). This necessitates that one is cautious when interpreting differences in accuracy between MEEG components unless one has a good way to estimate differences in noise ceilings. Such estimations are possible with encoding models (Kay et al., 2008) or with representational similarity analysis (Nili et al., 2014), but it is presently an unresolved issue for decoding models and further work in this field is important for ensuring the validity of comparisons of decoding accuracies. It should be emphasized that the issue is not likely to be dramatic and presently a rough estimate of noise ceiling may be achieved by prior knowledge of decoding accuracies across different tasks for various brain regions/components.

Univariate tests are of course sensitive to differences that are present on all epochs, but crucially they can, in addition, be sensitive to differences that appear only on some epochs, but show some average difference between conditions (e.g., aware/unaware). This has important implications for the attempt to separate NCC-pr, NCC, and NCC-co. In **Figure 2**, we show simulated data with three components for which there are average differences between trials reported as "aware" and "unaware" by a participant. We would expect the actual NCC to vary consistently with the conscious experience – whenever the participant has an experience of the stimulus, the relevant component should reflect this. The NCC-pr, however, might be present without the NCC on some trials (i.e., one particular prerequisite of conscious experience was present on a trial, but perhaps some others were not, and the participant thus had no experience) in which case the component becomes an unreliable predictor and should not be assigned high weights by the classifier when all data are taken into account, and it should

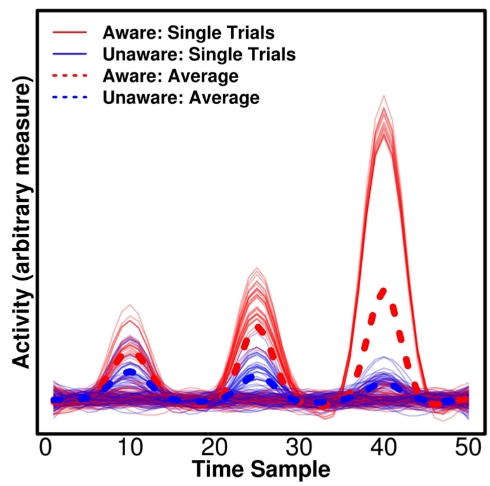


**FIGURE 2 | Consistency of the neural correlates of consciousness (NCC).** Three simulated, hypothetical signals of differing consistency and strength are plotted. All could be candidate NCC, thus reflecting differences between trials classified as "aware" and "unaware" by a participant. For the first component, there is a small average difference, but the component is not consistently larger for "aware" trials, making it unlikely that the component reflects awareness. The component could reflect a prerequisite for consciousness (NCC-pr) as it has to be present for awareness, but it does not guarantee awareness. For the second component, there is a medium average difference, and the component is consistently larger for "aware" trials. On the single trial level, the component thus reflects awareness and it may thus be an actual NCC. Finally, for the third component, there is a large average difference, but the component is only found on a subset of "aware" trials, and it does thus not consistently reflect awareness. The component could thus reflect processes that are consequences of awareness (NCC-co), which occur exclusively for "aware" trials, but may not occur on every single aware trial. Note that traditional univariate statistics based averaged participant-specific averages would erroneously find more evidence for the last component being the NCC proper in this example.

produce suboptimal decoding accuracy when used to train/test the classifier alone. This corresponds to the first component in **Figure 2**. The NCC-co, on the other hand, might not occur after each single NCC component (even if it occurs after some NCC components), and it should never occur without an NCC component. It is thus expected to be similarly suboptimal for decoding even if it produces very large responses on some trials and a large average difference. This corresponds to the third component in **Figure 2**. The actual NCC is thus expected to be consistently the most predictive at the single trial level even if it does not produce the largest average difference. This corresponds to the second component in **Figure 2**. As mentioned above, multivariate decoding approaches are able to identify the most consistent correlates, but traditional univariate analyses typically base statistics on participant-specific means and would in our example find significant evidence in favor of the third component even though it only occurs on some trials. Importantly, if the aim is to compare components, as in our example (**Figure 2**), univariate tests are not readily interpretable. There is no straightforward interpretation of what a difference in amplitude between components means (Luck, 2014). In comparison, the interpretation of differences in decoding accuracy is straightforward – it simply means that the pattern holds more information about the label of the state, say "aware" or "unaware."

In cases where the confounding processes occur on every single trial with an awareness response, multivariate decoding on its own will not be able to distinguish between NCC and NCC-pr/NCC-co as all responses could be equally predictive. For this reason, we believe that the optimal paradigm is a combination of decoding and the methods suggested by Melloni et al. (2011) and Aru et al. (2012). One way to combine methods would be to use cross-task decoding – i.e., using several tasks resulting in similar conscious experiences and training/testing on different tasks using a leave-one-out procedure. In this case, decoding performance should be best for components that generalize across experimental contexts.

Using multivariate decoding on MEG data, a study by our group have found that conscious experience during binocular rivalry was predicted relatively accurately by activity around 130–320 ms after stimulus onset and that an earlier and a later component was not consistently predictive (Sandberg et al., 2013). In an additional (ongoing) MEG study, multivariate decoding furthermore showed that activity around this time was the most predictive of small, graded differences in the clarity of conscious experience on the single trial level (Andersen et al., in preparation). Similarly, decoding can be used on different brain areas in turn in order to compare how consistently predictive these are separately (and/or combined; Norman et al., 2006). For binocular rivalry, this was done for V1–V3 by Haynes and Rees (2005) and across the cortex by Sandberg et al. (2013). Lastly, it should be acknowledged that when doing multivariate analyses, "decoding" is not strictly necessary. There are ways of doing "encoding" as well, where one can extract parameters from the model, as in classical univariate models. Encoding applications are at the moment, however, less available than decoding applications, both theoretically and practically, but see Allefeld and Haynes (2014) for a novel approach.

## OTHER POSSIBILITIES USING MULTIVARIATE DECODING

The use of multivariate decoding opens up for potential research, which would otherwise be difficult or even impossible to conduct. For MEG, conscious experience can be decoded using only a few milliseconds of data gathered within the first 200 ms after stimulus presentations (Sandberg et al., 2013, 2014). Particularly, if near-perfect, near real-time decoding can be achieved, it may be possible to exploit such speed in the control of brain-computer interfaces. At present, one study was able to achieve above 85% decoding accuracy for three of eight participants (and around 95% for one; Sandberg et al., 2013). In comparison, univariate decoding (i.e., using the single best sensor at the single best time point) resulted in lower accuracies (around 10% lower), and would furthermore require both time point and sensor to be specified in advance. Additionally, other studies have shown cases in which multivariate decoding is above chance in the absence of an average activity difference (Sterzer et al., 2008).

Because decoding can be accomplished prior to report, it raises the possibility that an MEG based brain-computer interface could be used to generate changes in the environment even before they are produced by the motor behavior of the individual, which could be of key importance in the study of overt behavior and sense of agency. Furthermore, neural correlates can be analyzed before and after the preparation to report in the attempt to filter out correlates of introspection, metacognition, and motor preparation. And finally, fast and accurate decoding allows for manipulations of stimuli or brain activity (using TMS, for instance) around the time where an event is experienced, but before it is reported, and it may allow for the study of awareness without report.

Haynes and Rees (2006) emphasized the importance of the then unresolved issue of how well activity generalizes over time, across situations (paradigms) and even across participants. This can be examined by conventional methods using correlations, but decoding provides a method of examining whether minor changes are critical or whether the overall patterns are generally maintained. Haynes and Rees (2005) used fMRI to examine drops in decoding accuracy across days, but the first long-term study was conducted by Sandberg et al. (2014), who found that the decrease in decoding accuracy within participants across 2.5 years was only around 1%, which was comparable to the drop across a few days. This study also found that the drop when attempting to generalize across participants (even at the source level) was much greater (around 10%). Further studies examining whether minor details in patterns of activity predict related changes in perceptual experience can be used to address theoretical questions about multiple realization in the brain.

It has also been established that it is possible to decode the conscious experience of one individual using a classifier trained on a different individual although the accuracy is lower than for within-individual decoding (Poldrack et al., 2009; Haxby et al., 2011; Sandberg et al., 2013, 2014). This opens up possibilities that so far have been outside the reach of cognitive neuroscience methods. One might apply multivariate decoding to investigate whether neural correlates generated in experiments using one paradigm can be used to train a classifier to decode the experience in other paradigms as we discuss above. Furthermore, between-participant decoding opens possibilities of decoding across groups for which it is uncertain whether one has conscious experiences, such as vegetative or minimally conscious patients. When consciousness has been examined in non-human animals, methods such as flash suppression have been used to ensure the validity of report as the stimuli are bistable but conscious perception can be manipulated by the experimental setup (Sheinberg and Logothetis, 1997). Such or similar methods could in principle also be used with patients, and it could be possible to decode both within individuals but also to examine how well classifiers generalize from healthy individuals to reduced consciousness patients. Here again, the improved accuracy of multivariate decoding provides an advantage compared to univariate approaches.

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## REFERENCES

Allefeld, C., and Haynes, J.-D. (2014). Searchlight-based multi-voxel pattern analysis of fMRI by cross-validated MANOVA. *Neuroimage* 89, 345–357. doi: 10.1016/j.neuroimage.2013.11.043

Andrews, T. J., Schluppeck, D., Homfray, D., Matthews, P., and Blakemore, C. (2002). Activity in the fusiform gyrus predicts conscious perception of Rubin's vase-face illusion. *Neuroimage* 17, 890–901. doi: 10.1006/nimg.2002.1243

Aru, J., Bachmann, T., Singer, W., and Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neurosci. Biobehav. Rev.* 36, 737–746. doi: 10.1016/j.neubiorev.2011.12.003

Baars, B. (1994). A Thoroughly Empirical Approach To Consciousness. *Psyche* 1, 1–25.

Babiloni, C., Vecchio, F., Buffo, P., Buttiglione, M., Cibelli, G., and Rossini, P. M. (2010). Cortical responses to consciousness of schematic emotional facial expressions: a high-resolution EEG study. *Hum. Brain Mapp.* 31, 1556–1569. doi: 10.1002/hbm.20958

Christensen, M. S., Ramsøy, T. Z., Lund, T. E., Madsen, K. H., and Rowe, J. B. (2006). An fMRI study of the neural correlates of graded visual perception. *Neuroimage* 31, 1711–1725. doi: 10.1016/j.neuroimage.2006.02.023

Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nat. Neurosci.* 4, 752–758. doi: 10.1038/89551

Haxby, J. V., Guntupalli, J. S., Connolly, A. C., Halchenko, Y. O., Conroy, B. R., Gobbini, M. I., et al. (2011). A common, high-dimensional model of the representational space in human ventral temporal cortex. *Neuron* 72, 404–416. doi: 10.1016/j.neuron.2011.08.026

Haynes, J.-D. (2009). Decoding visual consciousness from human brain signals. *Trends Cogn. Sci.* 13, 194–202. doi: 10.1016/j.tics.2009.02.004

Haynes, J.-D., and Rees, G. (2005). Predicting the stream of consciousness from activity in human visual cortex. *Curr. Biol.* 15, 1301–1307. doi: 10.1016/j.cub.2005.06.026

Haynes, J.-D., and Rees, G. (2006). Decoding mental states from brain activity in humans. *Nat. Rev. Neurosci.* 7, 523–534. doi: 10.1038/nrn1931

Hesselmann, G., Hebart, M., and Malach, R. (2011). Differential BOLD activity associated with subjective and objective reports during "blindsight" in normal observers. *J. Neurosci.* 31, 12936–12944. doi: 10.1523/JNEUROSCI.1556-11.2011

Jannati, A., and Di Lollo, V. (2012). Relative blindsight arises from a criterion confound in metacontrast masking: implications for theories of consciousness. *Conscious. Cogn.* 21, 307–314. doi: 10.1016/j.concog.2011.10.003

Kamitani, Y., and Tong, F. (2006). Decoding seen and attended motion directions from activity in the human visual cortex. *Curr. Biol.* 16, 1096–1102. doi: 10.1016/j.cub.2006.04.003

Kay, K. N., Naselaris, T., Prenger, R. J., and Gallant, J. L. (2008). Identifying natural images from human brain activity. *Nature* 452, 352–355. doi: 10.1038/nature06713

Kjaer, T. W., Nowak, M., Kjaer, K. W., Lou, A. R., and Lou, H. C. (2001). Precuneus-prefrontal activity during awareness of visual verbal stimuli. *Conscious. Cogn.* 10, 356–365. doi: 10.1006/ccog.2001.0509

Koivisto, M., Mäntylä, T., and Silvanto, J. (2010). The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. *Neuroimage* 51, 828–834. doi: 10.1016/j.neuroimage.2010.02.042

Kornmeier, J., and Bach, M. (2004). Early neural activity in Necker-cube reversal: evidence for low-level processing of a gestalt phenomenon. *Psychophysiology* 41, 1–8. doi: 10.1046/j.1469-8986.2003.00126.x

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends Cogn. Sci.* 10, 494–501. doi: 10.1016/j.tics.2006.09.001

Lau, H. C. (2008). A higher order Bayesian decision theory of consciousness. *Prog. Brain Res.* 168, 35–48. doi: 10.1016/S0079-6123(07)68004-2

Lau, H. C., and Passingham, R. E. (2006). Relative blindsight in normal observers and the neural correlate of visual consciousness. *Proc. Natl. Acad. Sci. U.S.A.* 103, 18763–18768. doi: 10.1073/pnas.0607716103

Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique,* 2nd Edn. Cambridge, MA: The MIT Press.

Lumer, E. D., Friston, K. J., and Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science* 280, 1930–1934. doi: 10.1126/science.280.5371.1930

Melloni, L., Schwiedrzik, C. M., Müller, N., Rodriguez, E., and Singer, W. (2011). Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. *J. Neurosci.* 31, 1386–1396. doi: 10.1523/JNEUROSCI.4570-10.2011

Nili, H., Wingfield, C., Walther, A., Su, L., Marslen-Wilson, W., and Kriegeskorte, N. (2014). A toolbox for representational similarity analysis. *PLoS Comput. Biol.* 10:e1003553. doi: 10.1371/journal.pcbi.1003553

Norman, K. A., Polyn, S. M., Detre, G. J., and Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends Cogn. Sci.* 10, 424–430. doi: 10.1016/j.tics.2006.07.005

Overgaard, M. (2004). Confounding factors in contrastive analysis. *Synthese* 141, 217–231. doi: 10.1023/B:SYNT.0000043019.64052.e0

Overgaard, M. (2006). Introspection in science. *Conscious. Cogn.* 15, 629–633. doi: 10.1016/j.concog.2006.10.004

Overgaard, M. (2010). How consciousness will change our view on neuroscience. *Cogn. Neurosci.* 1, 224–225. doi: 10.1080/17588928.2010.497585

Overgaard, M. (2011). Visual experience and blindsight: a methodological review. *Exp. Brain Res.* 209, 473–479. doi: 10.1007/s00221-011-2578-2

Poldrack, R. A., Halchenko, Y. O., and Hanson, S. J. (2009). Decoding the large-scale structure of brain function by classifying mental States across individuals. *Psychol. Sci.* 20, 1364–1372. doi: 10.1111/j.1467-9280.2009.02460.x

Sandberg, K., Bahrami, B., Kanai, R., Barnes, G. R., Overgaard, M., and Rees, G. (2013). Early visual responses predict conscious face perception within and between subjects during binocular rivalry. *J. Cogn. Neurosci.* 25, 969–985. doi: 10.1162/jocn_a_00353

Sandberg, K., Barnes, G. R., Rees, G., and Overgaard, M. (2014). Magnetoencephalographic activity related to conscious perception is stable within individuals across years but not between individuals. *J. Cogn. Neurosci.* 26, 840–853. doi: 10.1162/jocn_a_00525

Sergent, C., Baillet, S., and Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nat. Neurosci.* 8, 1391–1400. doi: 10.1038/nn1549

Sheinberg, D. L., and Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proc. Natl. Acad. Sci. U.S.A.* 94, 3408–3413. doi: 10.1073/pnas.94.7.3408

Silvanto, J., Lavie, N., and Walsh, V. (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cereb. Cortex* 15, 1736–1741. doi: 10.1093/cercor/bhi050

Smith, A. T., Kosillo, P., and Williams, A. L. (2011). The confounding effect of response amplitude on MVPA performance measures. *Neuroimage* 56, 525–530. doi: 10.1016/j.neuroimage.2010.05.079

Sterzer, P., Haynes, J.-D., and Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. *J. Vis.* 8, 10.1–12. doi: 10.1167/8.15.10

Sterzer, P., and Rees, G. (2008). A neural basis for percept stabilization in binocular rivalry. *J. Cogn. Neurosci.* 20, 389–399. doi: 10.1162/jocn.2008.20039


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# Appendix II

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Original Article

ORIGINAL ARTICLE

# Occipital MEG Activity in the Early Time Range (<300 ms) Predicts Graded Changes in Perceptual Consciousness

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## Abstract

Two electrophysiological components have been extensively investigated as candidate neural correlates of perceptual consciousness: An early, occipitally realized component occurring 130–320 ms after stimulus onset and a late, frontally realized component occurring 320–510 ms after stimulus onset. Recent studies have suggested that the late component may not be uniquely related to perceptual consciousness, but also to sensory expectations, task associations, and selective attention. We conducted a magnetoencephalographic study; using multivariate analysis, we compared classification accuracies when decoding perceptual consciousness from the 2 components using sources from occipital and frontal lobes. We found that occipital sources during the early time range were significantly more accurate in decoding perceptual consciousness than frontal sources during both the early and late time ranges. These results are the first of its kind where the predictive values of the 2 components are quantitatively compared, and they provide further evidence for the primary importance of occipital sources in realizing perceptual consciousness. The results have important consequences for current theories of perceptual consciousness, especially theories emphasizing the role of frontal sources.

**Key words:** classification, consciousness, magnetoencephalography, neural correlate of consciousness, perception



## Introduction

Ever since Baars (1988) argued for the possibility of investigating perceptual consciousness using contrastive analyses, perceptual consciousness has been investigated with a number of methods. For example, functional magnetic resonance imaging (fMRI) studies have identified activity in frontal (Dehaene et al. 2001; Lau and Passingham 2006) and occipital (Ffytche et al. 1998) areas as candidate neural correlate(s) of consciousness (NCC(s)). Electroencephalographic studies have shown that there are at least 3 event-related potentials (ERPs) of interest for perceptual consciousness, about 100, 200, and 400 ms after the onset of a stimulus with source reconstructions localizing them in the occipital lobes, occipito-temporal lobes, and fronto-parietal lobes, respectively (Sergent et al. 2005; Fahrenfort et al. 2007; Veser et al. 2008), which is in agreement with the above-mentioned fMRI findings. Magnetoencephalographic (MEG) studies have reported event-related fields (ERFs) corresponding to these ERPs (Vanni et al. 1996; Liu et al. 2012; Sandberg et al. 2013). In this study, we examine which spatial and temporal components of the MEG are the most predictive of graded levels of perceptual consciousness in a visual identification task. Before describing our study in greater detail, some theoretical distinctions must be made and some theories must be recounted.

The main distinctions relate to the definition of consciousness. Most importantly, it should be noted that we investigate conscious contents and not conscious states. Examples of differences in conscious states are differences between being awake, being asleep, being in a coma, etc. (Laureys et al. 2004). An example of a difference in conscious content is whether or not a briefly flashed stimulus was perceived. A further distinction can be made between becoming conscious of a stimulus and remaining conscious of that stimulus. Most commonly, stimuli are presented briefly or obscured in some manner in consciousness experiments, and the activity that predicts whether or not a stimulus was perceived consciously is examined. It is this "becoming conscious" of a stimulus that we examine in this study. Alternatively, one might examine the sustained activity related to consciously perceiving a stimulus for as long as it is presented. We do not examine this aspect as it would require a very different experimental paradigm.

A final distinction can be made between phenomenal consciousness, the experience of perceiving something, and access consciousness, the availability of these perceptions for action preparation, verbal report, etc. (Block 2005). Although conceptually important, this distinction is nevertheless very difficult to make experimentally as most studies, including the present, rely on participants' reports for separating trials into what degree stimuli were consciously perceived. For this reason, we do not interpret our findings in terms of access and phenomenal consciousness, and we do not make any claims as to whether our results reflect one or the other.

The experimental findings mentioned in the first paragraph are reflected in a number of theories about which specific activities correlate directly with perceptual consciousness. Crucially for the present study, these theories differ as to whether "early" differences in occipital activity around 130–300 ms (the N1 and N2 components) or "late" differences in frontal activity after 300–600 ms (the P3a) constitute the proper NCC (Aru, Bachmann, et al. 2012). There are also studies suggesting that changes in the P1 component (100 ms; Pins and Ffytche 2003; Veser et al. 2008) correlate with differences in perceptual consciousness, but these differences are reported much less consistently than for the N1, N2, and P3a components [for a review, see Koivisto and Revonsuo (2010)]. Evidence has also been reported for the P1 component correlating with differences in attention (Aru, Axmacher, et al. 2012) rather than perceptual consciousness per se. For these reasons, the P1 is generally not considered a main candidate for the correlate of perceptual consciousness, and the components of interest in the present study are thus the N1/N2 and the P3a.

In the Global Workspace Theory (GWT) of Baars (2005), the variation of it by Dehaene et al. (2006) and Dehaene (2014), and in the Higher-Order Thought (HOT) theory of consciousness (Lau and Rosenthal 2011), differences in late (P3a) frontal activity correlate with differences in perceptual consciousness. The frontal activity is theorized to reflect global broadcasting of perceptually integrated stimuli, and it is this broadcasting that makes it conscious according to the GWT. Sergent et al. (2005) argued that frontal components after 300 ms correlate with perceptual consciousness in a bimodal manner: Absent when participants are not conscious of a stimulus, and present when participants are conscious of a stimulus.

The P3a component has been observed to be bimodal in several experiments (Del Cul et al. 2007; Koivisto and Revonsuo 2010), including infant studies (Kouider et al. 2013), and to be absent in patients with prefrontal damage (Del Cul et al. 2009). According to GWT proponents, the bimodality of the proposed NCC suggests that perceptual consciousness is dichotomous: You either see something or you do not. We thus have one set of theories and studies, arguing that consciousness is dichotomous and related to the late P3a component and to activity (mainly) in frontal cortical areas.

In contrast, in the recurrent processing theory of Lamme (2006) and the research on the Visual Awareness Negativity (VAN) of Koivisto and Revonsuo (2010), differences in early occipital activity (N1/N2) are found to be the best correlate of differences in perceptual consciousness. Recurrent processing between higher and lower regions of the occipital lobes is theorized to be sufficient for perceptual consciousness in Lamme's theory (2006).

Furthermore, several behavioral studies have indicated that perceptual consciousness is better understood as graded with levels between conscious and unconscious (Overgaard et al. 2006, 2010; Sandberg et al. 2010; Nieuwenhuis and de Kleijn 2011; Wierzchoń et al. 2012).

An important consequence of the proposal that perceptual consciousness is graded is that more than one NCC may exist. Hypothetically, each grade of experience may be associated with activity in a different cortical area, or it may depend on different levels of activity in a single area. For instance, the Perceptual Awareness Scale (PAS; Ramsøy and Overgaard 2004), used in numerous studies (Ruzzoli et al. 2010; Melloni et al. 2011; Ludwig et al. 2013; Faivre and Koch 2014), has 4 qualitatively different ratings. The differences between the neighboring ratings can be summarized as follows: First and second ratings: the presence of subjective experience as such; second and third ratings: the presence of (unclear) content; third and fourth ratings: the presence of perceptually clear and unambiguous content. It is thus possible that we should not just be looking for one all-or-none component predicting perceptual consciousness, but instead several components or a graded modulation of a single component. The occipito-temporal N2 has been observed to vary in a graded manner (Sergent et al. 2005), and it may thus be argued that this component is in fact a more likely correlate of perceptual consciousness.

Recent electrophysiological studies also cast doubt on whether late frontal components specifically correlate with perceptual consciousness. Melloni et al. (2011) found that sensory expectations influence the amplitude of the late frontal component, but not that of the early occipital component. Pitts et al. (2012) found that the late frontal component disappeared for conscious percepts that were not task-associated. Even with no task association, the early occipital component still correlated with perceptual consciousness. Koivisto and Revonsuo (2007) found that the late frontal component interacted with selective attention, whereas the early occipital component did not. Sandberg et al. (2013) were able to decode which of 2 rivaling percepts the participant was conscious of, using only activity at occipital and temporal sources around 130–320 ms, and activity from these sources was more predictive than that at frontal sources at any time point.

Taken together, one set of theories and experimental findings argue in favor of a dichotomous, late frontal component being the main correlate of perceptual consciousness, and another set of theories and experimental findings argue in favor of graded, earlier occipital or occipito-temporal activity. We have previously suggested that one way of providing evidence relevant to this debate is to examine the predictive power of the components in question (Sandberg et al. 2014). Specifically, we have argued that the correlate of perceptual consciousness should be at least as predictive of reports on a perceptual consciousness scale as any process that is only a prerequisite of perceptual consciousness (which may sometimes lead to perceptual consciousness and sometimes not) or a potential consequence of consciousness (which may or may not occur consistently every time perceptual consciousness is present). For this reason, we conducted an MEG study of masked visual identification examining which spatial and temporal components of the MEG signal were the most predictive of perceptual consciousness. Specifically, we examined whether participants reported graded levels of perceptual consciousness, and whether these levels could be decoded from the MEG signal using multivariate classification algorithms trained and tested on data from a wide set of cortical sources primarily at the time windows of the P3a and the VAN (N1/N2).

## Materials and Methods

### Participants

Nineteen right-handed male participants with a normal or corrected-to-normal vision gave written informed consent to participate. Their age was 26.6 years on average (range: 21–37 years, SD: 4.4 years). The local ethics committee, De Videnskabsetiske Komitéer for Region Midtjylland, provided written confirmation that no ethical approval was required for the study according to the Danish law, specifically Komitéloven §7 and §8.1.

One participant misunderstood instructions and did not respond on the identification task when he had no experience of the target. With 2 other participants, there were problems with their Head Position Indicator (HPI) coils and head positions could thus not be monitored. Two participants reported claustrophobic reactions and did not complete the experiment. One participant did not use the "Almost Clear Experience" (ACE) rating at all (see definitions below) and could thus not be included in the analyses comparing the PAS ratings. Submission of the data to the MaxFilter (see below) of another participant returned an error that could not be resolved. Finally, one participant's contrasts were uniformly distributed among all possible contrasts, indicating that the staircase did not work for him. In summary, data from 8 participants were thus excluded before analyses.

### Stimuli and Procedure

A visual masking paradigm was used (Fig. 1A). Participants were seated 60 cm from the screen. A Panasonic PT-D10000E projector was used with a resolution of 1200 × 1024 pixels and a frequency of 60 Hz. A fixation cross was presented for 500, 1000, or 1500 ms,

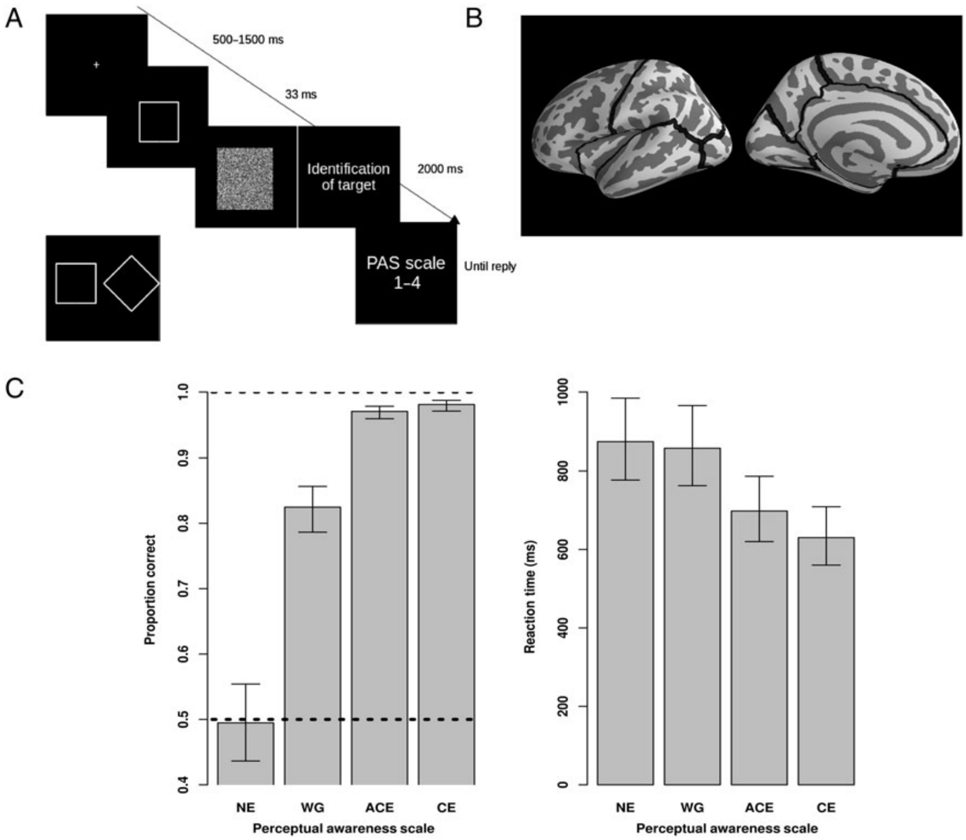


**Figure 1.** Paradigm, stimuli, and behavioral results. (*A*) Paradigm and stimuli: First, a fixation cross was presented for either 500, 1000, or 1500 ms. Following that, the target (1 of 2 figures, rectangle or rotated rectangle) was presented for 33.3 ms. This was immediately followed by a static noise mask presented for 2000 ms. During these 2000 ms, participants reported the identity of the target by a button press with one hand. Finally, they indicated the clarity of their experience using the PAS (Table 1). A contrast staircase, a modified 2-up-1-down, was used throughout the experiment. In the lower left of A are the 2 target stimuli used throughout the experiment. (*B*) Definition of lobes: Lobes overlaid on inflated cortex (left hemisphere) of the fsaverage map. A lateral (left) and a medial (right) view is shown with the borders between the lobes highlighted (*C*) Behavioral results: Only responses that were within the time limit are plotted. Proportion correct and response times are shown for the identification task, which have been categorized according to the subsequently reported PAS rating. Mean proportion correct (left) for each PAS rating. Error bars are 95% confidence intervals. The punctured lines represent chance and ceiling. Response times (right) for each PAS rating with 95% confidence intervals.

**Table 1** The Perceptual Awareness Scale (PAS)

| Label | Description [from Ramsøy and Overgaard (2004)] |
|---|---|
| (1) No Experience (NE) | No impression of the stimulus. All answers are seen as mere guesses. |
| (2) Weak Glimpse (WG) | A feeling that something has been shown. Not characterized by any content, and this cannot be specified any further. |
| (3) Almost Clear Experience (ACE) | Ambiguous experience of the stimulus. Some stimulus aspects are experienced more vividly than others. A feeling of almost being certain about one's answer. |
| (4) Clear Experience (CE) | Non-ambiguous experience of the stimulus. No doubt in one's answer. |

Note: Scale steps and their descriptions.

followed by 1 of 2 target rectangles, presented for 33.3 ms (2 frames), which were rotated 45° relative to each other (size: 1.34 × 1.02° of visual angle; Fig. 1A). Presentation of the target was followed by a static random noise mask that was presented for 2000 ms. During these 2000 ms, participants were to identify the presented figure by a button press on a response box (ID box). Following the identification of the target, participants were to rate their conscious experience on the PAS using 1 of 4 categories (Table 1). No Experience (NE): Nothing at all was seen; Weak Glimpse (WG): A feeling of having seen something, which cannot be described further; Almost Clear Experience (ACE): An ambiguous experience of the stimulus, some aspects are experienced more clearly than others; Clear Experience (CE): An unambiguous and clear experience. Pressing the upper button of a second response box (PAS box) enabled participants to cycle through the 4 categories. The lower button was used to confirm the selection of the PAS category that the cursor was situated on. At the beginning of PAS selection, the cursor was not present on the screen. By the first press of the upper button, it would appear on the NE category. In the beginning of the experiment, the ID box was the box in the participant's right hand and the PAS box the one in the participant's left hand. In every 36 trials, the functions of the 2 boxes swapped such that the ID box became the one in the left hand and the PAS box the one in the right hand or vice versa.

Before participants were tested in the magnetically shielded room, they completed a short practice session of 32 trials of varying contrast. The purpose of the session was to accustom participants to the experimental procedure and to instruct them in how to use the PAS categories. During the practice session, participants received feedback about the correctness of their identifications. Participants were instructed to use "No Experience" (NE) when they had no conscious experience at all, "Weak Glimpse" (WG) when they had a conscious experience of a target appearing on the screen, but with no experience of its features, "Almost Clear Experience" (ACE) when they had a conscious experience of a target and some of its features, and "Clear Experience" (CE) when they had a conscious experience of a target and all of its features. Extra care was given in instructing participants in the difference between ACE and CE, because their names are semantically very close to one another. Participants were given as an example of an ACE contra a CE the clearer experiencing of the 2 lines that make up the upper left angle of a rectangle versus the equally clear experiencing of all 4 lines of a rectangle. All participants except one had used all categories after the practice session and reported that the 4 categories were experientially distinguishable to them. Finally, they were instructed that they were to describe the clarity of their experiences and not how confident they were in having made the correct identification.

In the magnetically shielded room, participants went through 1 practice block and 11 experimental blocks, each consisting of 72 trials. Participants received feedback on the identification task only during the practice trials. Between blocks, participants were encouraged to rest a little and move their limbs (not their heads). Furthermore, participants were notified by a message every 36 trials that the functions of the response boxes changed, in the manner explained earlier.

Because our planned statistical contrasts included the 4 levels of PAS ratings, a sufficient amount of responses for each PAS rating was necessary, and a contrast staircase was therefore used. All stimuli were white/gray on a black (RGB value of 0, 0, 0) background. The staircase had 26 contrast levels with the clearest level equivalent to a contrast of 77% (with 100% equivalent to an RGB value of 255, 255, 255) and the dimmest level equivalent to a contrast of 2% (with 0% equivalent to an RGB value of 0, 0, 0). All steps were of 3%. During the practice block and the first experimental block, 2 successive correct answers on the identification task resulted in going 2 levels down the staircase (making the stimulus dimmer), whereas 1 wrong answer resulted in going 1 level up the staircase (making the stimulus brighter). The contrast level was 14% or lower for all participants at the end of the practice trials. For each experimental block after the first, that is, blocks 2–11, the staircase adapted based on which PAS rating the participant had responded the least with throughout the experiment so far. If NE had been used the least number of times during a block, 3 levels were subtracted after 2 successive correct answers, and only 1 added for a wrong answer. If WG had been used the least number of times, 2 levels were subtracted and 1 added. For ACE, 1 level was subtracted and 2 added. Finally, for CE, 1 level was subtracted and 3 added.

Distributed pseudorandomly across the experiment, approximately 72 "catch trials" containing no stimulus were presented.

## Magnetoencephalography

MEG data were recorded in a magnetically shielded room with an Elekta Neuromag Triux system with 102 magnetometers and 204 orthogonal planar gradiometers with a recording frequency of 1000 Hz. Offline, a Maxwell Filter was used to apply spatio-temporal Signal Space Separation (tSSS), which separates the brain signal from the external disturbances outside the sensor array, leaving only the brain signal. After applying tSSS, movement compensation was applied based on continuous HPI measurements with a step size of 30 ms. tSSS and movement compensation were both performed using the MaxFilter, version 2.2 (Elekta). Five HPI coils were used, one behind each ear, one on the left and right temples, respectively, and the final one on the forehead. Head shape was digitized using a Polhemus Fasttrack Digitizer (Colchester, Vermont, USA). The head shape of the participant was later used to create the forward model for each participant.

Data were analyzed using MNE-python (Gramfort et al. 2013). The data were bandpass-filtered (0.5–15 Hz, Butterworth) and epoched into epochs of −200 to −600 ms around the target and downsampled to 250 Hz. The upper boundary of 15 Hz was selected as both components of interest, the VAN and the P3a, have a frequency of approximately 7 Hz. Therefore, a filter removing frequencies above this will generate the greatest statistical power. Independent component analysis (Hyvärinen and Oja 2000) was used to remove eye blinks and eye movements by removing the component that correlated most with the horizontal and vertical electrooculograms.

### Source Reconstruction

Source reconstruction was done using the minimum norm estimate (MNE) algorithm (Hämäläinen et al. 1993). MNE assumes minimal prior information, only that the source currents are spatially restricted. We aimed to model 8196 sources for each participant based on participant-specific cortical reconstructions and volumetric segmentations. The cortical reconstructions were modeled using FreeSurfer (http://surfer.nmr.mgh.harvard.edu/ [date last accessed; 11 May 2015]; Dale et al. 1999).

Dynamic statistical parametric mapping was used to overcome the superficial bias of MNE (Dale et al. 2000). We ran a separate source reconstruction for each of the 3 PAS comparisons. For each comparison, we used the shared maximum number of trials for each PAS rating. Because differences in stimuli contrasts can induce differences in a given NCC (Fisch et al. 2009), we only used trials with the same contrast level in our tests. Furthermore, we ensured that there was an equal amount of left-handed and right-handed responses to prevent the classifier from using motor activity associated with a perceptual state to classify trials (Sandberg et al. 2013).

Owing to individual anatomical differences, participants had different numbers of reconstructed sources in each lobe. The average amount of modeled sources in each participant was 8194 (min. = 8175, max. = 8196). For the frontal lobe, it was 2490 (min. = 2283, max. 2654); for the occipital lobe, it was 698 (min. = 585, max. = 821); for the parietal lobe, it was 2254 (min. = 2165, max. 2298); and for the temporal lobe, it was 1426 (min. = 1289, max. = 1539). The lobes were defined using the Desikan–Killiany Atlas (Desikan et al. 2006). See Figure 1B for the lobes displayed on the “fsaverage” template from FreeSurfer.

### Multivariate Analyses (Within Participants)

We used a logistic regression classifier (Bishop 2006). We conducted 5 different runs with the classifier per PAS comparison (NE versus WG, WG versus ACE, and ACE versus CE), one with all sources included, and one with occipital, temporal, parietal, and frontal sources separately. The analyses were run within participants. We used stratified 5-fold cross-validation to ensure an equal amount of trials with left- and right-handed responses in each training set. Only correct trials were included, such that the influence of performance on decoding accuracy was minimized.

Thus, classification accuracy was calculated for each source group for each participant tested. The theoretical chance level was 50% since there was an equal number of trials for each comparison. We used L1-regularization, sparse weighting.

This classification analysis was run for an early range (VAN: 132–320 ms) and for a late range (P3a: 324–512 ms). These ranges were of equal duration (i.e., the number of temporal features was controlled) to ensure that they could be compared meaningfully (Sandberg et al. 2014). We thus specifically tested whether the early range or the late range was the more informative by comparing their classification accuracies to one another. For the 3 PAS comparisons, this resulted in the following median number of trials per participant: NE versus WG = 24, WG versus ACE = 34, and ACE versus CE = 30. It should be noted that the number of trials used in the analysis for a given participant did not predict classification accuracy (see control analysis reported in Fig. 5B).

### Group-Level Analysis

The main objective of this analysis was to compare frontal and occipital lobes as to which was the better for classifying perceptual consciousness. We investigated this in the VAN time range and in the P3a time range since both these have been reported as correlating with perceptual consciousness. This was done for each of the 3 neighboring PAS comparisons, NE–WG, WG–ACE, and ACE–CE. More exploratively, the temporal and parietal lobes and the full brain were also investigated.

We fitted models with accuracy of the classifier as the dependent variable. Participants were modeled as having a unique intercept, that is, a random effect. Three fixed effects were of interest: PAS comparison (3 levels: NE–WG, WG–ACE, and ACE–CE), Lobe (5 levels: all, frontal, occipital, parietal, and temporal), and Time Range (2 levels: VAN and P3a; Fig. 3). We performed model comparisons between models that did or did not include the fixed effects and their interactions to find the best compromise between an explanatory and a parsimonious model. This was done using the log-likelihood ratio between the 2 models because this ratio approximates a $\chi^2$ distribution. A $\chi^2$ test can thus be used to assess whether 2 models differ significantly, where the test statistic is the log-likelihood ratio and the degrees of freedom is the difference in free parameters of the 2 models.

## Results

### Behavioral Results

The behavioral results showed differences in accuracy and response times for the 4 perceptual ratings. For the behavioral analyses, all data points were used, despite differences in contrasts. The analysis was performed to show the relationship between performance and perceptual clarity.

The proportion correct per PAS rating (4) was modeled using a logistic regression model. Each participant (11) was modeled with an individual intercept. Comparing this model with a null model, which assigns an identical proportion correct to each PAS rating, we found that the model including PAS ratings fitted proportion correct significantly better than the null model, $\chi^2(3) = 1943.3$, $P < 0.001$. This means that the accuracies differed significantly across PAS ratings. It can be seen from the confidence intervals of proportion correct (Fig. 1C) that performance was not significantly different from chance when participants reported NE. For the remaining PAS ratings, performance was significantly different from chance and different from one another in an ordered manner, that is, $WG_{ACC} > NE_{ACC}$, $z = 19.18$, $P < 0.001$; $ACE_{ACC} > WG_{ACC}$, $z = 14.21$, $P < 0.001$; and $CE_{ACC} > ACE_{ACC}$, $z = 2.16$, $P = 0.031$. $CE_{ACC} > ACE_{ACC}$ was not significant when Bonferroni-corrected (3), $P_{BONF} = 0.092$.

Log response times per PAS rating (4) for the identification task were modeled factorially. Each participant (11) was modeled with an individual intercept. Comparing this model against a null model, we found that the model including PAS ratings explained significantly more than the null model, $\chi^2(3) = 1818.8$, $P < 0.001$. Response times decreased with clarity of experience: $WG_{RT} <$

$NE_{RT}$, z = 2.14, P = 0.032; $ACE_{RT} < WG_{RT}$, z = 23.87, P < 0.001; $CE_{RT} < ACE_{RT}$, z = 11.11, P < 0.001. $WG_{RT} < NE_{RT}$ was not significant when Bonferroni-corrected, $P_{BONF} = 0.097$. Overall, performance (measured using accuracy and response time) increased in relation to the clarity of perceptual consciousness.

The median number of trials per PAS rating used by a participant was: NE = 183; WG = 150; ACE = 177; CE = 121, indicating that participants used the scale in a graded manner.

## Catch Trials

The median number of times participants used the 4 different PAS ratings on catch trials was: NE = 61; WG = 11; ACE = 0; and CE = 0.

This indicates that the sensory characteristics, figure-present versus figure-absent, correlates well with perceptual characteristics, that is, PAS rating, even though participants occasionally experienced a WG when no target was presented, indicating that some visual confabulation took place.

## Illustrations of Components Found

We created grand averages for illustration (Fig. 2). In Figure 2A, the difference topographies for the differing neighboring comparisons are seen. In Figure 2B, an example of an ERF is shown from a temporal magnetometer. As can be seen, the components behind the VAN difference and the P3a difference are elicited. No formal statistics were done on these ERFs, since all statistics were done in source space using multivariate analyses. Nevertheless, it can be seen that the 2 components, VAN (130–320 ms) and P3a (320–510 ms), have comparable mean amplitude differences between conditions (Fig. 2A), indicating that any difference found using multivariate statistics reflects the consistency of information on the single trial level (Sandberg et al. 2014). The ratios (all close to 1) between peak differences for the VAN time range and the P3a time range for the 3 PAS comparisons indicated that they were indeed comparable. The peak differences over magnetometers were for NE–WG: VAN = 25.2 fT, P3a = 28.4 fT, ratio = 1.12; WG–ACE: VAN = 29.1 fT, P3a = 27.8 fT, ratio = 1.05; ACE–CE: VAN = 23.9 fT, P3a = 25.5 fT, ratio = 1.07.

## Group-Level Analysis of Results From the Multivariate Decoding

To investigate which spatio-temporal features classified perceptual consciousness the best, the 3 effects of interest, PAS comparison (3), Lobe (5), and Time Range (2), and their interactions were modeled and evaluated for significance (the decoding accuracies are plotted in Fig. 3). Models including these effects were compared against a null model, which modeled accuracy as a constant. The Time Range model was not significantly different from the null model: $\chi^2(1) = 1.1$, P = 0.29. The PAS comparisons and Lobe models were, however, $\chi^2(2) = 38.9$, $P < 0.001$ and $\chi^2(4) = 20.6$, $P < 0.001$. None of the possible interactions between the fixed effects made a significant difference (for all tests, $P > 0.30$). Comparisons of the different levels of Lobe revealed that occipital sources were significantly better for classification than frontal sources, z = 4.46, $P < 0.001$. Occipital sources were also better for classification than temporal sources, z = 3.81, $P < 0.001$. These tests were also significant when Bonferroni-corrected for 10 comparisons. There was furthermore evidence of occipital sources classifying significantly better than parietal sources, z = 2.28, P = 0.023, and all sources together, z = 2.31, P = 0.021. Evidence of all sources together classifying better than frontal sources was also found, z = 2.15, P = 0.031. Finally, there was also evidence of parietal sources classifying better than frontal sources, z = 2.19, P = 0.029. These 4 comparisons were not significant when Bonferroni-corrected for multiple comparisons (10).

Comparisons of the different levels of PAS revealed that both the WG–ACE comparison and the ACE–CE comparison were more accurate than the NE–WG comparison, z = 5.25, $P < 0.001$, and z = 6.11, $P < 0.001$, respectively. Both survived Bonferroni-correction for multiple comparisons (3).

## Time Courses of the Classification

The analyses above focused on the classification accuracies over extended time periods. To investigate the earliest time post-stimulus that perceptual consciousness could be decoded (the time point at which no later information contributed to increased decoding accuracy), we performed classifications per time point in a cumulative manner as well (Fig. 4). For these analyses, the *n*th analysis included all time points up to and including the *n*th time point. The time range was from 200 ms pre-target to 600 ms post-target. With the downsampled frequency of 250 Hz, this resulted in 201 classification analyses being run for each of the 3 PAS comparisons. Only frontal and occipital lobes were tested, and all classifications were run within-participant.

The steepest rise in classification accuracy for the occipital sources (Fig. 4A) occurred in the VAN range, whereas the P3a range in the frontal sources did not seem to be associated with any change in classification accuracy (Fig. 4B). Paired *t*-tests corroborated this: for the occipital lobe, the difference in classification accuracy between 320 and 130 ms was significantly different from zero for all 3 PAS comparisons: NE–WG: $t_{(10)} = 3.06$, P = 0.012; WG–ACE: $t_{(10)} = 2.97$, P = 0.014; ACE–CE: $t_{(10)} = 2.67$, P = 0.023, whereas for the frontal lobe the difference in classification accuracy between 510 and 320 ms was not significantly different from zero for any of the 3 PAS comparisons: NE–WG: $t_{(10)} = 0.45$, P = 0.66; WG–ACE: $t_{(10)} = 1.74$, P = 0.11; ACE–CE: $t_{(10)} = -0.075$, P = 0.94.

## Comparison Between the 2 Ranges

The multivariate analyses showed that only the occipital sources contain information for decoding all 3 PAS comparisons above chance (Fig. 3), and that only the VAN time range was associated with a significant increase in classification accuracy (Fig. 4A). Note that the temporal sources did not classify above chance for the NE–WG comparison. This fits well with the notion that temporal sources only start playing a role when the difference in experience is about content (Goodale and Milner 1992). However, it might be that all necessary processing takes place in the occipital lobe (e.g., V4), and that the temporal lobe is not necessary for an experience of content. This is entirely possible, especially because of evidence that V4 can process complex information such as shapes (Desimone and Schein 1987).

## Analysis of Catch Trials

Six participants had enough catch trials rated NE and WG to do a classification between NE and WG. This number had to be greater than the number of folds (5). The trials were processed and analyzed in the same manner as described for the figure-present trials. Classifications were run for frontal and occipital sources in the VAN range and the P3a range. A mixed model was fitted with Lobe (2) and Time Range (2) as fixed effects and Participant (6) with random intercepts and with accuracy of the classifier as

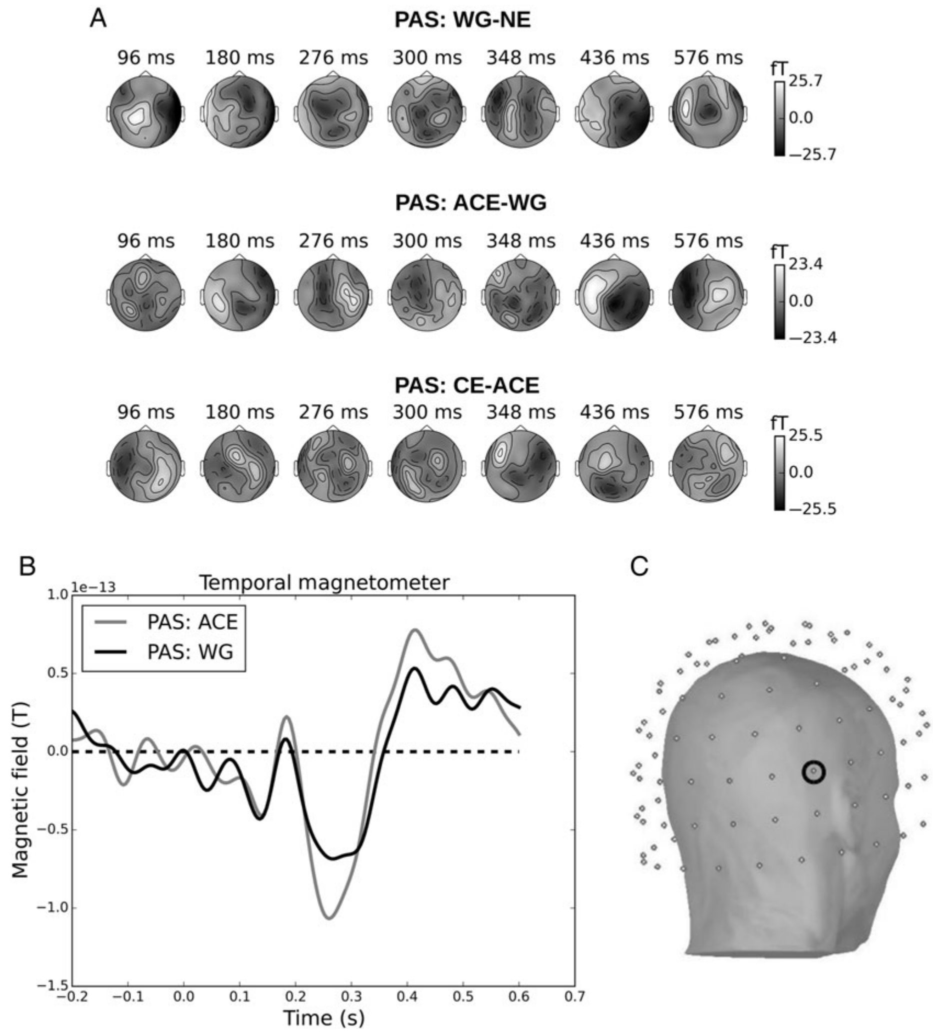


Figure 2. Sensor space data. (A) Topographic maps of the grand average difference waves between the neighboring PAS ratings. (B) Activity recorded at an example sensor (right temporal magnetometer) showcasing the components elicited, here exemplified by the WG–ACE comparison from the grand average over participants. The VAN difference (~270 ms) and the P3a difference (~440 ms) are both visible. (C) The position of the magnetometer on a participant.

the dependent variable. The model with Lobe did not explain significantly more than a model with just an intercept, $\chi^2(1) = 1.86$, $P = 0.17$, but a model with Time Range did, $\chi^2(1) = 6.20$, $P = 0.013$. Adding the interaction between Time Range and Lobe did not explain significantly more, $\chi^2(2) = 5.47$, $P = 0.065$.

The effect of Time Range was driven by the P3a range, mean = 0.581, 95% CI [0.502; 0.660], classifying significantly better than the VAN range, mean = 0.435, 95% CI [0.356; 0.514]. The P3a range was thus marginally better than chance for classifying perceptual state. This was not a planned analysis, and the effect is marginal, but finding evidence for the P3a range being related to, and the VAN range unrelated to, illusory perception is interesting in its own right. An interpretation of this finding is that P3a reflects accumulation of internal evidence, veracious or not, resulting in a given report and does not reflect perceptual consciousness itself (Melloni et al. 2011). We will return to this discussion later.

## Difference in Lobe Size

A potential confound of the present analysis is that the tested lobes differ in regard to the number of reconstructed sources they each contain. Specifically, it may be expected that given a fixed number of examples (trials), a very high number of spatial features (sources) could reduce the ability of the classifier to find an optimal border in the data to distinguish PAS responses. To address this potential issue, we trained new classifiers based on frontal and occipital lobes using 1) various fractions of the available sources and 2) different numbers of trials. To address the potential issue of the number of spatial features, we first randomly sampled one-tenth of the available sources for each lobe and each time range, VAN or P3a, respectively. This was repeated 100 times, each time with a new and independent sample. A multivariate analysis was run for each sampling, otherwise using the same parameters as in earlier analyses. This procedure was also run for the following fractions: two-, three-, four-, five-, six-, seven-, eight-, and nine-tenths. These analyses were run within-participant. For each range, VAN and P3a, the mean classification accuracy across participants was calculated for each lobe, frontal and occipital (Fig. 5A). We modeled Accuracy with PAS comparison (3) and Fraction as fixed effects and Participants (11) modeled as having a random intercept. No correlations were found between Fraction and Accuracy, and also no interaction between Fraction and PAS comparison, occipital $Fs < 1$ and frontal $Fs < 0.01$. There seemed to be an effect of PAS comparison, all $Fs$

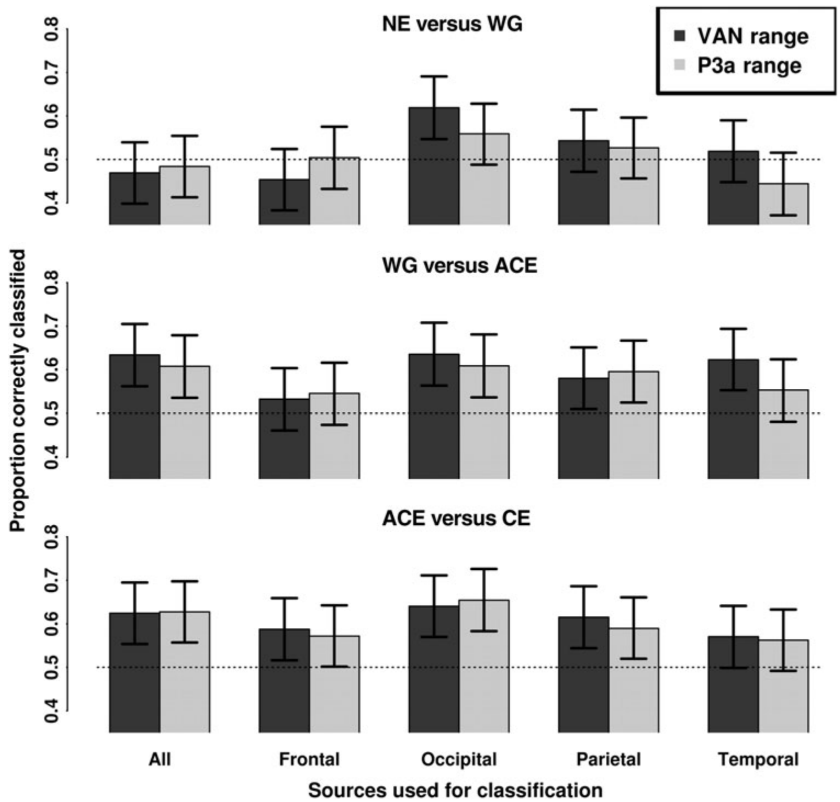


**Figure 3.** Mean classification accuracies for each of the 5 lobes tested for the 3 PAS comparisons for each of the 2 ranges: The VAN range (132–312 ms) and the P3a range (324–512 ms). NE versus WG is the difference of a subjective experience as such. WG versus ACE is the experiential difference of content. ACE versus CE is the experiential difference of unambiguity. Of special importance is it that occipital sources can be used to classify all PAS comparisons significantly above chance. The error bars are 95% confidence intervals tested against chance, bootstrapped using 10 000 simulations, from a mixed model having Time Range (2) and PAS comparison (3), and Lobe (5) as fixed effects including all possible interactions. Participants (11) were modeled with individual intercepts (random effect).

> 2.95 reflecting the results of the main analysis, but no formal test was done as this is unrelated to a test of the potential confound. Taken together, the analyses thus revealed that the difference in source number between the lobes could not explain the results of the main analysis as the multivariate model was indifferent to the fraction of sources used as long as one-tenth or more of the sources are used, corresponding to approximately 70 and approximately 240 spatial features for the occipital and frontal lobes, respectively. It should be noted that previous studies have found poor classification accuracy when a very low number of spatial features (below 20) was used (Haynes and Rees 2005; Sandberg et al. 2013), but the number of spatial features was significantly higher for all analyses in the present study.

### Number of Trials Used for Classification

The second potential confound mentioned earlier was that differing amount of trials were used for the classifications, and that this could be related to the accuracy of the classification. A linear regression (Fig. 5B) was run to investigate this relationship for the occipital sources in the VAN time range, $\rho = 0.061$, $t_{(31)} = 0.34$, $P = 0.73$. The number of trials thus appears to be unrelated to the accuracy of the classifier.

### Physical Characteristics Versus Perceptual Characteristics

A third potential confound was that some of the within-participant classification trial sets contained unequal amounts of trials with the 2 figures, a rectangle and a 45° rotated rectangle. It is possible that successful classification was based on decoding representations of physical properties, that is, orientation, rather than perceived clarity, that is, differences in perceptual consciousness. Therefore, we investigated the correlation between accuracy of the classification and how unequally the figures were distributed between the trials of that classification. Two linear regressions (Fig. 5C) were run for the occipital sources in the VAN time range, one with all data points, $\rho = 0.21$, $t_{(31)} = 1.17$, $P = 0.25$, and one with the rightmost outlier removed, $\rho = 0.056$, $t_{(30)} = 0.31$, $P = 0.76$. This indicates that there is no relation between variability of physical characteristics, that is, orientation of target stimuli, and the ability of the classifier to decode perceptual consciousness, that is, PAS ratings.

## Discussion

In this study, we examined the neural activity related to becoming conscious of a visual stimulus. We found evidence that the MEG signal originating in the frontal lobe decoded graded differences in perceptual consciousness (measured using the PAS) significantly worse than the signal originating in the occipital lobe. Furthermore, the frontal activity could only be used to decode 1 out of the 3 PAS contrasts above chance (Fig. 3), and neither in the VAN nor P3a time ranges did frontal sources add to the predictive value of a classification algorithm (Fig. 4). While we found no mean difference in predictability of activity in the VAN and P3a range, only occipital sources in the VAN time

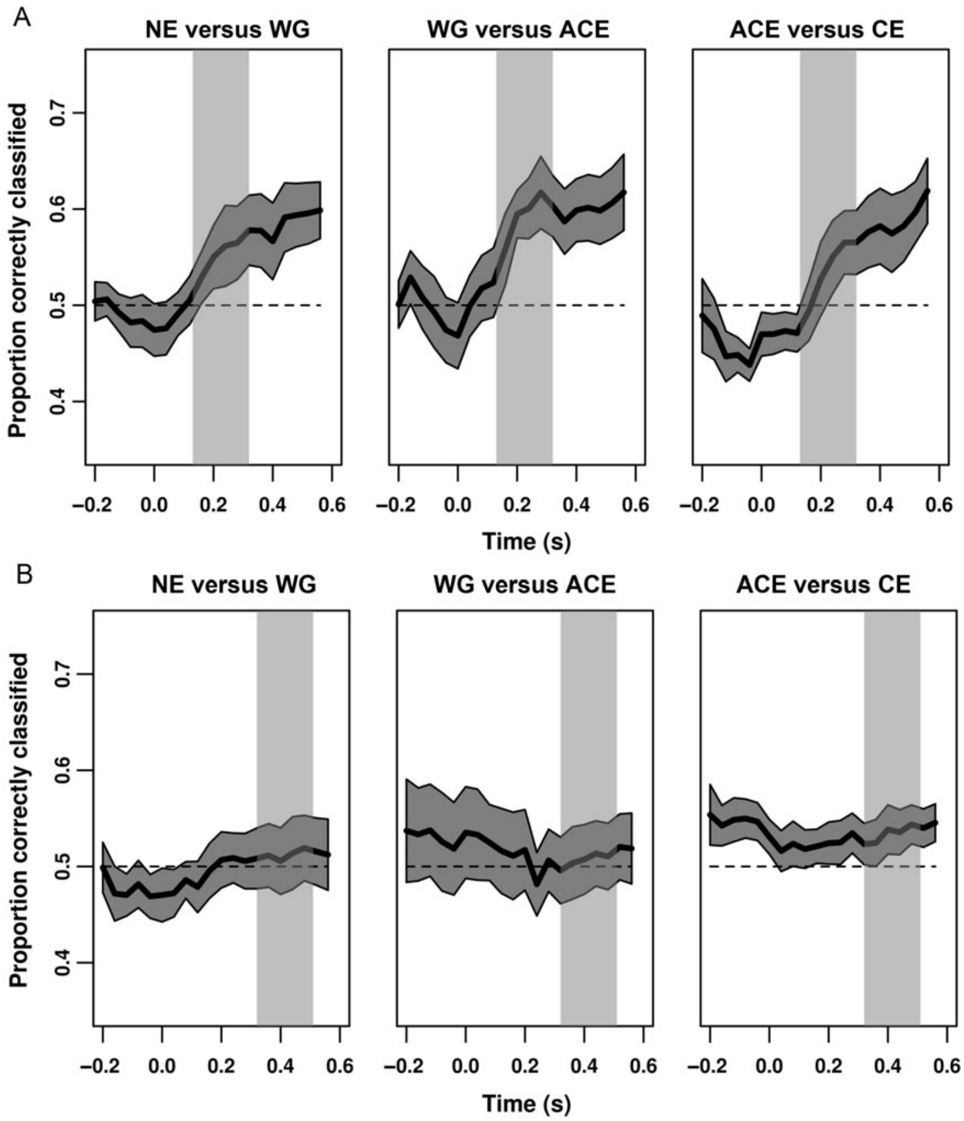


**Figure 4.** Mean cumulative time point classification accuracies (*A*) for the occipital lobe and (*B*) for the frontal lobe tested for the 3 PAS comparisons. The light gray indicates the VAN range (*A*) and the P3a range (*B*), respectively. Note that the largest increase in decoding accuracy occurred during the VAN at occipital sources. The darker gray area indicates 1 SEM. Curves have been smoothed by only plotting every 10th point. These points are based on the mean of the 9 samples that came before them. The SEM is calculated over 10 points as well.

range could be used to decode all 3 PAS comparisons (Fig. 3), and the greatest increase in predictive values was found during the VAN time range (Fig. 4). These results were unrelated to differences in the number of sources in the lobes (Fig. 5*A*), differences in the number of trials used to train the classifier (Fig. 5*B*), and differences in stimuli proportions (Fig. 5*C*).

Our results thus indicate that there are neural activations that systematically differ between experienced differences in perceptual consciousness. Taken together with previous behavioral experiments (Overgaard et al. 2006; Sandberg et al. 2010), this study provides evidence that perceptual consciousness is graded, and that differences between each gradation are best explained by the conglomerate activity of the neurons in the occipital lobe during the VAN time range, 130–320 ms. It should be noted that in this study, we do not distinguish between gradual/graded and partial awareness (Kouider et al. 2010), where gradual/graded awareness can be interpreted as meaning that the entire conscious percept is either more clear or less clear, whereas the partial awareness hypothesis states that the individual perceptual features are consciously perceived in an all-or-none manner.

Taken together, these results thus indicate that occipital activity seems a more likely candidate for a neural correlate of perceptual consciousness than does prefrontal activation. It should be noted that other studies (e.g., Sandberg et al. 2013) have found that other perceptual sources in, for instance, the temporal lobe are as predictive of conscious perception as occipital sources. It is likely that this difference is due to differences in stimuli. The simple stimuli used in the present experiment are expected to be processed mainly in relatively early visual areas, such as V4 (Pasupathy and Connor 2001). Had we used more complex stimuli, for example, tools or visual scenes, temporal sources might have been equally predictive. It is important to note that differences in activation patterns in perceptual areas across different conscious experiences do not, in themselves, imply a role for frontal areas. Based on the current findings, a likely explanation

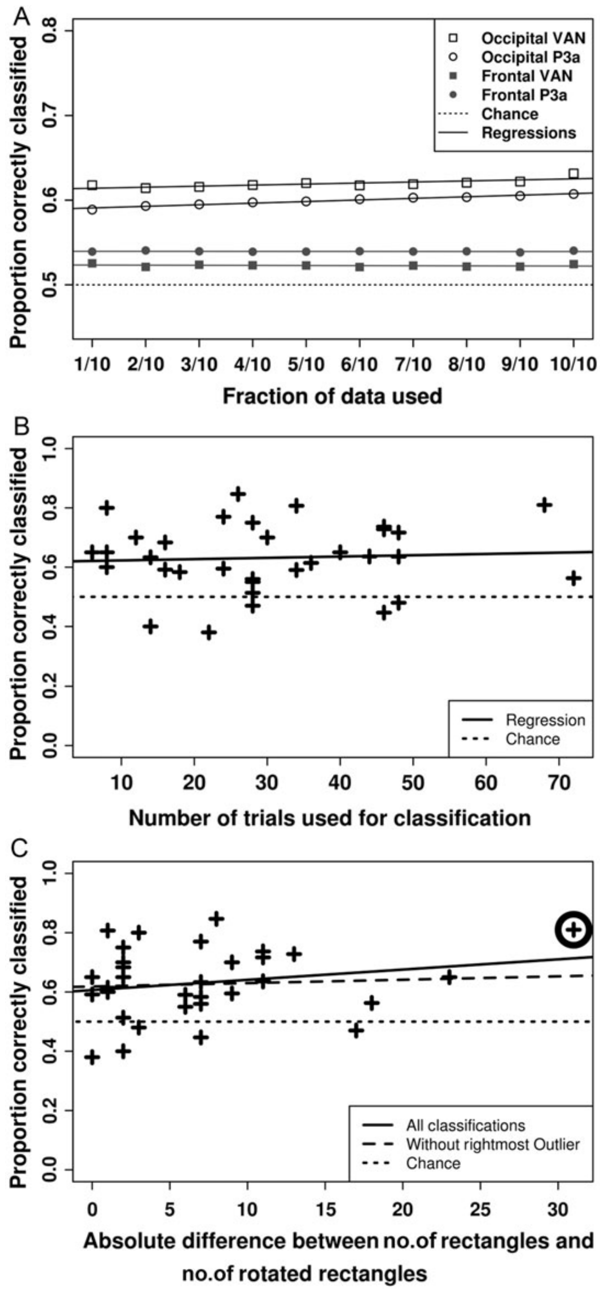


**Figure 5.** Control analyses: (A) Controlling for lobe size: Classification accuracies for the occipital lobe and for the frontal lobe collapsed over the 3 PAS comparisons. Separate lines are plotted for the VAN time range and the P3a range. All slopes are close to 0, $\rho_{\min} = -0.00070$, $\rho_{\max} = 0.048$, indicating that classification with the occipital lobe is best not simply because of differences in the number of reconstructed sources in the multivariate models across lobes. (B) Controlling for differences in the number of trials used for each classification: Individual observations, 3 for each participant, 1 for each PAS comparison, showing the relationship between classification accuracy for the occipital lobe for the VAN range and the number of trials used for classification. The linear regression line is drawn, $\rho = 0.061$. This indicates that the results are not a consequence of differences in the number of trials used for classification. (C) Controlling for differences in the number of trials with each stimulus used for classification: Individual observations showing the relationship between classification accuracy for the occipital lobe for the VAN time range and the difference between the number of rectangles and the number of rotated rectangles among the trials for that classification. Two linear regression lines are drawn, one with all observations, $\rho = 0.21$, and one with the rightmost outlying observation (encircled) removed, $\rho = 0.056$. This indicates that the results are not a consequence of differences in physical characteristics of the stimuli.

is that activity in perceptual areas is the main correlates of conscious perception of stimuli processed in those areas.

In HOT (Lau and Rosenthal 2011) and Information Integration Theory (Tononi 2004), it is proposed that consciousness is associated with prefrontal activations. The same is predicted by at least some versions of GWT (Baars 2005; Dehaene 2014). The present finding that sources in the frontal lobe decode differences in PAS levels significantly worse than those in the occipital lobe is thus not what one should expect seen from the vantage point of these theories. Furthermore, activity in the frontal sources could only be used to decode 1 out of the 3 PAS comparisons above chance (Fig. 3), and neither in the VAN or P3a time ranges did frontal sources seem to add a predictive value (Fig. 4B).

In contrast, the results of the experiment are consistent with theories that associate occipital activation with differences in perceptual consciousness such as Lamme's feedback theory (Lamme 2006), associating perceptual consciousness with recurrent processing within the occipital and temporal lobes, and the above-mentioned VAN proposed by Koivisto and Revonsuo (2010).

In the Neural GWT, the occipito-temporal VAN is often associated with construction of the percept, and the more frontal P3a is associated with becoming conscious of that content (Sergent et al. 2005). This interpretation appears somewhat inconsistent with the results of two of our main analyses. We have previously argued (Sandberg et al. 2014) that a prerequisite of perceptual consciousness (such as the construction of the percept) should not be more predictive of conscious perception than the actual correlate of conscious perception. As we found occipital activity to be more predictive than frontal activity, it thus appears unlikely that the occipital activity is only a prerequisite, especially given the similar mean differences between the 2 signals across the PAS comparisons (Fig. 2A). Additionally, in our spatio-temporal analyses (Fig. 4), frontal activity appeared completely unrelated to classification accuracy throughout the time range. If frontal activity in the P3a time range correlates with perceptual consciousness, we would instead have expected to see an increase in classification accuracy (Fig. 4B) around this time window. These results suggest that frontal activity may be related to processes typically (but somewhat inconsistently) occurring on trials with reported conscious perception. In an experimental context, these processes could be report, overt consideration, or memory consolidation. This interpretation is consistent with the studies mentioned in the introduction showing a decrease in the size of the P3a when a perceived stimulus is not task relevant (Pitts et al. 2012), and when it is expected (Melloni et al. 2011).

While our study did not provide evidence of a role for frontal sources, it is nevertheless not possible to conclusively dismiss a role of the late P3a time range as activity in this time range was not significantly less predictive than the VAN time range, although occipital sources were driving the accuracy in both ranges. One argument against the P3a being the key NCC is that it did not distinguish all PAS ratings as did the VAN (Fig. 3). Another argument is that no predictive value was added during the P3a time range as one might expect (Fig. 4), but proponents of GWT might argue that this is expected as all information is present in a preconscious state during the VAN range.

We also found evidence that activity during the P3a time range classified the NE–WG difference in catch trials better than that in the VAN time range, and we failed to reject the hypothesis that any cortical lobe performed better than the other. One interpretation of this finding, opposite to the general gist of our argument, is that P3a reflects perceptual consciousness better than VAN since it accounts for this illusory perception difference. However, if this were the case, it is surprising that the P3a was not more predictive of perceptual consciousness on veridical trials, and it is surprising that frontal sources could not be used to decode the NE–WG difference on such trials. Frontal sources in the P3a time range thus appeared to be predictive of the report of perception only when no stimulus was presented. For these reasons, an alternative explanation is that the P3a reflects differences in the accumulation of internal evidence for how to map perceptual consciousness onto PAS ratings (Melloni et al. 2011), and thus not perceptual consciousness itself. Based on the present experiment, however, it is not possible to conclude decisively about this matter.

In the NCC theories mentioned above, consciousness is often discussed and investigated by contrasting perceptual states dichotomously. PAS and other non-dichotomous scales allow for more options: One interpretation may be that there is more than one NCC, that is, one NCC per neighboring PAS comparison. If one maintains that there is only one proper NCC, then one has to decide on the defining feature of perceptual consciousness: that something is experienced at all (the difference between NE and WG), that one can specify the content of the experience (the difference between WG and ACE), or unambiguousness (the difference between ACE and CE). Assuming that for Lamme's theory, the defining feature of perceptual consciousness is an experience of content, it is noteworthy that temporal sources in the VAN time range can classify both the difference between ACE and WG and the difference between CE and ACE, providing some suggestive evidence for the involvement of temporal sources in the recurrent feedback to occipital sources. The present results also indicate that whether the dichotomously defining feature of perceptual consciousness is taken to be the difference between NE and WG or the difference between WG and ACE, there was no evidence for frontal sources decoding perceptual consciousness above chance (Fig. 3). It is of course possible that this is a question of statistical power, but importantly we found positive evidence for occipital sources classifying significantly better than frontal sources.

The REFCON model (Overgaard and Mogensen 2014) suggests that consciousness is related to information integrated in a "situational algorithmic strategy" (SAS) that is realized by a complex system of feed-forward and feed-backward mechanisms. Consciousness is seen as gradual, directly related to how integrated given information is in SAS, determined by its relevance, according to top-down expectations and evaluations. Thus, REFCON would predict that consciousness does not relate directly to one cortical structure, but rather, the structures that are "set up" in a given individual to realize particular functions. REFCON would predict that, in most cases, occipital regions are relatively more related to weak visual experiences than other cortical regions, but that more brain regions will be activated in an increasingly individual manner as a cascade as more information becomes available and the stimulus becomes more clearly experienced. Thus, REFCON does not assume that any correlation to a mental state is static but rather dynamic and may vary greatly between individuals. Such more theoretical aspects of REFCON are not directly reflected in the results of this experiment. However, its predictions related to gradual integration, the relatively stronger involvement of occipital regions for visual consciousness, and the increasing involvement of other cortical regions seem consistent with the results.

In summary, we found that participants reported differences in perceptual consciousness in a graded manner, and that occipital sources have the greatest predictive value for decoding these graded differences in perceptual consciousness, thus strengthening VAN and occipital lobe recurrent processing theories. The REFCON model is also compatible with the present results. In the context of this experiment, frontal activations did not appear directly related to perceptual consciousness, which is consistent with studies relating it to differences in, for example, attention and expectations. Using the Perceptual Awareness Scale made it possible to distinguish how different degrees of perceptual consciousness each are related to brain activity, highlighting an often neglected conceptual point that one needs to define a neural correlate of perceptual consciousness in order to find it—for example, as experience per se (as in the difference between NE and WG) or the experience of content (as in the difference between WG and ACE). Using the PAS is a possible way to approach and explore these different neural correlates of perceptual consciousness in more detail.

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## Notes

*Conflict of Interest*: None declared.

## References

Aru J, Axmacher N, Lam ATAD, Fell J, Elger CE, Singer W, Melloni L. 2012. Local category-specific gamma band responses in the visual cortex do not reflect conscious perception. J Neurosci. 32:14909–14914.

Aru J, Bachmann T, Singer W, Melloni L. 2012. Distilling the neural correlates of consciousness. Neurosci Biobehav Rev. 36: 737–746.

Baars BJ. 1988. A cognitive theory of consciousness. NY, USA: Cambridge University Press.

Baars BJ. 2005. Global workspace theory of consciousness: toward a cognitive neuroscience of human experience. In: Laureys S, editor. Progress in Brain Research. The Boundaries of Consciousness: Neurobiology and Neuropathology. Oxford, UK: Elsevier. pp. 45–53.

Bishop CM. 2006. Pattern recognition and machine learning. Cambridge, UK: Springer.

Block N. 2005. Two neural correlates of consciousness. Trends Cogn Sci. 9:46–52.

Dale AM, Fischl B, Sereno MI. 1999. Cortical surface-based analysis. I. Segmentation and surface reconstruction. NeuroImage. 9:179–194.

Dale AM, Liu AK, Fischl BR, Buckner RL, Belliveau JW, Lewine JD, Halgren E. 2000. Dynamic statistical parametric mapping. Neuron. 26:55–67.

Dehaene S. 2014. Consciousness and the brain: deciphering how the brain codes our thoughts. NY, USA: Penguin.

Dehaene S, Changeux J-P, Naccache L, Sackur J, Sergent C. 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. Trends Cogn Sci. 10:204–211.

Dehaene S, Naccache L, Cohen L, Bihan DL, Mangin J-F, Poline J-B, Rivière D. 2001. Cerebral mechanisms of word masking and unconscious repetition priming. Nat Neurosci. 4:752–758.

Del Cul A, Baillet S, Dehaene S. 2007. Brain dynamics underlying the nonlinear threshold for access to consciousness. PLoS Biol. 5:e260.

Del Cul A, Dehaene S, Reyes P, Bravo E, Slachevsky A. 2009. Causal role of prefrontal cortex in the threshold for access to consciousness. Brain J Neurol. 132:2531–2540.

Desikan RS, Ségonne F, Fischl B, Quinn BT, Dickerson BC, Blacker D, Buckner RL, Dale AM, Maguire RP, Hyman BT, et al. 2006. An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. NeuroImage. 31:968–980.

Desimone R, Schein SJ. 1987. Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. J Neurophysiol. 57:835–868.

Fahrenfort JJ, Scholte HS, Lamme VAF. 2007. Masking disrupts reentrant processing in human visual cortex. J Cogn Neurosci. 19:1488–1497.

Faivre N, Koch C. 2014. Inferring the direction of implied motion depends on visual awareness. J Vis. 14:1–14.

Ffytche DH, Howard RJ, Brammer MJ, David A, Woodruff P, Williams S. 1998. The anatomy of conscious vision: an fMRI study of visual hallucinations. Nat Neurosci. 1:738–742.

Fisch L, Privman E, Ramot M, Harel M, Nir Y, Kipervasser S, Andelman F, Neufeld MY, Kramer U, Fried I, et al. 2009. Neural "Ignition": enhanced activation linked to perceptual awareness in human ventral stream visual cortex. Neuron. 64:562–574.

Goodale M, Milner D. 1992. Separate visual pathways for perception and action. Trends Neurosci. 15:20–25.

Gramfort A, Luessi M, Larson E, Engemann DA, Strohmeier D, Brodbeck C, Goj R, Jas M, Brooks T, Parkkonen L, et al. 2013. MEG and EEG data analysis with MNE-Python. Front Neurosci. 7, doi: 10.3389/fnins.2013.00267.

Hämäläinen MS, Hari R, Ilmoniemi RJ, Knuutila J, Lounasmaa OV. 1993. Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. Rev Mod Phys. 65:413–497.

Haynes J-D, Rees G. 2005. Predicting the stream of consciousness from activity in human visual cortex. Curr Biol. 15:1301–1307.

Hyvärinen A, Oja E. 2000. Independent component analysis: algorithms and applications. Neural Netw. 13:411–430.

Koivisto M, Revonsuo A. 2007. Electrophysiological correlates of visual consciousness and selective attention. Neuroreport. 18:753–756.

Koivisto M, Revonsuo A. 2010. Event-related brain potential correlates of visual awareness. Neurosci Biobehav Rev. 34:922–934.

Kouider S, de Gardelle V, Sackur J, Dupoux E. 2010. How rich is consciousness? The partial awareness hypothesis. Trends Cogn Sci. 14:301–307.

Kouider S, Stahlhut C, Gelskov SV, Barbosa LS, Dutat M, de Gardelle V, Christophe A, Dehaene S, Dehaene-Lambertz G. 2013. A neural marker of perceptual consciousness in infants. Science. 340:376–380.

Lamme VAF. 2006. Towards a true neural stance on consciousness. Trends Cogn Sci. 10:494–501.

Lau HC, Passingham RE. 2006. Relative blindsight in normal observers and the neural correlate of visual consciousness. Proc Natl Acad Sci USA. 103:18763–18768.

Lau HC, Rosenthal D. 2011. Empirical support for higher-order theories of conscious awareness. Trends Cogn Sci. 15:365–373.

Laureys S, Owen AM, Schiff ND. 2004. Brain function in coma, vegetative state, and related disorders. Lancet Neurol. 3:537–546.

Liu Y, Paradis A-L, Yahia-Cherif L, Tallon-Baudry C. 2012. Activity in the lateral occipital cortex between 200 and 300 ms distinguishes between physically identical seen and unseen stimuli. Front Hum Neurosci. 6, doi: 10.3389/fnhum.2012.00211.

Ludwig K, Sterzer P, Kathmann N, Franz VH, Hesselmann G. 2013. Learning to detect but not to grasp suppressed visual stimuli. Neuropsychologia. 51:2930–2938.

Melloni L, Schwiedrzik CM, Müller N, Rodriguez E, Singer W. 2011. Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. J Neurosci Off J Soc Neurosci. 31:1386–1396.

Nieuwenhuis S, de Kleijn R. 2011. Consciousness of targets during the attentional blink: a gradual or all-or-none dimension? Atten Percept Psychophys. 73:364–373.

Overgaard M, Mogensen J. 2014. Visual perception from the perspective of a representational, non-reductionistic, level-dependent account of perception and conscious awareness. Philos Trans R Soc B Biol Sci. 369:20130209.

Overgaard M, Rote J, Mouridsen K, Ramsøy TZ. 2006. Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task. Conscious Cogn. 15: 700–708.

Overgaard M, Timmermans B, Sandberg K, Cleeremans A. 2010. Optimizing subjective measures of consciousness. Conscious Cogn. 19:682–684.

Pasupathy A, Connor CE. 2001. Shape representation in area V4: position-specific tuning for boundary conformation. J Neurophysiol. 86:2505–2519.

Pins D, Ffytche D. 2003. The neural correlates of conscious vision. Cereb Cortex. 13:461–474.

Pitts MA, Martínez A, Hillyard SA. 2012. Visual processing of contour patterns under conditions of inattentional blindness. J Cogn Neurosci. 24:287–303.

Ramsøy TZ, Overgaard M. 2004. Introspection and subliminal perception. Phenomenol Cogn Sci. 3:1–23.

Ruzzoli M, Marzi CA, Miniussi C. 2010. The neural mechanisms of the effects of transcranial magnetic stimulation on perception. J Neurophysiol. 103:2982–2989.

Sandberg K, Andersen LM, Overgaard M. 2014. Using multivariate decoding to go beyond contrastive analyses in consciousness research. Conscious Res. 5:1250.

Sandberg K, Bahrami B, Kanai R, Barnes GR, Overgaard M, Rees G. 2013. Early visual responses predict conscious face perception within and between subjects during binocular rivalry. J Cogn Neurosci. 25:969–985.

Sandberg K, Timmermans B, Overgaard M, Cleeremans A. 2010. Measuring consciousness: Is one measure better than the other? Conscious Cogn. 19:1069–1078.

Sergent C, Baillet S, Dehaene S. 2005. Timing of the brain events underlying access to consciousness during the attentional blink. Nat Neurosci. 8:1391–1400.

Tononi G. 2004. An information integration theory of consciousness. BMC Neurosci. 5:42.

Vanni S, Revonsuo A, Saarinen J, Hari R. 1996. Visual awareness of objects correlates with activity of right occipital cortex. Neuroreport. 8:183–186.

Veser S, O'Shea RP, Schröger E, Trujillo-Barreto NJ, Roeber U. 2008. Early correlates of visual awareness following orientation and colour rivalry. Vision Res. 48:2359–2369.

Wierzchoń M, Asanowicz D, Paulewicz B, Cleeremans A. 2012. Subjective measures of consciousness in artificial grammar learning task. Conscious Cogn. 21:1141–1153.

# Appendix III

**Task differences induce differences in magnetoencephalographic correlates of consciousness**

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## Abstract

Neural correlates of perceptual consciousness have been examined using primarily the method of contrastive analysis in which conscious states are compared with unconscious states. Differences in cognitive context, such as differences in task requirements have been seen as confounding factors for finding the minimal conditions sufficient for conscious experience. This approach assumes that consciousness is independent of the cognitive context, and that there is one proper neural correlate of consciousness similar across all confounding differences. In contrast, according to integrative approaches in which perceptual consciousness and cognitive context are not considered independent, neural correlates of perceptual consciousness are not expected to be uniquely spatio-temporally localizable, but may differ according to differences in task requirements. In this study, we examined whether differences in task requirements give rise to spatio-temporal neural differences in *when* and *where* different gradations of perceptual consciousness could be discerned from one another. Using magnetoencephalography (MEG), we found that occipital activity in general predicted perceptual consciousness more accurately than frontal activity, but crucially we also found that task requirements changed the latency, with the abstraction level of the task influencing when perceptual consciousness could be classified: early on, < 320 ms for a perceptual task, and later on, > 320 ms, for a conceptual task. This points towards an integrative view of perception and cognitive context, which has the consequence that one may need to abandon the search for one unique spatio-temporal neural correlate of perceptual consciousness.

*Keywords: neural correlates of consciousness, perception, magnetoencephalography, classification, task requirements*

## Introduction

The search for the neural correlates of perceptual consciousness has been defined as the search for the minimal conditions sufficient for realizing a conscious representation (Chalmers, 2000). Using contrastive analyses (Baars, 1988; Crick & Koch, 1990) much research has been done on isolating the minimal conditions sufficient for realizing a conscious representation, what we here call perceptual consciousness. An important question, often not explicitly addressed, is what it means for neural conditions to be minimally sufficient for perceptual consciousness. One possibility is that there is *one* uniquely identifiable spatio-temporal pattern of neural activity that is constant across differences in task requirements, differences in performance, differences in working memory load etc. Seen from this viewpoint, any of these differences would be confounding factors in the search for what might be called the proper neural correlates of perceptual consciousness (NCC-proper). A second possibility is that the minimally sufficient conditions are dependent on the cognitive context. Seen from this viewpoint, differences in task requirements, differences in performance, differences in working memory etc. are not necessarily confounding factors. They may rather be necessary to understand the specifics of the realization of perceptual consciousness. From the first viewpoint, consciousness is something that is either attached to a representation or not. If consciousness is attached to the representation, even if it be in a graded manner, it should be possible to find unique neural correlates of this. These would then be the NCC-proper. From the second viewpoint, consciousness is integrated into the representation. If representations differ because of differences in the cognitive context such as differences in task requirements, then from this viewpoint we should also expect differences in the neural correlates of perceptual consciousness. From this viewpoint, these neural correlates would be evidence of what might be called an NCC-context. This name reflects the integration of cognitive context and perceptual consciousness in the representation. For example, if one is counting the number of people in a crowd, there is no need to process each of their faces, but if one is looking for a particular person, there is. In these 2 cases, the representations of the people in the crowd should differ in terms of the extent of face processing, and conscious representation, consequently, is expected to differ as well.

In most studies, it seems that experimenters have been aiming for the NCC-proper. This is evident from the much debated distinction between phenomenal consciousness and access consciousness (Block, 2005). Phenomenal consciousness is defined as being the subjective experience as such whereas access consciousness is the availability of the content of that subjective experience for cognitive control and motor control. It is much debated whether this is just a conceptual distinction or whether it is also empirically tractable (Block, 2007; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Lamme, 2006). Lamme (2006, 2010) argues that phenomenal consciousness is demonstrably empirically real, and that in order to find the NCC-proper, we must determine its minimal conditions, which he argues to be early (< 300 ms) occipital reentrant activity. Dehaene (2014) on the other hand argues that only the study of access consciousness, if there at all be such a thing as phenomenal consciousness, is a scientifically reputable endeavour. He argues that late (> 300 ms) frontal activity reflects the minimal conditions for realizing access consciousness. Common to these seemingly conflicting viewpoints is that they both assume that there is *one* underlying NCC-proper. Much of the debate then revolves around whether phenomenal or access consciousness is the NCC-proper. Another way to characterize this debate is by the conceptual divisions of Aru, Bachmann, Singer & Melloni (2012). They divide the correlates that can be found by contrastive analyses into 3 kinds: NCC-prerequisites, NCC-proper and NCC-consequences. NCC-prerequisites are enabling conditions that allow for the NCC-proper whereas NCC-consequences arise because of the cognitive context, such as differences in task requirements and attention. In electroencephalographic (EEG) studies using contrastive analysis, differences have been found in both an occipito-temporally realized component (~130-320 ms) and a fronto-parietally realized component (~320-510 ms) (Koivisto & Revonsuo, 2010). Using the terminology of Aru et al. (2012), seen from the framework of Dehaene (2014) the occipital activity is an NCC-prerequisite, what they call perceptual integration (Sergent, Baillet, & Dehaene, 2005), and the frontal activity is seen as the NCC-proper. From the framework of Lamme (2006, 2010), it is the other way around, with the occipital activity seen as the NCC-proper and the frontal activity seen as an NCC-consequence. Again, it is evident that both assume the existence of *the* NCC-proper.

On the other hand, there has not been many studies on the neural correlates of perceptual consciousness where the cognitive context has been manipulated. One interesting study is that of Melloni, Schwiedrzik, Müller, Rodriguez & Singer (2011) where they found that differences in top-down expectations changed the latency of neural correlates of perceptual consciousness. This indicates that perception and cognitive context may be integrated into one another. In terms of theoretical accounts, some accounts do exist wherein it is proposed that perception and cognitive context are integrated. Windey & Cleeremans (2015), for example, argued that whether perceptual consciousness takes a graded or an all-or-none form is dependent on the level of experience. Low-level stimuli such as geometrical shapes are subjectively experienced in a graded manner whereas high-level stimuli with semantic content are subjectively experienced in a more dichotomous manner (Windey, Gevers, & Cleeremans, 2013; Windey, Vermeiren, Atas, & Cleeremans, 2014). From this account, one should thus expect that differences in task requirements should give rise to different neural correlates dependent on context (NCC-context). Another account is the REFCON account of Overgaard & Mogensen (2014). In this account cognitive context and perceptual consciousness are integrated in such a manner that the NCC-context represents the neural information that is most relevant to the task at hand given the cognitive context. It is important here to emphasize that what neural information is most relevant may change depending on both external, e.g. task requirements, and internal differences e.g. differences in the clarity of subjective experience. That is, the optimal cognitive strategy is dependent on both availability of information and the goal associated with interpreting that information. According to REFCON, potential differences between tasks should be greatest for the graded ratings. If an experience is crisp and clear such that all relevant features can be extracted, any strategy should be available. When an experience, on the other hand, is less than perfectly clear, the available strategies may differ between tasks due to sub-optimal extraction of features. Thus, according to REFCON, if cognitive strategies differ, neural correlates of perceptual consciousness should also differ.

So far, we thus have 2 incompatible viewpoints of what constitute the minimal conditions for realizing perceptual consciousness. One where minimal conditions exclude cognitive context, the NCC-proper, and one where minimal conditions include cognitive context, the NCC-context. To test these viewpoints against one another, we created a paradigm with differences in cognitive context, but minimal differences in stimuli. We manipulated the cognitive context by manipulating the task requirements. The so-called classification tasks of Posner & Mitchell (1967) are examples of tasks that differ in regards of cognitive requirements despite them having similar stimuli. A pair of letters is presented and participants have to indicate whether the letters are "same" or "different". This can for example be according to physical identity, e.g. "bb", or rule identity, e.g. both are vowels. Using a slightly different vocabulary, we created a *perceptual* task, corresponding to physical identity, and a *conceptual* task, corresponding to rule identity. We chose the terms *perceptual* and *conceptual to* illustrate that when judging physical identity, one can rely on one's perceptual system to differentiate them, even if one does not know what they symbolize. When judging rule identity, however, one has to conceptualize the shown letters as vowels and consonants to be able to perform the task correctly.

We used the Perceptual Awareness Scale (PAS) (Ramsøy & Overgaard, 2004) to measure perceptual consciousness. PAS has four ratings, No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) (Table 1). The differences between neighbouring points can be described as *there being a subjective experience at all*, (No Experience versus Weak Glimpse), *there being a subjective experience of content*, (Weak Glimpse versus Almost Clear Experience) and finally *there being a subjective experience of unambiguousness of the content*, (Almost Clear Experience versus Clear Experience).

The 2 viewpoints, one associated with an NCC-proper and one associated with an NCC-context, entailed 2 hypotheses each that we could test. From the view of there existing an NCC-proper, the hypotheses are that either the early (< 320 ms) occipital activity, also called the Visual Awareness Negativity (VAN) (Koivisto & Revonsuo, 2010), or the late (> 320 ms) frontal activity, the P3a (Sergent et al., 2005), correlates with PAS ratings across the 2 tasks. From the view of there existing NCC-context(s), 2 hypotheses could be formed based on the accounts that we discussed earlier. According to the account of Windey & Cleeremans (2015), it can be hypothesized that perceptual consciousness is graded for the perceptual task and dichotomous for the conceptual task. According to the account of Overgaard & Mogensen (2014), it can be hypothesized that perceptual consciousness will be graded, and that potential differences between tasks will be the greatest for the graded ratings. This means that there may not be one specific spatio-temporal pattern of activity that correlates with perceptual consciousness across tasks.

**Table 1:** The Perceptual Awareness Scale (PAS)

| Label | Description (from Ramsøy and Overgaard 2004) |
|---|---|
| (1) No Experience (NE) | No impression of the stimulus. All answers are seen as mere guesses |
| (2) Weak Glimpse (WG) | A feeling that something has been shown. Not characterized by any content, and this cannot be specified any further |
| (3) Almost Clear Experience (ACE) | Ambiguous experience of the stimulus. Some stimulus aspects are experienced more vividly than others. A feeling of almost being certain about one's answer |
| (4) Clear Experience (CE) | Non-ambiguous experience of the stimulus. No doubt in one's answer |

*Note: Scale steps and their descriptions*

To test these hypotheses, magnetoencephalographic recordings with subsequent multivariate analyses done on source reconstructed data from the occipital, frontal, temporal and parietal lobes were used to investigate the potential differential effects that task requirements may have on potential neural correlates of perceptual consciousness, whether they be NCC-proper or NCC-context. From a more explorative angle, we also included analyses of source reconstructed data from the parietal and temporal lobes since areas in both lobes have been found to be involved in processing of letters (Scott, Blank, Rosen, & Wise, 2000; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002).

# Methods

## Participants

40 right-handed participants, 18 women and 22 men, with normal or corrected-to-normal vision provided written informed consent to participate. The median age was 23 years (range: 20 to 31 years). The experiment was approved by the local ethics committee, De Videnskabsetiske Komitéer for Region Midtjylland.

Two participants were excluded from the study, one because she did not finish the experiment in the allotted time, and the other because he had remains of metallic dental braces in his mouth.

## Stimuli and procedure

Participants were seated 137 cm from a screen onto which a Panasonic PT-D10000E projector projected an image with a resolution of 1280 × 800 pixels and a refresh rate of 60 Hz. A fixation cross was presented for 1000 ms followed by a delay of 1000 ms (to prevent forward masking), which was followed by a pair of letters, the target, presented for 33.3 ms. After the target a mask was presented until the participant performed the same/different judgement, which they were instructed to do as fast and accurately as possible (Fig. 1). Participants were administered one of 2 tasks. 19 participants performed the *perceptual* task, and 19 participants performed the *conceptual* task. Task was determined by participant order with odd numbered participants performing the perceptual task and even numbered participants performing the conceptual task. In the *perceptual* task the target letters were defined as “same” if they were identical, e.g. “rr”, and “different” in all other cases. For the *conceptual* task, the target letters were defined as “same” if they were of the same type according to whether they were consonants or vowels, e.g. “eu” or “sv”, and “different” if they were of opposite types, e.g. “ev”. After the participant had performed a same/different judgement, they were to report perceptual consciousness on the Perceptual Awareness Scale. All stimuli were presented using PsychoPy (Peirce, 2009). Participants were administered 800 trials in blocks of 100 trials each where 10 trials in each block were catch trials where no stimulus was shown. After each block the response hand changed for the “same”/”different” response.

The background was black (RGB value, 0, 0, 0). The fixation cross was white (RGB value, 255, 255, 255). The colour of the target letters was set based on a thresholding procedure as described below, and the height of the letters were 0.75 ° of visual angle and presented with a monospaced font (http://gnome-look.org/content/show.php/DigiTalk-mono+%5Bdigital+clock+font%5D?content=132902, [date last accessed: 31 July 2015]).

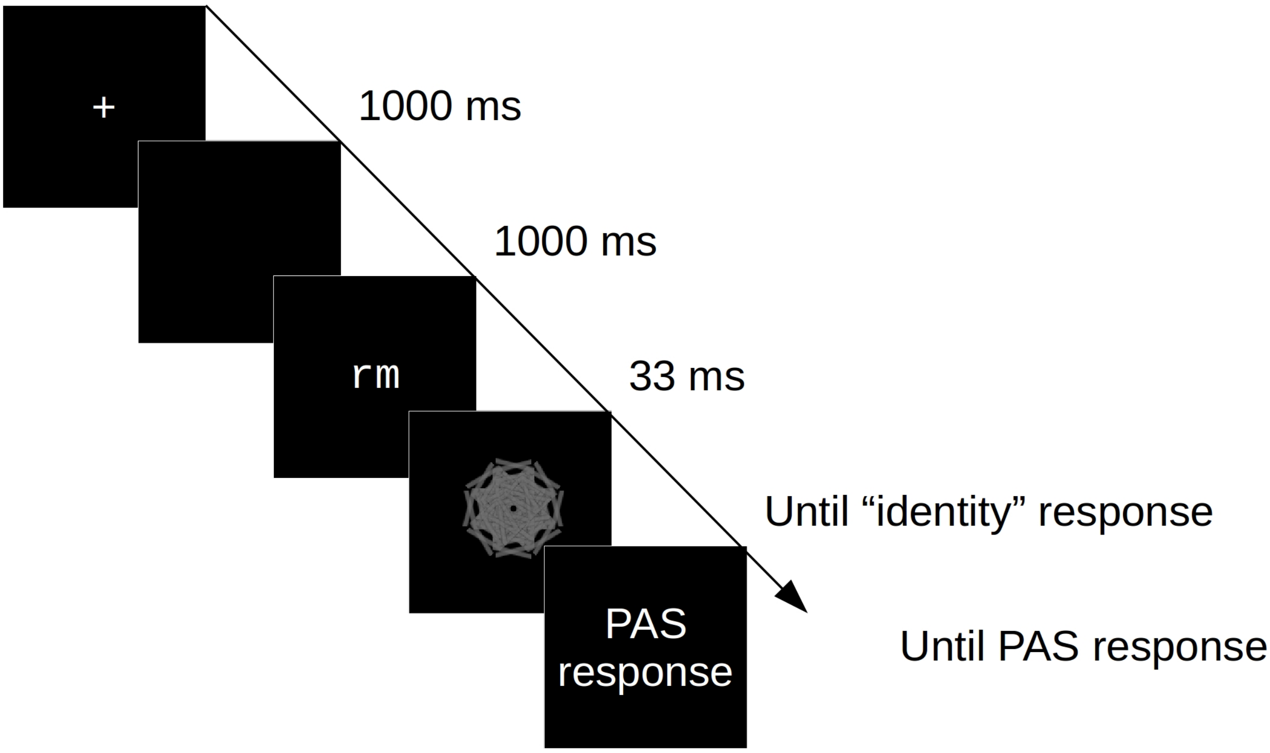



**Figure 1:** Paradigm: A fixation cross was presented for 1000 ms, followed by a delay of 1000 ms, to prevent forward masking of the target stimulus. A pair of letters was then presented for 33 ms immediately followed by a mask that remained on until the participant indicated whether the 2 letters were “same” or “different”. In the *perceptual* task the target letters were defined as “same” if they were identical, e.g. “rr”, and “different” in all other cases. For the *conceptual* task, the target letters were defined as “same” if they were of the same type according to whether they were consonants or vowels, e.g. “eu” or “sv”, and “different” if they were of opposite types, e.g. “ev”. After that participants had to indicate perceptual consciousness by one of 4 ratings, No Experience, Weak Glimpse, Almost Clear Experience or Clear Experience.

Before the participants were prepared for the magnetoencephalographic recording, they went through a practice session in the magnetically shielded room where the recording was made. This practice session consisted of 21 trials of varying contrasts. These trials were done to ascertain that participants understood the task they had been assigned.

After having been prepared for the magnetoencephalographic recording, participants went through a staircase-block that doubly served as practice and for setting a threshold.

### Threshold procedure

The target letters were presented in greyscale. All participants started at the grey hue exactly between black (RGB value, 0, 0, 0) and white (RGB value, 255, 255, 255). We used a stochastic approximation staircase to change the grey hue after each trial (Faes et al., 2007) aiming at a proportion correct of 75 % since this was where we expected all 4 PAS ratings to be represented (Sandberg, Bibby, Timmermans, Cleeremans, & Overgaard, 2011). The thresholded contrast was held constant after this staircase-block.

### Behavioural analyses

We used mixed models to model the proportion correct and response times of participants.

### Magnetoencephalography (MEG)

Before the magnetoencephalographic recording we fastened 4 head position indicator coils (HPI-coils) on the participants, one behind each ear and one on the left and right temples respectively. Head shape and positions of the HPI-coils were digitized using a Polhemus Fasttrack Digitizer (Colchester, Vermont, USA). The coordinate system of this digitization was based on the nasion and the left and right pre-auricular points of the participants. The individual head shapes of participants were later used to create forward models for each participant individually. We also recorded horizontal and vertical electrooculographic data and electrocardiographic data.

MEG data were recorded in a magnetically shielded room with an Elekta Neuromag Triux system with 102 magnetometers and 204 orthogonal planar gradiometers with a recording frequency of

1000 Hz. Offline, a Maxwell filter was used to apply spatiotemporal signal space separation (tSSS), which estimates the signals originating inside the sensor array, the disturbances arising outside the array, and noise/artefacts located close to the sensors and subsequently suppresses the latter two. After applying tSSS, movement compensation was applied based on the continuous HPI measurements with a step size of 30 ms. tSSS and movement compensation were both performed using MaxFilter (version 2.2, Elekta).

Subsequently, data were analysed using MNE-python (Gramfort et al., 2013). The data were bandpass filtered using an infinite impulse response filter (1-15 Hz) and separated into epochs with an interval of [-200; 600] ms around target onset time and subsequently downsampled to 250 Hz. Epochs were rejected if the response of any magnetometer was greater than 4 pT or the response of any gradiometer was greater than 400 pT/m. Independent component analysis (Hyvärinen & Oja, 2000) was used to remove eye blinks, eye movements and heart beats by removing the component that correlated most with horizontal and vertical electrooculograms and the electrocardiogram respectively.

### Source reconstruction

Source reconstruction was done using the minimum norm estimate algorithm (MNE) (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). MNE assumes minimal prior information, namely only that source currents are spatially restricted. Source reconstructions were done for each participant based on participant-specific cortical reconstructions and volumetric segmentations modelled using FreeSurfer (http://surfer.nmr.mgh.harvard.edu/) (Dale, Fischl, & Sereno, 1999).

Dynamic statistical parametric mapping was used to overcome the superficial bias of MNE (Dale et al., 2000). Furthermore, the occipital, frontal, temporal and parietal sources were defined as those reconstructed to the occipital, frontal, temporal and parietal lobes as defined by the Desikan-Killiany Atlas (Desikan et al., 2006).

### Characteristics of the classifiers

Based on the source reconstructions, we tested whether trials that only differed on how perceptual consciousness was subjectively rated using PAS could statistically be told apart. We used multinomial logistic regression (Bishop, 2006) to classify perceptual consciousness, the 4 PAS ratings. The input to the classifier was either the reconstructed time courses of occipital, frontal, temporal or parietal sources. Half the trials were right-handed responses and the other half were left-handed responses such that motor activity would not bias the classifier. We used stratified 5-fold cross-validation. Separate classification analyses were run for an early range (VAN: 132-320 ms) and for a late range (P3a: 324-512 ms). Importantly, these ranges were of equal duration and thus included equal numbers of temporal features. This secures unbiased comparisons of the ranges (Sandberg, Andersen, & Overgaard, 2014). We used grid search to find the optimal regularization parameters. These analyses were run within-participant. We ran 2 types of analyses on the source reconstructed data, explicated below.

### Number of trials

Only participants that had at least 30 trials of each PAS rating were admitted to the analysis. This criterion was conservative and excluded 28 of our 38 participants, and made 4 remain from the conceptual task and 6 from the perceptual task. Setting the number of trials to 20 did not increase the number of participants in the conceptual task. Since the planned analyses were multinomial with 4 categories, we judged that we could not go lower on trials without this resulting in bad model fits. Thus, despite the low number of participants we chose to go with 30 trials since this should result in better model fits.

### Time sample analysis

We ran multinomial analyses for each of the 201 time samples, -200 ms to 600 ms, where we tested how classification accuracy evolved over time, but also how the 4 different ratings were mistaken for one another. This was done for each of the 4 lobes, occipital, frontal, temporal and parietal.

### Range analysis

For each participant a multinomial logistic classification analysis was run 8 times total, one for each of the combinations of Time Range (2 levels: VAN; P3a) and Lobe (4 levels: occipital; frontal; temporal; parietal). We used mixed models to model the probability for the classifier to label a trial as any of the 4 PAS ratings across participants. The probability for each label was modelled as dependent on 5 fixed effects and their interactions: Time Range (2 levels: VAN; P3a), Task (2 levels: perceptual; conceptual), Lobe (4 levels: occipital; frontal; temporal; parietal), Actual PAS (4 levels: No Experience Weak Glimpse; Almost Clear Experience; Clear Experience) and Classified PAS (4 levels: No Experience; Weak Glimpse; Almost Clear Experience; Clear Experience).

## Results

### Behavioural performance

We created mixed models testing how the proportion of correct responses and response times were dependent on PAS rating and Task. Accuracy was modelled as a binomial parameter (Fig. 2A). As fixed effects, we included PAS rating (4 levels: No Experience; Weak Glimpse; Almost Clear Experience; Clear Experience), Task (2 levels: perceptual; conceptual), and the interaction between them. Individual intercepts were modelled for each Participant (38). The interaction could *not* be dropped without a significant change in log likelihood, $\chi^2(38) = 82.0$, $p < 0.001$. The interaction between Task and PAS rating was driven by a significantly higher accuracy for Weak Glimpses, Almost Clear Experiences, and Clear Experiences for participants doing the perceptual task compared to participants doing the conceptual task, Weak Glimpse: $z = 2.69$, $p = 0.0072$; Almost Clear Experience: $z = 5.56$, $p < 0.001$; Clear Experience: $z = 4.81$, $p < 0.001$. There was no significant difference between tasks when participants reported No Experience: $z = 0.74$, $p = 0.46$.

In both tasks, accuracy increased significantly with perceptual clarity. In the perceptual task: Weak Glimpse versus No Experience: $z = 11.1$, $p < 0.001$; Almost Clear Experience versus Weak Glimpse: $z = 19.5$, $p < 0.001$; Clear Experience versus Almost Clear Experience: $z = 10.6$, $p < 0.001$. In the conceptual task: Weak Glimpse versus No Experience: $z = 6.35$, $p < 0.001$; Almost

Clear Experience versus Weak Glimpse: $z = 17.5$, $p < 0.001$; Clear Experience versus Almost Clear Experience: $z = 15.4$, $p < 0.001$.

Response times were log-transformed and modelled factorially (Fig. 2B). The fixed and random effects were the same as in the accuracy model. Again, the interaction between Task and PAS ratings could *not* be dropped without a significant change in log-likelihood, $\chi^2(3) = 315.8$, $p < 0.001$.

The interaction was driven by slower response times in the conceptual task for PAS ratings: Weak Glimpse: $z = -3.61$, $p < 0.001$; Almost Clear Experience: $z = -4.25$, $p < 0.001$; Clear Experience: $z = -2.94$, $p = 0.0032$. There was no significant difference for No Experience: $z = 0.13$, $p = 0.90$.

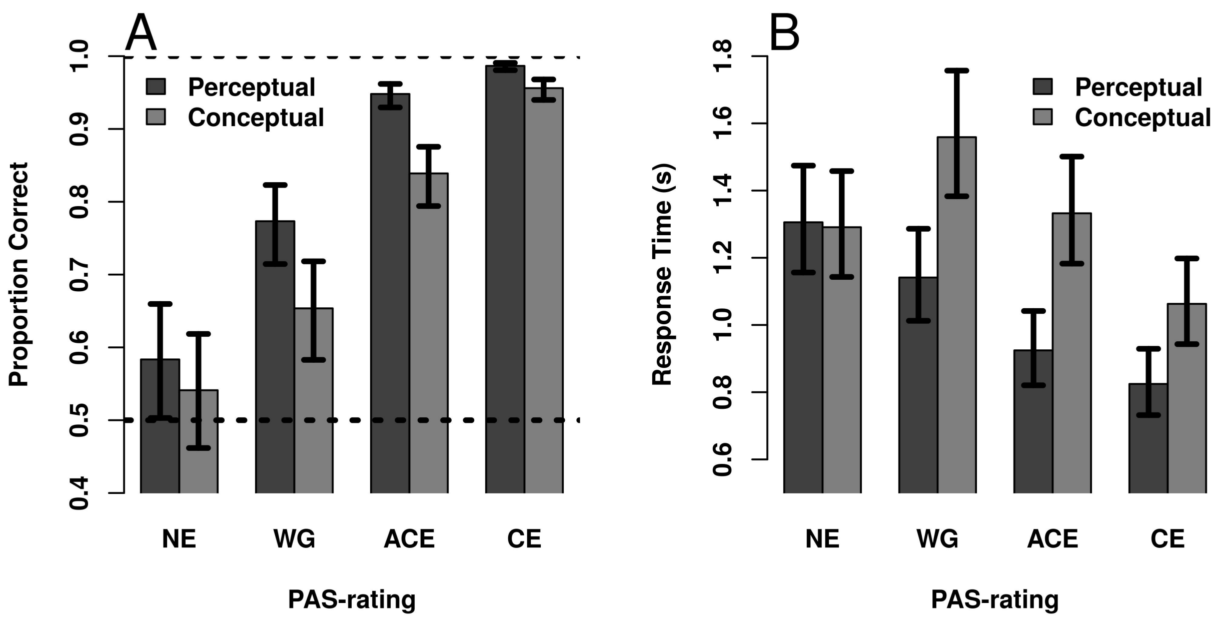



**Figure 2:** Behavioural results: (A) accuracy increased as a function of rated perceptual clarity. A significant interaction and subsequent paired tests indicated that Weak Glimpses (WG), Almost Clear Experiences (ACE) and Clear Experiences (CE) were more accurate in the perceptual task compared to the conceptual task. Error bars are 95 % confidence intervals. (B) response times decreased from Weak Glimpse to Almost Clear Experience to Clear Experience across the 2 tasks. For these 3 ratings, participants were faster on the perceptual task than on the conceptual task. Error bars are 95 % confidence intervals. No significant differences in response times or accuracy was found for No Experiences between tasks.

For the perceptual task, response times decreased with increasing PAS ratings: Weak Glimpse versus No Experience: $z = -8.69$, $p < 0.001$; Almost Clear Experience versus Weak Glimpse: $z = -19.5$, $p < 0.001$; Clear Experience versus Almost Clear Experience: $z = -11.4$, $p < 0.001$. For the conceptual task, however, there was an increase of response times when going from No Experience to Weak Glimpse, $z = 12.2$, $p < 0.001$. Thereafter, response times decreased with increasing PAS ratings: Almost Clear Experience versus Weak Glimpse: $z = -15.0$, $p < 0.001$; Clear Experience versus Almost Clear Experience: $z = -21.2$, $p < 0.001$. A possible interpretation of this pattern for the conceptual task is that random guessing, which subjectively speaking is what subjects do when they rate a trial as No Experience, should take equally long for both the conceptual and the perceptual task. Please note that these analyses included all 38 participants since the behavioural analyses could be performed independently of whether there were 30 trials available.

### Catch trials

The median number of catch trials for each PAS rating was as follows. For the perceptual task: No Experience = 71, Weak Glimpse = 8, Almost Clear Experience = 0, Clear Experience = 0. For the conceptual task: No Experience = 74, Weak Glimpse = 2, Almost Clear Experience = 0, Clear Experience = 0. This supports that participants were using the scale in the intended manner.

### Illustration of event-related fields

We found that our tasks elicited components in the VAN range and the P3a range indicating that our paradigm had worked as intended (Fig. 3A) (Koivisto & Revonsuo, 2010).

### Time sample analysis

We did a classification per time sample in the epoch period. Means were taken across participants for each time sample for occipital sources (Fig. 4), frontal sources (Fig. 5), temporal sources (Sup. Fig. 1) and parietal sources (Sup. Fig. 2).

Looking at the occipital sources first, we found for the perceptual task that the period up to (~ 130 ms) and around the peak of VAN (~ 270 ms) (Fig. 4E-H) saw a steep rise in classification accuracy. Thereafter, classification accuracy started declining. This mirrored the finding that perceptual consciousness is graded, and that occipital sources during the VAN time range correlates with ratings of perceptual consciousness (Andersen, Pedersen, Sandberg, & Overgaard, 2015). When Weak Glimpses were misclassified, it was mostly as No Experiences, and Almost Clear Experiences were mostly misclassified as Clear Experiences.

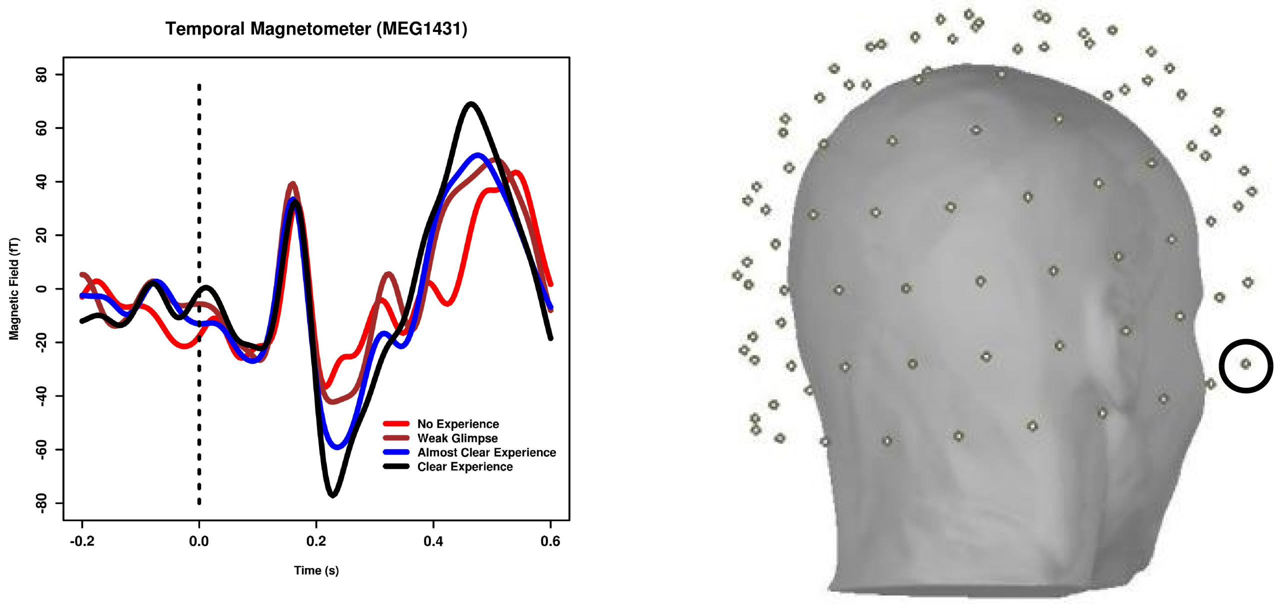



**Figure 3:** A) An example of an MEG response: grand average over 10 participants. Graded differences are visible in the Visual Awareness Negativity Range (130-320 ms), and a less graded difference is present around the P3a (~430 ms). B) The positions of magnetometers and gradiometers around the head of an example participant. Encircled is the magnetometer shown in A.

For the conceptual task (Fig. 4A-D), we found that only No Experiences and Clear Experiences could be clearly separated from the others during the VAN time range. Almost Clear Experiences became more separated from the others during the P3a time range, while Weak Glimpses only showed one narrow peak around 300 ms. It thus seems that the conceptual task resulted in a more dichotomous pattern where Weak Glimpses and Almost Clear Experiences were not separable from the other ratings judging from the sample-by-sample occipital activity during the VAN time range. An interesting thing to notice is that classification accuracy was sustained during the P3a time range for the conceptual task, which it was not in the perceptual task. This might indicate further processing of the stimuli required for assessing the vowel-/consonanthood of the presented stimuli with graded experiences.

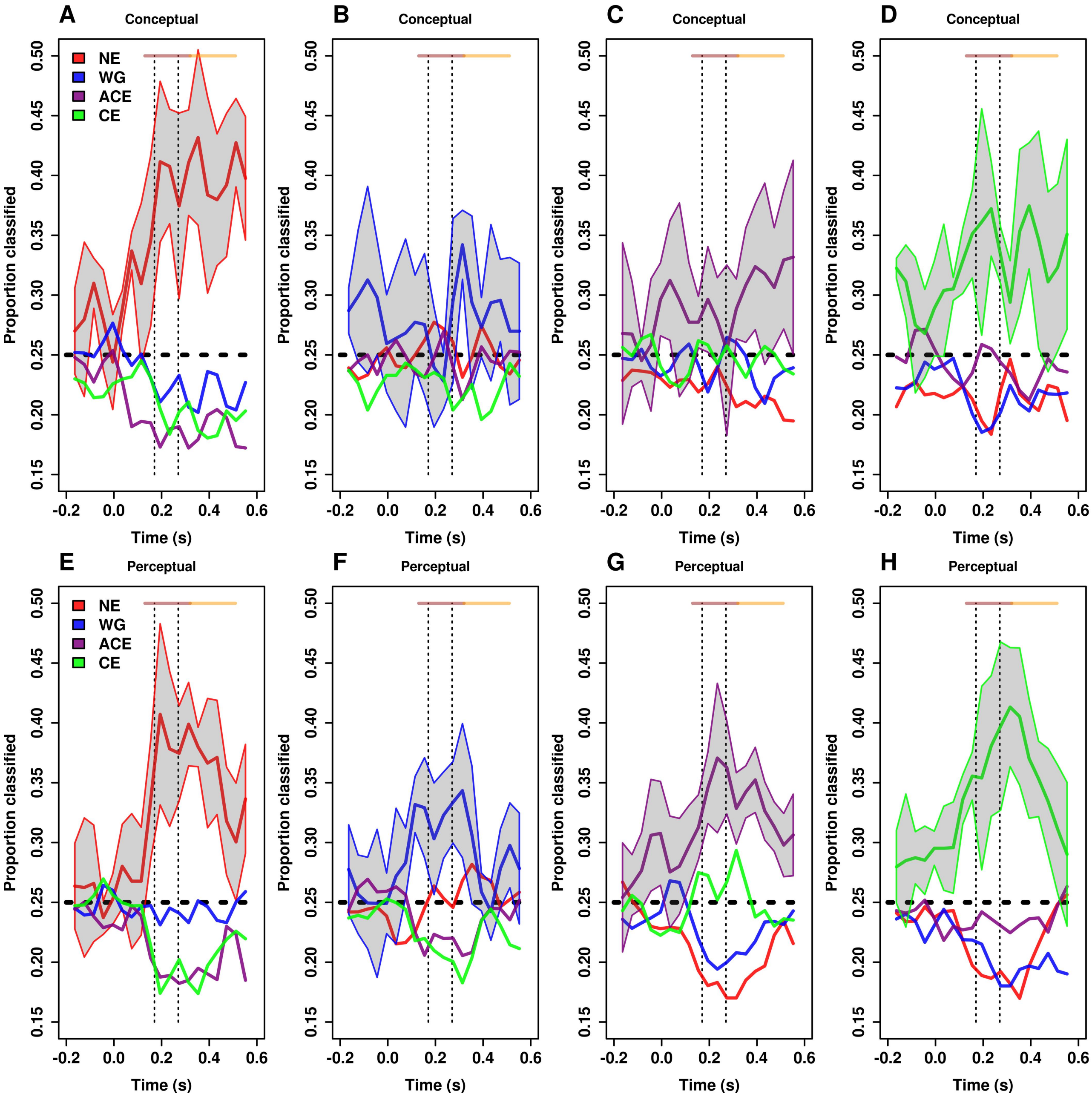



**Figure 4:** Sample-by-sample analyses for occipital sources: the upper row of panels (A-D) shows conceptual sources classification for No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) respectively. The lower row of panels (E-H) shows the same for the perceptual task. Mean classification accuracies across participants, smoothed by taking every 10$^{th}$ sample and taking the mean across that sample and the 10 samples on each side, are shown for all classifications. Shaded regions are standard errors of the mean smoothed the same way. The 2 bars at the top indicate the width of the 2 time ranges tested in other analyses. Vertical lines indicate 170 ms and 270 ms respectively.

We then investigated the frontal sources (Fig 5.)

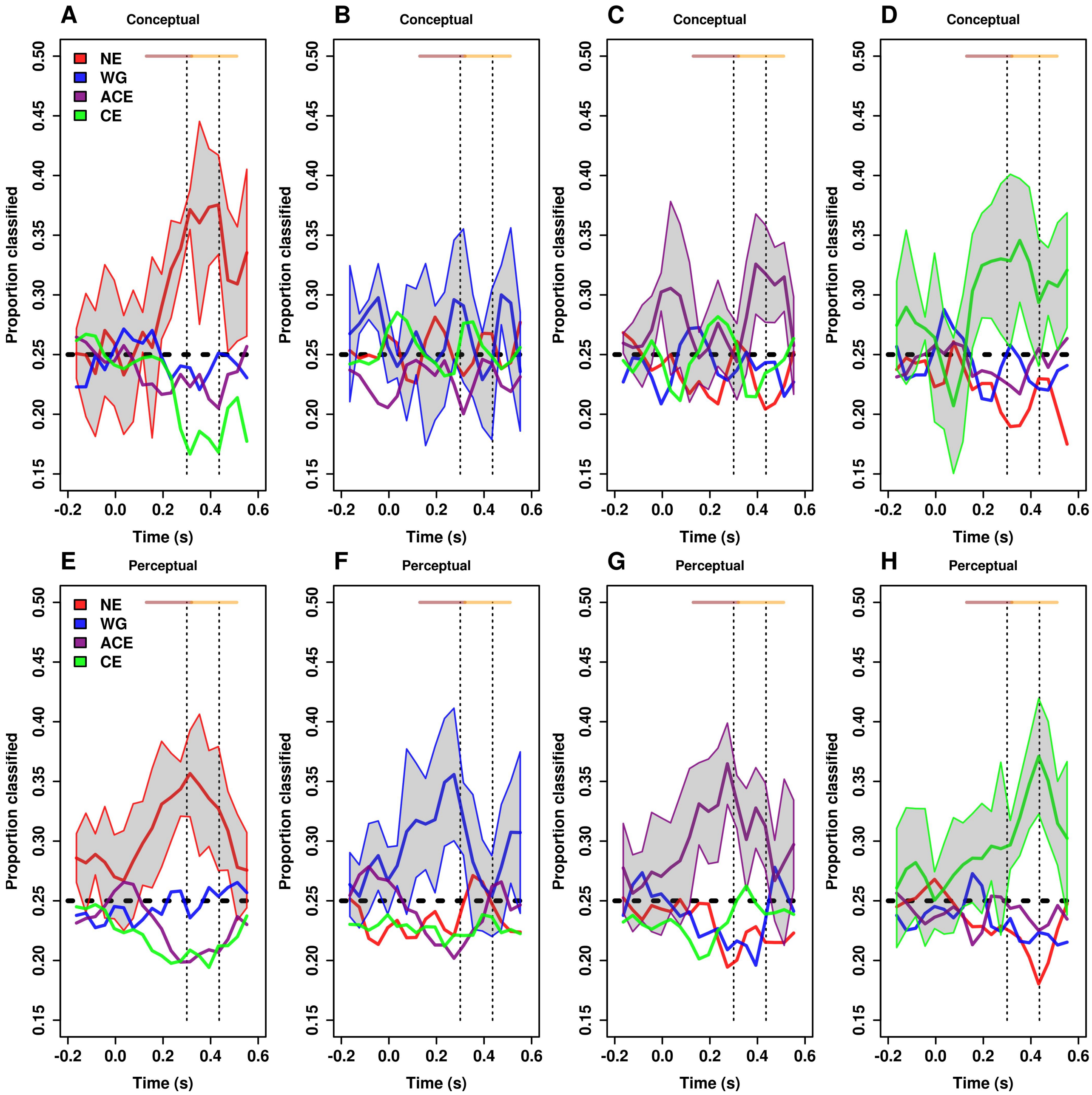



**Figure 5:** Sample-by-sample analyses for frontal sources: the upper row of panels (A-D) shows conceptual sources classification for No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) respectively. The lower row of panels (E-H) shows the same for the perceptual task. Mean classification accuracies across participants, smoothed by taking every 10$^{th}$ sample and taking the mean across that sample and the 10 samples on each side, are shown for all classifications. Shaded regions are standard errors of the mean smoothed the same way. The 2 bars at the top indicate the width of the 2 time ranges tested in other analyses. Vertical lines indicate 300 ms and 436 ms respectively.

We found that for the perceptual task (Fig. 5E-H), classification accuracies for No Experiences, Weak Glimpses and Almost Clear Experiences all peaked around ~ 300 ms probably reflecting the N3, which Sergent et al. (2005) reported to be fronto-temporally realized and bimodal.

After ~ 300 ms, classification accuracies started declining for these 3 ratings. Clear Experiences, however, peaked around ~ 430 ms, probably reflecting the P3a (Koivisto & Revonsuo, 2010; Sergent et al., 2005). Around the P3a peak, Weak Glimpses and Almost Clear Experiences could not be told apart from the other ratings.

In the conceptual task (Fig. 5A-D), only No Experiences and Clear Experiences peaked around the N3 showing the bimodal character that Sergent et al. (2005) reported. Their task required conceptualization of the letters. We thus found a bimodal pattern in the conceptual task, but a more graded pattern in the perceptual, thus it seems probable that the bimodal character they reported is due to the conceptual character of their task.

The temporal and parietal time courses were very similar with classification accuracies for the perceptual task rising and peaking for all PAS ratings in the VAN time range and the conceptual task only able to classify the extreme ratings accurately during the VAN Range (Sup. Figs. 1 & 2)

### Range Analysis

In this analysis, all 4 categories of PAS (No Experience; Weak Glimpse; Almost Clear Experience; Clear Experience) were tested against one another based on the conglomerate activity from 2 predefined ranges (Andersen et al., 2015). We investigated the confusion matrices. A confusion matrix has a row and a column for each label classified, one for each PAS rating. One dimension represents the *actual* categories and the other dimension represents what they were *classified* as. The sum of the matrix is 120 (30 trials × 4 PAS ratings). Counts on the diagonal are correctly classified trials. With a multinomial analysis, it is possible to test if there is any pattern in how trials are misclassified. They might provide evidence for whether perceptual consciousness is graded or dichotomous. We fitted a mixed model based on 5 fixed effects: Time Range (2 levels: VAN; P3a), Task (2 levels: perceptual; conceptual), Lobe (4 levels: occipital; frontal; temporal; parietal), Actual PAS (4 levels: No Experience; Weak Glimpse; Almost Clear Experience; Clear Experience) and Classified PAS (4 levels: No Experience; Weak Glimpse; Almost Clear Experience; Clear

Experience) with a random intercept for each Participant (10) and a random effect, Classified PAS, whose addition to the model resulted in a significant change in log-likelihood: $\chi^2(9) = 52.6$, $p < 0.001$. The 4 remaining effects did not: Time Range: $\chi^2(2) = 0.00$, $p = 1.0$; Lobe: $\chi^2(9) = 0.00$, $p = 1.0$; Actual PAS: $\chi^2(9) = 0.00$, $p = 1.0$; Task: $\chi^2(2) = 0.00$, $p = 1.0$. Among the fixed effects, the 4-way interaction Time Range × Task × Actual PAS × Classified PAS could not be removed without a significant change in log-likelihood, $\chi^2(9) = 19.8$, $p = 0.019$, and neither could the 3-way interaction Lobe × Actual PAS × Classified PAS, $\chi^2(27) = 75.0$, $p < 0.001$ (see Appendix A for the full analysis of the model).

We investigated these 2 interactions further, but restricted the analyses to the proportion of correct trials (for the full model, see Figs. 7 & 8).

The Lobe interaction revealed 5 significant effects of the 24 tested comparisons (6 for each PAS rating: Fig. 6A: see Appendix B for a table of all the tests) and was driven by significant differences within No Experiences, Almost Clear Experiences and Clear Experiences. No significant differences were found for Weak Glimpses. For No Experiences, occipital sources were more predictive than frontal sources, $z = 2.37$, $p = 0.018$, and so were parietal sources, $z = 2.54$, $p = 0.011$. For Almost Clear Experiences, parietal sources were more predictive than temporal sources, $z = 2.31$, $p = 0.021$. For Clear Experiences, occipital sources were more predictive than frontal sources, $z = 2.48$, $p = 0.013$, and were more predictive than temporal sources, $z = 3.12$, $p = 0.0018$. Extreme awareness ratings, No Experiences and Clear Experiences, were thus classified more accurately by occipital sources than by frontal sources. No significant differences were found, however, for graded ratings, Weak Glimpses and Almost Clear Experiences (Fig. 6A).

The Time Range × Task interaction revealed 8 significant effects of the 24 tested comparisons (6 for each PAS rating: Fig. 6B: see Appendix C for a table of all the tests). For No Experiences, the P3a time range was more predictive in the conceptual task than in the perceptual task, $z = 2.00$, $p = 0.045$. For Weak Glimpses in the perceptual task, the VAN time range was more predictive than all other combinations of Task and Time Range: Conceptual VAN, $z = 2.31$, $p = 0.021$; Perceptual P3a, $z = 2.42$, $p = 0.015$; Conceptual P3a, $z = 2.52$, $p = 0.012$. Compared to Almost Clear Experiences in the VAN time range for the conceptual task, all remaining combinations of Task and Time Range were significantly more predictive, Perceptual VAN, $z = 3.27$, $p = 0.0011$; Perceptual P3a, $z = 3.37$, $p < 0.001$; Conceptual P3a, $z = 2.13$, $p = 0.033$. For Clear Experiences in the P3a time range, the perceptual task was significantly more predictive than the conceptual task, $z = 2.07$, $p = 0.038$ (Fig. 6B).

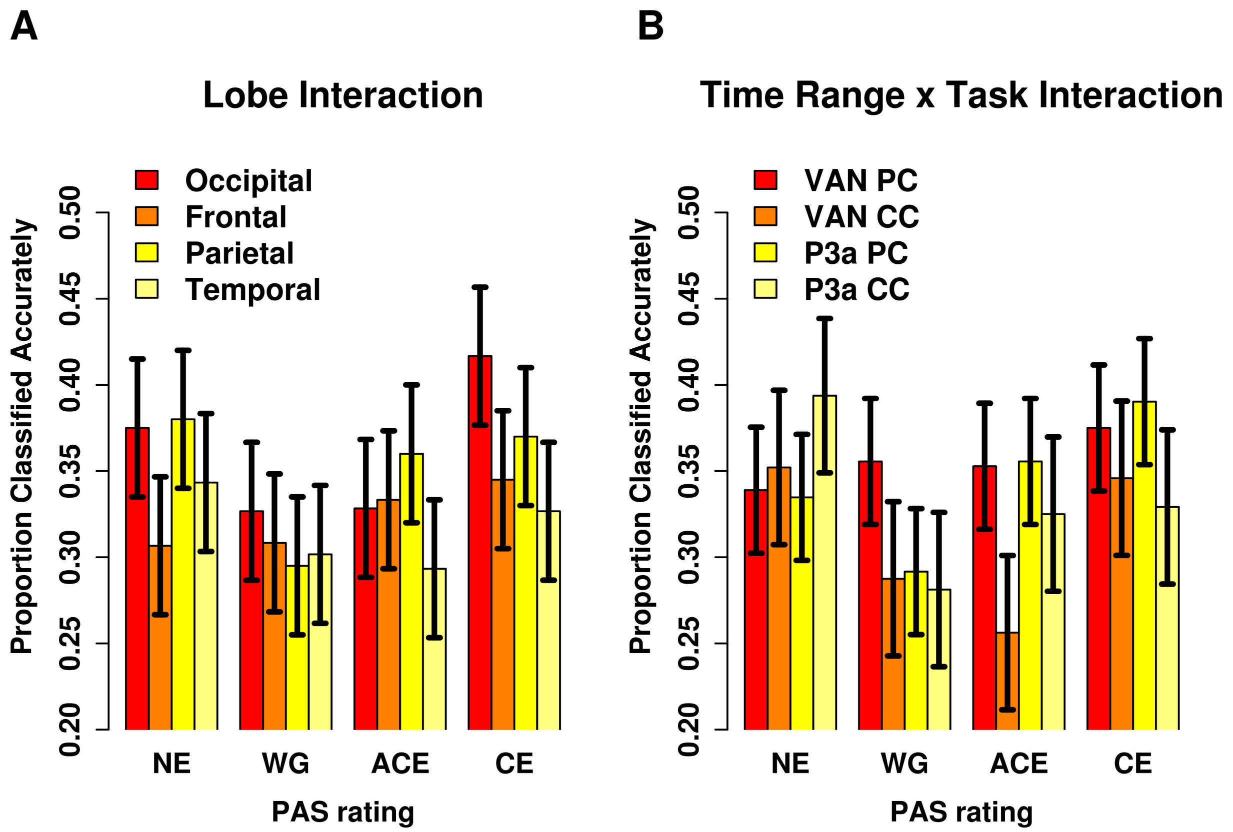



**Figure 6:** Illustration of the effects that Lobe and the Time Range × Task interaction had on classification accuracy. For extreme ratings, NE and CE, occipital sources were found to be significantly more accurate than frontal sources, whereas the interaction between time range and task was driven by graded ratings, WG and ACE, being affected differently by the 2 tasks administered. Error bars are 95 % confidence intervals.

This concurs with the impression from the sample-by-sample analyses, namely that the greatest differences between tasks were in the graded ratings, Weak Glimpses and Almost Clear Experiences. Weak Glimpses were dependent on early activity for successful classification, and this was only possible in the perceptual task. We thus found evidence of a dissociation for tasks and for time ranges. We also found a dissociation between tasks and time ranges for Almost Clear Experiences, namely a greater dependence on late activity for successful classification, but crucially so only in the conceptual task.

Having investigated what was driving the differences in classification accuracy, we investigated the estimates for the full model looking at both classification accuracy and how often a PAS rating was confused for another (Fig. 7). To interpret to which degree each PAS rating could be discerned from the other 3 possible ratings, we tested whether classification accuracy was significantly different from the misclassification probability for each PAS rating (Fig. 8). The motivation for investigating the full model was that the statistical analyses showed that all 5 fixed effects had an effect, thus the full model might reveal more about the individual classification accuracy estimates and could be used to ascertain whether or not perceptual consciousness was graded.

Looking at the *occipital* sources, first, we saw that during the VAN time range, all 4 PAS ratings could be classified above chance in the perceptual task (Figs. 7A & 8A). In general, a graded pattern was found during the VAN time range (Fig. 7A) where all ratings could be classified above chance and to a high degree could be discerned from one another (Figs. 8A & 8E)

For the conceptual task, the VAN time range could only classify No Experiences and Clear Experiences above chance (Fig. 7I). The P3a time range (Fig. 7M), however, could classify all PAS ratings above chance, and PAS ratings were less confused with one another (Figs. 8I & 8M). Thus, a dichotomous pattern was found during the VAN time range, but a graded pattern was found during the P3a time range. The graded pattern thus seemed to move from the VAN time range to the P3a time range between the 2 tasks.

Looking at the *frontal* sources, then, we found that during the VAN time range (Figs. 7B & 8B) for the perceptual task that the graded ratings, Weak Glimpses and Almost Clear Experiences, could be classified above chance probably peaking at a graded N3 (~ 300 ms) (Fig. 5F-G). The P3a time range (Fig. 7F), however, could classify only Almost Clear Experiences and Clear Experiences above chance.

For the conceptual task, the frontal sources could not classify anything above chance during the VAN time range (Fig. 7J), and during the P3a time range (Fig. 7N), only Almost Clear Experiences were classified above chance, while the other ratings were mostly confused for one another. Thus, frontal sources were surprisingly best for graded ratings in the perceptual task.

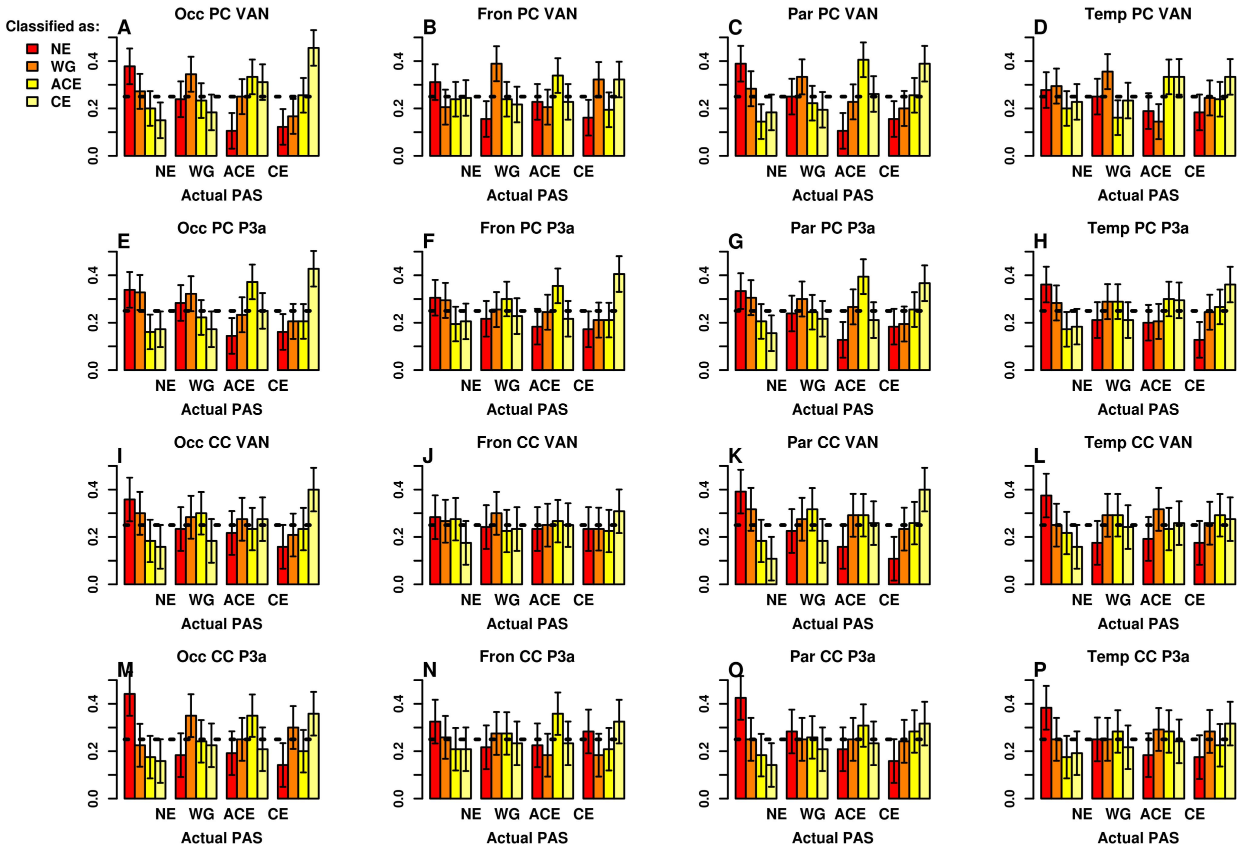



**Figure 7:** Multinomial classifications for all combinations of time ranges (VAN: Visual Awareness Negativity and P3a), tasks (PC: perceptual and CC: conceptual) and lobes (Occ: occipital; Fron: frontal; Tem = temporal; Par = parietal). For each PAS rating, the probability of classifying that rating as any of the 4 PAS ratings is shown. Error bars are 95 % confidence intervals.

For the *parietal* sources, in the perceptual task all 4 PAS ratings could be classified above chance in the VAN time range, thus showing a graded pattern (Fig. 7C). The frontal sources do thus seem less apt for classifying graded perceptual consciousness than both occipital and parietal sources as the interactions found suggested (Fig. 6A).

In the conceptual task, only the extreme ratings, No Experiences and Clear Experiences, could be classified above chance (Fig. 7K) in the VAN time range and only No Experiences in the P3a time range. The graded pattern from the perceptual task thus seemed to become a more dichotomous pattern in the conceptual task.

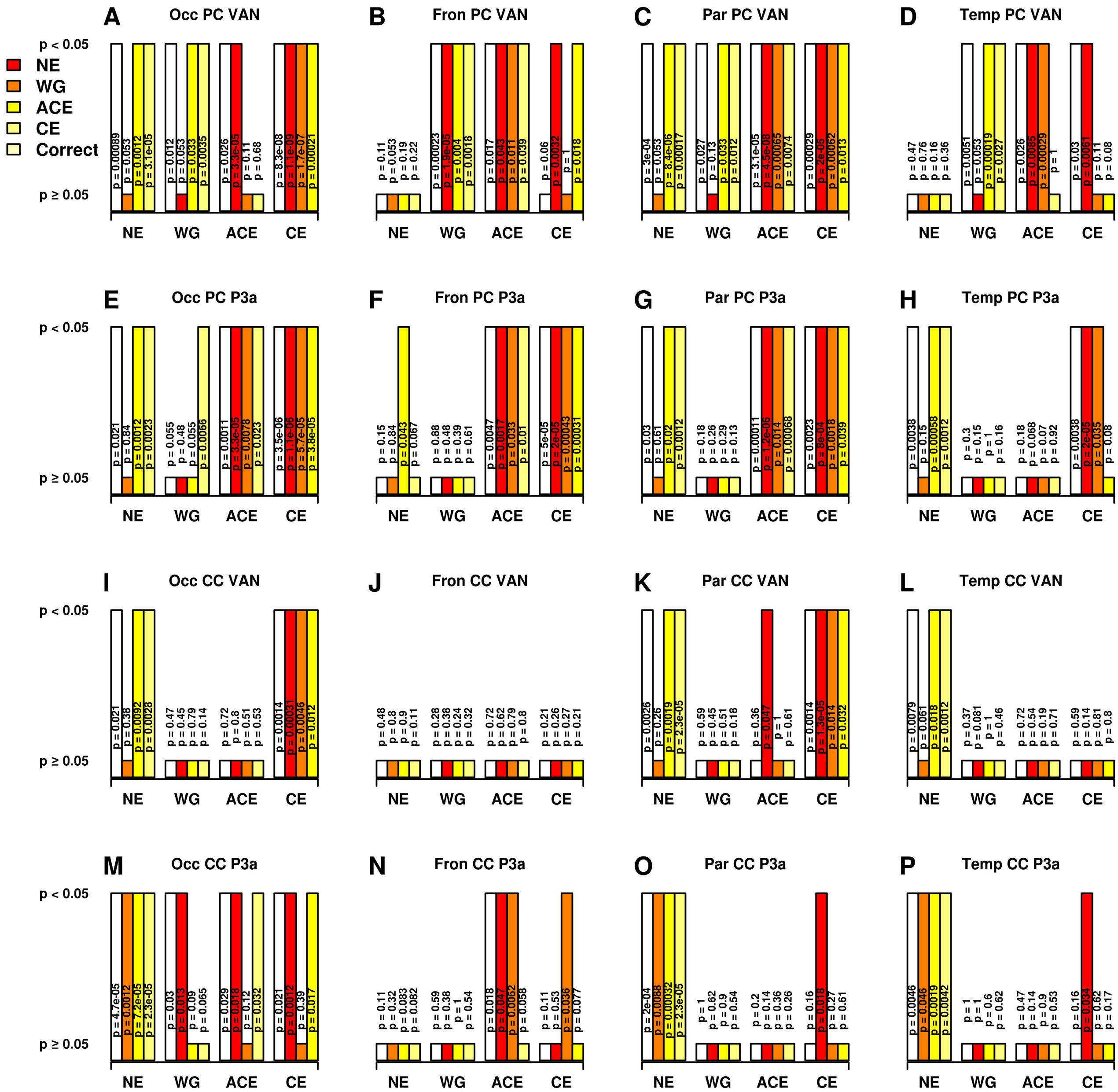



**Figure 8:** Plots showing for each PAS rating (*x*-axis) whether they could be significantly be told apart from from the other ratings (column on *y*-axis) indicated by the heat colours. White bars show whether the PAS rating could be classified above the theoretical chance level (25 %).

For the *temporal* sources, in the perceptual task the graded ratings, Weak Glimpses and Almost Clear Experiences, could be classified during the VAN time range, but not during the P3a time range. In the conceptual task, only No Experiences were classified above chance. The temporal sources do thus seem less apt for classifying graded perceptual consciousness than occipital and parietal sources as the interactions found suggested (Fig. 6A).

In general the full model, showed, as the interaction effects revealed (Fig. 6A), how occipital sources, in terms of being above chance for all gradations of perceptual consciousness, were more predictive of PAS ratings than frontal sources and temporal sources. The interaction effect between Task and Time Range (Fig. 6B) was also clearly visible in the perceptual task being associated with higher classification accuracies for the graded ratings, Weak Glimpses and Almost Clear Experiences, than the conceptual task.

The overall picture of these multinomial analyses is that the differences in task requirements induced differences in *when* and *where* perceptual consciousness could be classified. Most notable were the differences in how classification accuracies for the graded ratings, Weak Glimpses and Almost Clear Experiences, differed between tasks, and how occipital sources were superior to frontal sources on the extreme ratings, No Experiences and Clear Experiences. More specifically how will be discussed below.

## Discussion

The behavioural results revealed, despite our efforts to control the performance levels, that participants in the conceptual task performed significantly worse than participants in the perceptual task in terms of accuracy. Crucially, this was only for Weak Glimpses, Almost Clear Experiences and Clear Experiences. Thus, there were no significant difference when participants rated No Experience. For Weak Glimpses and above, above-chance performance was found for both tasks (Fig 2A). The above-chance performance for Weak Glimpses is evidence for participants being able to code letters into vowels and consonants even when they report having no experience of the content. The distributions of response times showed an interesting pattern. In the perceptual task, there was an approximately linear decrease of response times as perceptual ratings increased. For the conceptual task, however, there was only an approximately linear decrease from Weak Glimpses to Clear Experiences (Fig. 2B). The response times for No Experiences were very similar between the 2 tasks and were actually faster than the Weak Glimpses in the conceptual task. The similarity of these responses may reflect the cognition that is involved in assessing that no information is present and that a random response must be given. It seems reasonable to assume that the cognition for both tasks span the same temporal timeline when no information is present to operate on. From this view it is coincidental that No Experiences appear to be part of a linear decrease in the perceptual task. The increase in response time from No Experience to Weak Glimpse in the conceptual task thus makes sense if one assumes that uninformed guesses, No Experiences, undergo different kinds of processes, which are independent of task requirements, than informed guesses, Weak Glimpses and above, which are dependent on task requirements. If this interpretation is correct, we thus should expect that neural processing of No Experiences should not differ much between tasks. We will return to this point later.

The multinomial analyses (Figs. 4, 5 & 6) indicated that there was no unique spatio-temporal correlate of perceptual consciousness across differences in task requirements. Judging from the perceptual task only, occipital sources in the VAN time range could predict all 4 PAS ratings, as we have found earlier in a perceptual task, (Andersen et al., 2015) (Figs. 7A & 8A) whereas this predictive capability had moved to the P3a time range for the conceptual task (Figs. 7M & 8M). This speaks against occipital activity during either time range exclusively being an NCC-proper. The same goes for frontal activity, which could not differentiate all 4 PAS ratings from chance in any of the tasks or time ranges (Figs. 7B, F, J, & N). Thus our results are not as would be hypothesized from the viewpoint of there existing an NCC-proper, where cognitive context and perceptual consciousness are seen as not interacting. On the other hand, these results are compatible with such an interaction between cognitive context and perceptual consciousness. The cognitive context, most notably, influenced how predictive the VAN time range was for graded ratings (Fig. 6B). Initially, the hypothesis based on the account of Windey & Cleeremans (2015) that the perceptual task would result in graded perceptual consciousness and that the conceptual task would result in dichotomous perceptual consciousness seems to be corroborated. During the VAN time range, we found that all 4 PAS ratings could be distinguished in the perceptual task by occipital sources, which is evidence of gradedness (Fig. 7A), and that only No Experiences and Clear

Experiences could be told apart in the conceptual task, which might be taken as evidence of dichotomousness (Fig. 7I). Even in the conceptual task, however, there was evidence of occipital sources being capable of telling all 4 PAS ratings apart; this capability had just moved to the P3a time range (Fig. 7M & 8M). The account of Windey & Cleeremans (2015) offers no immediate explanation of this finding.

The hypothesis made based on the REFCON account (Overgaard & Mogensen, 2014) that perceptual consciousness would be graded and that the greatest differences between tasks would be found for graded differences can be interpreted as corroborated by these findings (Figs. 7A & 7M). The question is then why there should be in a shift in latency for when perceptual consciousness could be classified in a graded manner across tasks. According to REFCON, the cognitive strategies available depend on both availability of information, as measured by PAS, and the cognitive context associated with interpreting that information, as manipulated by the task requirements. So an answer as to why we found latency differences could be that the cognitive strategies available in the conceptual task for less than perfect information, that is for Weak Glimpses and Almost Clear Experiences, are different than the strategies available for the perceptual task. Not only the latency differences between tasks for the occipital sources may be a consequence of differences in cognitive strategies, also the differences in accuracy between tasks for frontal sources during the VAN time range peaking at N3 (~300 ms) may be reflecting differences in cognitive strategies available. For the perceptual task, there was evidence that frontal sources could classify PAS ratings in a graded manner (Figs. 5 E-H & 6B) whereas this ability was absent in the conceptual task. There is evidence that N3 reflects object processing and categorization but not the semantics associated with letters whereas later activity (~ 400 ms) has been associated with the extraction of semantics (Eddy, Schmid, & Holcomb, 2006; Hamm, Johnson, & Kirk, 2002; McPherson & Holcomb, 1999). The information processing reflected by N3 may be sufficient for performing the perceptual task above chance, and therefore according to REFCON, it is not surprising to see this correlating with differences in perceptual consciousness since this activity is directly relevant to behavioural goals in terms of task requirements. In contrast, the N3 activity will not be sufficient for performing the conceptual task above chance since the semantics, i.e. vowelhood and consonanthood, needs to be extracted. Interestingly, we also found that the Clear Experiences did not reach peak classification accuracy in the perceptual task until 436 ms (Fig. 5H). This might seem surprising because one might believe that this should mirror the patterns from the graded ratings. For graded ratings, the optimal strategy might be one of comparing shapes, (N3), but for a Clear Experience, this strategy might be backed by up a more explicit comparison of the letters, e.g. a conscious assessment of seeing *letters*, say, 2 *a*'s or an *e* and a *c*, not just about the similarity of shapes. The peak of 436 ms also coincides with P3a peak thought by Dehaene (2014) to signify entry into a global workspace. Our findings are thus compatible with a theory of a global neural workspace, but importantly such a theory would only be able to explain a subset of the phenomena observed, namely those for Clear Experiences, which are the only ones that show the P3a peak, but not for what we observed for the graded ratings. Proponents of a global workspace theory could bite the bullet and insist that only Clear Experiences are truly conscious and thus maintain a dichotomous view of perceptual consciousness. This would, however, mean that the dividing point between a conscious and an unconscious experience would be whether or not stimuli were *unambiguously* seen, not whether or not there was an experience of *content* (Table 1), which does not seem to be what most people have in mind when discussing perceptual consciousness (Chalmers, 1997; Dehaene, 2014; Lamme, 2006).

We believe that these findings taken together support a view of neural correlates of perceptual consciousness where cognitive context has to be taken into account, thus we cannot expect an NCC-proper, but must settle for an NCC-context. Our results furthermore suggest that in general (Fig. 6A), occipital and parietal sources predict perceptual consciousness better than frontal sources, that is for the extreme ratings, and that perceptual consciousness is graded such as was hypothesized based on the REFCON account.

Thus the general hypothesis that perceptual consciousness is graded and that cognitive context is integrated into perceptual consciousness, as predicted by REFCON, is compatible with these findings. Below, we explore how the interactions between time ranges and tasks may be explained in terms of REFCON.

First, the finding that the Weak Glimpses are best classified in the perceptual task by the VAN time range indicates that the cognitive strategy applied is more consistent (Sandberg et al., 2014) in terms of a spatio-temporal neural pattern than in the conceptual task. Furthermore, it was also more consistent than any pattern in the P3a time range. One interpretation of this may be that it is feedforward activity, which enables above-chance performance, but does not involve a perception of conscious content (Lamme, 2010). The frontal peak (Fig. 5F) at 300 ms may indicate that feedforward activity has reached the frontal lobe, which according to the earlier discussion can be sufficient for solving the perceptual task, but not the conceptual task. This would also explain why the P3a time range classified worse than the VAN time range since activity based on feedforward activity cannot be sustained if it is not recurrently processed, according to Lamme. This might also explain why the VAN time range in the conceptual task was worse than in the perceptual task for classification of Almost Clear Experiences (Fig. 6B). Again, the feedforward activity can be sufficient for solving the perceptual task. Differing from the classification of Weak Glimpses, however, was the finding that the P3a time range, for either task, was significantly better than VAN range activity in the conceptual task. This may be explained by recurrent interactions, as witnessed by the conscious perception of (ambiguous) content (Lamme, 2010). These allow in the conceptual task for a consistent strategy where the semantics are extracted as might be indicated by the rise in classification accuracy after 300 ms (Fig. 5C). Thus the differences found for graded ratings here may thus be consequences of differences in available cognitive strategies. It should be emphasized that these interpretations are tentative interpretations of why we see the differences that we do and were not *a priori* formed hypotheses.

For future experiments into whether task requirements, or other changes in cognitive context, affect which NCCs are found, we here propose that the greatest differences should be expected to be found for the graded ratings, Weak Glimpses and Almost Clear Experience (Fig. 6B), the theoretical reason being that these are the ratings where cognitive strategies should differ the most. For Clear Experiences, all cognitive strategies should in principle be available. For example, one can explicitly compare what the *letters* were instead of just comparing *shapes*. For No Experiences the cognitive strategy may be expected to be the same across tasks: first, ascertain the lack of information for the task at hand, second, carry out a random response, as participants were instructed to in case of No Experience. The behavioural results in terms of response times (Fig. 2B) support that cognition is similar across tasks for the No Experiences, but that it differs for all the other ratings. In further support of the strategy being similar for No Experiences, we found that classification accuracies peaked around the same time across tasks both in occipital sources (Figs. 4A & E: ~170 ms) and frontal sources (Figs. 5A & E: ~300 ms) (and also in temporal sources (Sup. Figs. 1A & E: ~ 300 ms) and parietal sources (Sup. Figs. 2A & E: ~ 170 ms). In general, it seems difficult to incorporate the different peaks found between and within tasks into a non-integrative view whereas an integrative view such as REFCON offers a cohesive explanation.

One potential concern about doing a between participants analysis is that any differences found may be driven by differences in intercepts between the 2 groups of participants. This does not seem to be the case in this analysis since No Experiences and Clear Experiences have comparable peaks and have comparable classification accuracies between the 2 tasks (Fig. 6B). The difference between tasks seems to be uniquely driven by differences in the NCCs for Weak Glimpses and Almost Clear Experiences, which are plausibly related to differences in cognitive strategy that give rise to differences in the NCCs based on cognitive context, i.e. NCC-context(s).

When choosing between an integrative and a non-integrative account, it is important to recognize that, in principle, no single experiment can decide between the two. Proponents of non-integrative accounts, who believe there is one unique NCC-proper, can with no logical fault insist that all confounds have not been accounted for yet, and that that is why we find differing NCCs between tasks in this experiment. We do propose, however, that an integrative view explains the differences that different cognitive contexts induce in a more elegant and cohesive way than non-integrative views. It can be argued that the non-integrative framework has been at a standstill for some time; no matter whether someone espouses late frontal activity or early occipital activity as the NCC-proper, both sides agree that both are almost always elicited by experimental contrasts of perceptual consciousness, but with alterations between paradigms. From the viewpoint of there existing an NCC-proper, these alterations are seen as noise. From the viewpoints of there existing multiple NCC-contexts, these alterations are seen as signal that can be predicted and explained where REFCON is one possible and plausible answer, namely that what correlates best with perceptual consciousness is dependent on what cognitive strategies one's degree of perceptual consciousness allows for in the current cognitive context. Of course, many more experiments need to be done to convincingly argue for the usefulness of REFCON or any other integrative theory. Based on this experiment, it seems that especially neural correlates of Weak Glimpses and Almost Clear Experiences may be expected to differ between different cognitive contexts.

## Conclusions

Task requirements affected *when* and *where* in the brain we found the neural activity that correlated the best with perceptual consciousness. They affected whether brain activity could classify graded ratings: in the perceptual task early activity showed a graded pattern, < 320 ms, whereas in the conceptual task late activity, > 320 ms, showed the most graded pattern.

Occipital and parietal sources provided more accurate classification of extreme ratings of perceptual consciousness than frontal sources did.

We argue that these results speak against a view of perceptual consciousness, where perceptual consciousness is realized by *one* unique spatio-temporal pattern of activity, a so-called NCC-proper. Instead our data are compatible with an integrated view of perceptual consciousness and cognitive context.

For vision, the realization of perceptual consciousness is thus more dependent on occipital activity than on frontal activity, but in terms of latency, the abstraction level of the task determines when perceptual consciousness can be classified: early on, < 320 ms, for the perceptual task, and later on, > 320 ms, for the conceptual task. This study points towards the necessity of investigating perceptual consciousness in differing cognitive contexts.

## References


Andersen, L. M., Pedersen, M. N., Sandberg, K., & Overgaard, M. (2015). Occipital MEG Activity in the Early Time Range (<300 ms) Predicts Graded Changes in Perceptual Consciousness. *Cerebral Cortex*, bhv108. http://doi.org/10.1093/cercor/bhv108

Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neuroscience & Biobehavioral Reviews*, *36*(2), 737–746. http://doi.org/10.1016/j.neubiorev.2011.12.003

Baars, B. J. (1988). *A Cognitive Theory of Consciousness*. NY, USA: Cambridge University Press.

Bishop, C. M. (2006). *Pattern recognition and machine learning*. Cambridge, UK: Springer, USA.

Block, N. (2005). Two neural correlates of consciousness. *Trends in Cognitive Sciences*, *9*(2), 46–52. http://doi.org/10.1016/j.tics.2004.12.006

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *The Behavioral and Brain Sciences*, *30*(5-6), 481–99; discussion 499–548. http://doi.org/10.1017/S0140525X07002786

Chalmers, D. J. (2000). What Is a Neural Correlate of Consciousness. In T. Metzinger (Ed.), *Neural Correlates of Consciousness*. USA: Massachusetts Institute of Technology.

Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, *2*, 263–275.

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage*, *9*(2), 179–94. http://doi.org/10.1006/nimg.1998.0395

Dale, A. M., Liu, A. K., Fischl, B. R., Buckner, R. L., Belliveau, J. W., Lewine, J. D., & Halgren, E. (2000). Dynamic Statistical Parametric Mapping: Combining fMRI and MEG for High-Resolution Imaging of Cortical Activity. *Neuron*, *26*(1), 55–67. http://doi.org/10.1016/S0896-6273(00)81138-1

Dehaene, S. (2014). *Consciousness and the Brain: Deciphering How the Brain Codes Our Thoughts*. NY, USA: Penguin.

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–11. http://doi.org/10.1016/j.tics.2006.03.007

Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., … Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*, *31*(3), 968–980. http://doi.org/10.1016/j.neuroimage.2006.01.021

Eddy, M., Schmid, A., & Holcomb, P. J. (2006). Masked repetition priming and event-related brain potentials: A new approach for tracking the time-course of object perception. *Psychophysiology*, *43*(6), 564–568. http://doi.org/10.1111/j.1469-8986.2006.00455.x

Faes, L., Nollo, G., Ravelli, F., Ricci, L., Vescovi, M., Turatto, M., … Antolini, R. (2007). Small-sample characterization of stochastic approximation staircases in forced-choice adaptive threshold estimation. *Perception & Psychophysics*, *69*(2), 254–262. http://doi.org/10.3758/BF03193747

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., … Hämäläinen, M. (2013). MEG and EEG data analysis with MNE-Python. *Brain Imaging Methods*, *7*, 267. http://doi.org/10.3389/fnins.2013.00267

Hämäläinen, M. S., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, *65*(2), 413–497. http://doi.org/10.1103/RevModPhys.65.413

Hamm, J. P., Johnson, B. W., & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology*, *113*(8), 1339–1350. http://doi.org/10.1016/S1388-2457(02)00161-X

Hyvärinen, A., & Oja, E. (2000). Independent component analysis: algorithms and applications. *Neural Networks*, *13*(4), 411–430.

Koivisto, M., & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience and Biobehavioral Reviews*, *34*(6), 922–34. http://doi.org/10.1016/j.neubiorev.2009.12.002

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501. http://doi.org/10.1016/j.tics.2006.09.001

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive*

*Neuroscience*, *1*(3), 204–220. http://doi.org/10.1080/17588921003731586

McPherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, *36*(1), 53–65. http://doi.org/10.1017/S0048577299971196

Melloni, L., Schwiedrzik, C. M., Müller, N., Rodriguez, E., & Singer, W. (2011). Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(4), 1386–96. http://doi.org/10.1523/JNEUROSCI.4570-10.2011

Overgaard, M., & Mogensen, J. (2014). Visual perception from the perspective of a representational, non-reductionistic, level-dependent account of perception and conscious awareness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130209. http://doi.org/10.1098/rstb.2013.0209

Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, *2*, 10. http://doi.org/10.3389/neuro.11.010.2008

Posner, M. I., & Mitchell, R. F. (1967). Chronometric Analysis of Classification. *Psychological Review*, *74*(5), 392–409. http://doi.org/http://dx.doi.org/10.1037/h0024913

Ramsøy, T. Z., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, *3*(1), 1–23. http://doi.org/10.1023/B:PHEN.0000041900.30172.e8

Sandberg, K., Andersen, L. M., & Overgaard, M. (2014). Using multivariate decoding to go beyond contrastive analyses in consciousness research. *Frontiers in Psychology*, *5*, 1250. http://doi.org/10.3389/fpsyg.2014.01250

Sandberg, K., Bibby, B. M., Timmermans, B., Cleeremans, A., & Overgaard, M. (2011). Measuring consciousness: Task accuracy and awareness as sigmoid functions of stimulus duration. *Consciousness and Cognition*, *20*(4), 1659–1675. http://doi.org/10.1016/j.concog.2011.09.002

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. S. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain*, *123*(12), 2400–2406. http://doi.org/10.1093/brain/123.12.2400

Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, *8*(10), 1391–400. http://doi.org/10.1038/nn1549

Simon, O., Mangin, J.-F., Cohen, L., Le Bihan, D., & Dehaene, S. (2002). Topographical Layout of Hand, Eye, Calculation, and Language-Related Areas in the Human Parietal Lobe. *Neuron*, *33*(3), 475–487. http://doi.org/10.1016/S0896-6273(02)00575-5

Windey, B., & Cleeremans, A. (2015). Consciousness as a graded and an all-or-none phenomenon: A conceptual analysis. *Consciousness and Cognition*, *35*, 185–191. http://doi.org/10.1016/j.concog.2015.03.002

Windey, B., Gevers, W., & Cleeremans, A. (2013). Subjective visibility depends on level of processing. *Cognition*, *129*(2), 404–409. http://doi.org/10.1016/j.cognition.2013.07.012

Windey, B., Vermeiren, A., Atas, A., & Cleeremans, A. (2014). The graded and dichotomous nature of visual awareness. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130282. http://doi.org/10.1098/rstb.2013.0282

# Appendices:

## Appendix A:

*The full model*

We fitted a mixed model based on 5 fixed effects: Time Range (2 levels: VAN; P3a), Task (2 levels: perceptual; conceptual), Lobe (4 levels: occipital; frontal; temporal; parietal), Actual PAS (4 levels: No Experience; Weak Glimpse; Almost Clear Experience; Clear Experience) and Classified PAS (4 levels: No Experience; Weak Glimpse; Almost Clear Experience; Clear Experience). a random intercept for each Participant (10) and Classified PAS as a random effect for each Participant, whose addition to the model resulted in a significant change in log-likelihood: $\chi^2(9) = 52.6$, $p < 0.001$. The 4 remaining effects did not: Time Range: $\chi^2(2) = 0.00$, $p = 1.0$; Lobe: $\chi^2(9) = 0.00$, $p = 1.0$; Actual PAS: $\chi^2(9) = 0.00$, $p = 1.0$; Task: $\chi^2(2) = 0.00$, $p = 1.0$.

*Optimization procedure*

For finding the best compromise between an explanatory and a parsimonious model, we first defined the *full model*, which included all possible interactions and main effects. We removed one term, main effect or interaction, at a time and performed a model comparison by comparing the log-likelihoods of the 2 models. 2 times the ratio between these 2 log-likelihoods approximates a $\chi^2$-distribution whose degrees of freedom is the difference in free parameters between the 2 models. If the observed ratio under the $\chi^2$-distribution was associated with a *p*-value less than 0.05, we put that term back in the model before removing the next term. Thus, only parameters whose removal would result in a significant drop in explanatory power, weighted relative to the number of parameters, were kept in the model. If a term was included in a higher-order interaction, it was not tested but left in the model.

*Steps of the optimization procedure*

The 5-way interaction could be removed without a significant change in log-likelihood: $\chi^2(27) = 20.0$, $p = 0.83$.

Among the 4-way interactions, the 4-way interaction: Lobe × Time Range × Task × Actual PAS, could be removed without a significant change in log-likelihood: $\chi^2(9) = 0.00$, $p = 1.0$; so could the 4-way interaction: Lobe × Time Range × Task × Classified PAS: $\chi^2(9) = 4.59$, $p = 0.87$; so could the 4-way interaction: Lobe × Task × Actual PAS × Classified PAS: $\chi^2(27) = 35.8$ , $p = 0.12$; so could the 4-way interaction: Lobe × Time Range × Actual PAS × Classified PAS: $\chi^2(27) = 36.5$, $p = 0.10$. The remaining 4-way interaction: Time Range × Task × Actual PAS × Classified PAS, however, could *not* be removed without a significant change in log-likelihood: $\chi^2(9) = 19.8$, $p = 0.019$.

Among the 3-way interactions, the 3-way interaction: Lobe × Task × Actual PAS: $\chi^2(9) = 0.00$, $p = 1.0$, could be removed without a significant change in log-likelihood; so could the 3-way interaction: Lobe × Time Range × Actual PAS: $\chi^2(9) = 0.00$, $p = 1.0$; so could the 3-way interaction: Lobe × Time Range × Task $\chi^2(3) = 0.00$, $p = 1.0$; so could the 3-way interaction: Lobe × Task × Classified PAS: $\chi^2(9) = 4.30$, $p = 0.89$; so could the 3-way interaction: Lobe × Time Range × Classified PAS: $\chi^2(9) = 5.40$, $p = 0.80$. The 3-way interaction: Lobe × Actual PAS × Classified PAS: $\chi^2(27) = 75.0$, $p < 0.001$ could *not* be removed without a significant change in log-likelihood. The remaining 3-way interactions were all part of the 4-way interaction kept in the model, thus they too were kept in the model.

All 2-way interactions were included in one of the higher-order interactions, and they were thus kept in the model.

All main effects were included in one of the higher-order interactions, and they were thus kept in the model.

*Optimal model*

The optimal model thus had the probability of a given classification as dependent on the 4-way interaction: Time Range × Task × Actual PAS × Classified PAS; and the 3-way interaction: Lobe × Actual PAS × Classified PAS and the random effect of Classified PAS across Participants.

## Appendix B:

**Supplementary Table 2:** All statistical tests, within PAS, from the Lobe comparisons

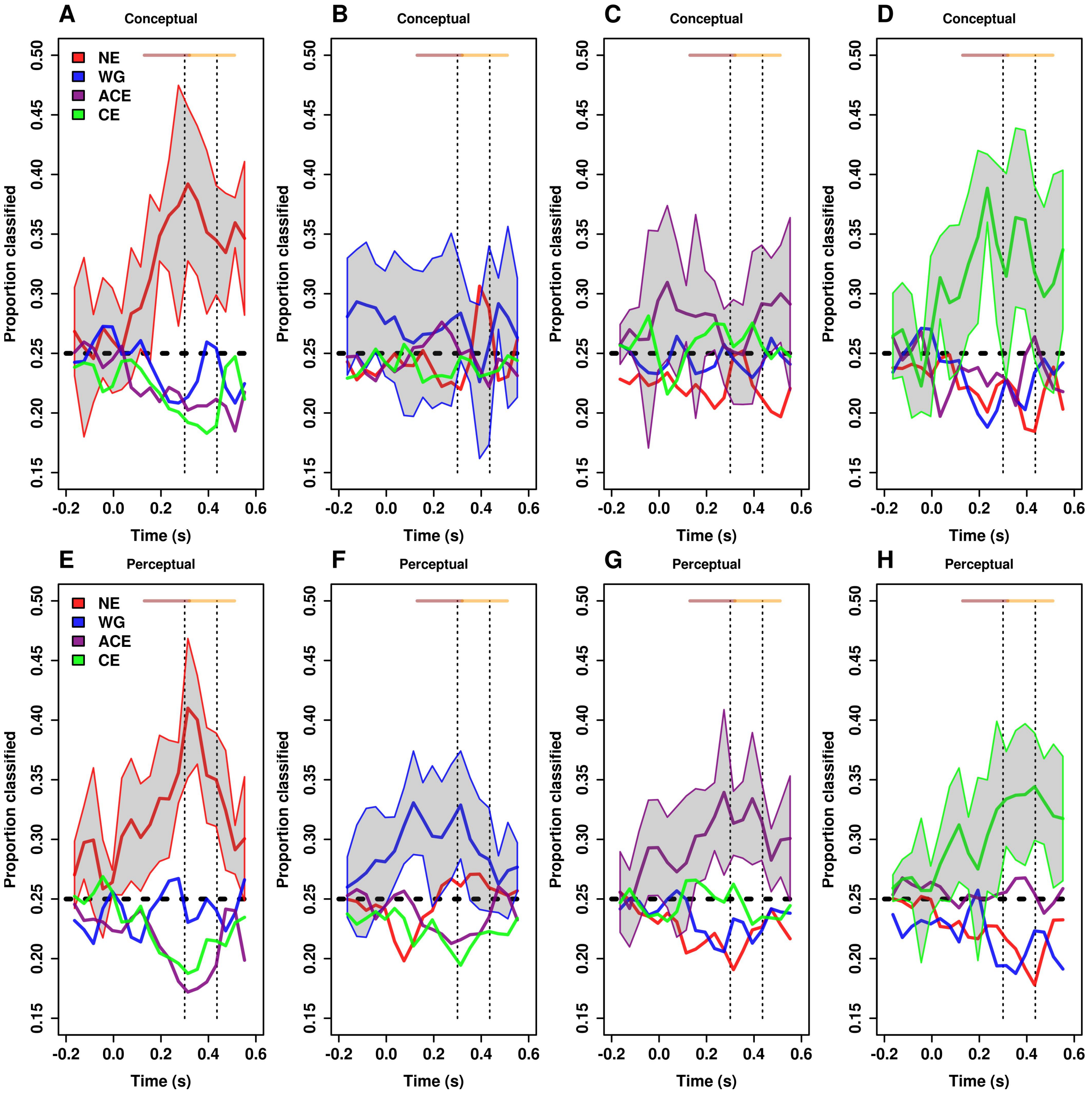
| PAS | Comparison | Estimated Effect | Standard Error | Z-value | P-value |
|---|---|---|---|---|---|
| NE | Occipital versus Frontal | -0.013 | 0.029 | -0.45 | 0.65 |
| NE | Occipital versus Parietal | 0.0042 | 0.026 | 0.16 | 0.87 |
| NE | Occipital versus Temporal | -0.055 | 0.029 | -1.9 | 0.063 |
| NE | Frontal versus Parietal | 0.017 | 0.029 | 0.59 | 0.56 |
| NE | Frontal versus Temporal | -0.042 | 0.032 | -1.3 | 0.2 |
| NE | Parietal versus Temporal | -0.059 | 0.029 | -2 | 0.045 |
| WG | Occipital versus Frontal | 0.068 | 0.029 | 2.3 | 0.021 |
| WG | Occipital versus Parietal | 0.064 | 0.026 | 2.4 | 0.015 |
| WG | Occipital versus Temporal | 0.074 | 0.029 | 2.5 | 0.012 |
| WG | Frontal versus Parietal | -0.0042 | 0.029 | -0.14 | 0.89 |
| WG | Frontal versus Temporal | 0.0063 | 0.032 | 0.19 | 0.85 |
| WG | Parietal versus Temporal | 0.01 | 0.029 | 0.35 | 0.72 |
| ACE | Occipital versus Frontal | 0.097 | 0.029 | 3.3 | 0.0011 |
| ACE | Occipital versus Parietal | -0.0028 | 0.026 | -0.11 | 0.92 |
| ACE | Occipital versus Temporal | 0.028 | 0.029 | 0.94 | 0.35 |
| ACE | Frontal versus Parietal | -0.099 | 0.029 | -3.4 | 0.00076 |
| ACE | Frontal versus Temporal | -0.069 | 0.032 | -2.1 | 0.033 |
| ACE | Parietal versus Temporal | 0.031 | 0.029 | 1 | 0.3 |
| CE | Occipital versus Frontal | 0.029 | 0.029 | 0.99 | 0.32 |
| CE | Occipital versus Parietal | -0.015 | 0.026 | -0.58 | 0.56 |
| CE | Occipital versus Temporal | 0.046 | 0.029 | 1.6 | 0.12 |
| CE | Frontal versus Parietal | -0.044 | 0.029 | -1.5 | 0.13 |
| CE | Frontal versus Temporal | 0.017 | 0.032 | 0.52 | 0.61 |
| CE | Parietal versus Temporal | 0.061 | 0.029 | 2.1 | 0.038 |

# Appendix C:

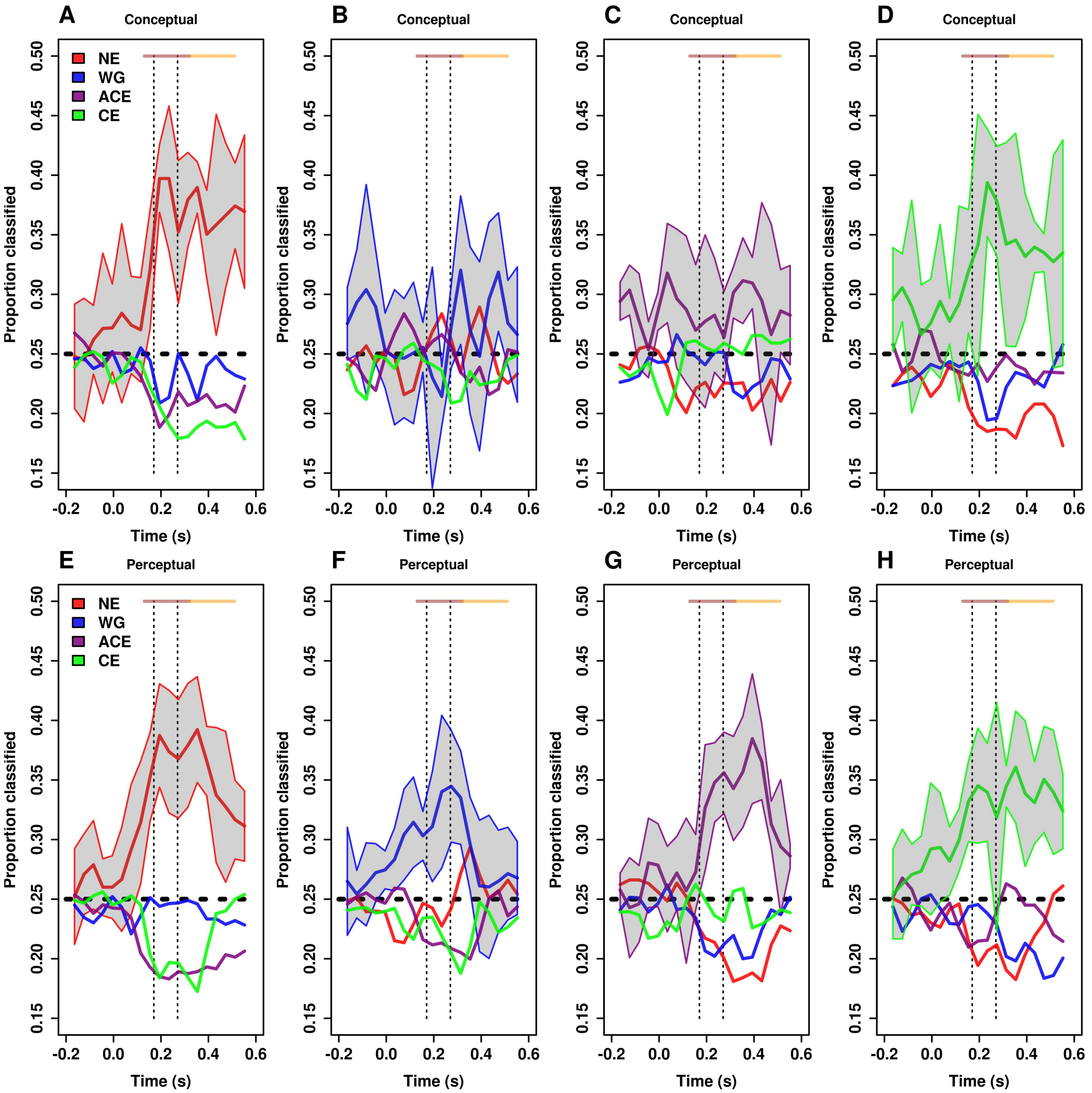
**Supplementary Table 3:** All statistical tests, within PAS, from the Time Range × Task interaction

| PAS | Comparison | Estimated Effect | Standard Error | Z-value | P-value |
|---|---|---|---|---|---|
| NE | VAN PC versus VAN CC | 0.024 | 0.046 | 0.52 | 0.6 |
| NE | VAN PC versus P3a PC | 0.022 | 0.037 | 0.59 | 0.55 |
| NE | VAN PC versus P3a CC | -0.039 | 0.046 | -0.85 | 0.39 |
| NE | VAN CC versus P3a PC | -0.0014 | 0.046 | -0.03 | 0.98 |
| NE | VAN CC versus P3a CC | -0.063 | 0.046 | -1.4 | 0.17 |
| NE | P3a PC versus P3a CC | -0.061 | 0.046 | -1.3 | 0.18 |
| WG | VAN PC versus VAN CC | 0.075 | 0.043 | 1.7 | 0.084 |
| WG | VAN PC versus P3a PC | 0.078 | 0.037 | 2.1 | 0.038 |
| WG | VAN PC versus P3a CC | 0.054 | 0.043 | 1.2 | 0.21 |
| WG | VAN CC versus P3a PC | 0.0028 | 0.043 | 0.064 | 0.95 |
| WG | VAN CC versus P3a CC | -0.021 | 0.046 | -0.45 | 0.65 |
| WG | P3a PC versus P3a CC | -0.024 | 0.043 | -0.54 | 0.59 |
| ACE | VAN PC versus VAN CC | 0.086 | 0.044 | 2 | 0.049 |
| ACE | VAN PC versus P3a PC | -0.028 | 0.037 | -0.74 | 0.46 |
| ACE | VAN PC versus P3a CC | -0.018 | 0.044 | -0.41 | 0.68 |
| ACE | VAN CC versus P3a PC | -0.11 | 0.044 | -2.6 | 0.0093 |
| ACE | VAN CC versus P3a CC | -0.1 | 0.046 | -2.3 | 0.023 |
| ACE | P3a PC versus P3a CC | 0.0097 | 0.044 | 0.22 | 0.82 |
| CE | VAN PC versus VAN CC | 0.035 | 0.045 | 0.78 | 0.44 |
| CE | VAN PC versus P3a PC | -0.028 | 0.037 | -0.74 | 0.46 |
| CE | VAN PC versus P3a CC | 0.047 | 0.045 | 1.1 | 0.29 |
| CE | VAN CC versus P3a PC | -0.062 | 0.045 | -1.4 | 0.16 |
| CE | VAN CC versus P3a CC | 0.013 | 0.046 | 0.27 | 0.78 |
| CE | P3a PC versus P3a CC | 0.075 | 0.045 | 1.7 | 0.094 |

## Supplementary Figures




**Supplementary Figure 1:** Sample-by-sample analyses for temporal sources: the upper row of panels (A-D) shows conceptual sources classification for No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) respectively. The lower row of panels (E-H) shows the same for the perceptual task. Mean classification accuracies across participants, smoothed by taking every 10th sample and taking the mean across that sample and the 10 samples on each side, are shown for all classifications. Shaded regions are standard errors of the mean smoothed the same way. The 2 bars at the top indicate the width of the 2 time ranges tested in other analyses. Vertical lines indicate 300 ms and 436 ms respectively.




**Supplementary Figure 2:** Sample-by-sample analyses for parietal sources: the upper row of panels (A-D) shows conceptual sources classification for No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) respectively. The lower row of panels (E-H) shows the same for the perceptual task. Mean classification accuracies across participants, smoothed by taking every 10th sample and taking the mean across that sample and the 10 samples on each side, are shown for all classifications. Shaded regions are standard errors of the mean smoothed the same way. The 2 bars at the top indicate the width of the 2 time ranges tested in other analyses. Vertical lines indicate 170 ms and 270 ms respectively.

# Appendix IV

# Top-down expectations affect the gradedness of perception and the evidence weighting of informative levels of perceptions

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## Abstract

Differences in top-down expectations are known to modulate response times. In this task, we investigated how differences in expectations might affect a subjective dimension, namely the gradedness of reports of perceptual consciousness. We found that participants reported more graded perceptual consciousness when their expectations towards the prospective stimulus were vague, involving any of 8 alternatives, compared to when they were distinct and consisted of only 2 possible alternatives. This difference in gradedness between different expectations was not accompanied by any solid differences in accuracy. We also found evidence of response times being modulated by differences in expectations, but only when participants reported that they had at least some experience of the target stimuli, that is when perceptual consciousness was informative. When participants reported no experience of the stimulus, which was accompanied by chance performance, expectations did not modulate response times. Across these manipulations of top-down expectation and sensory saliency, participants demonstrated excellent metacognitive knowledge and accurately reported when they had no conscious experience of the stimulus and no knowledge of the correct response. We argue that this is evidence for the exhaustiveness of the scale we used for rating perceptual consciousness, the so-called Perceptual Awareness Scale, namely that participants can use it to separate unconscious states, with no information relevant for the task, from conscious states, which were characterized by above-chance performance, that correlate with how clearly stimuli were perceived. We thus found evidence for top-down expectations modulating both perceptual consciousness and responses, but only when the responses were based on informative conscious states.

*Keywords: perception, visibility, expectations, informativeness, metacognition*

## Introduction

Human beings subjectively experience a rich visual world full of different objects. Looking at an object, say, a cat on a mat, one will under normal circumstances be visually conscious of that cat on that mat. A simple way to eliminate conscious visual content of the cat on the mat is to close one's eyes. From this simple example, it is natural to assume that perceptual consciousness is dichotomously divisible; either one is perceptually conscious of a potential visual object or one is not. However, there might be states that fall between conscious and unconscious. An everyday example of this is seeing something in the periphery of one's visual field. One may have a vague perception of something, and the object is not seen as clearly or vividly as something in central vision; thus, it seems that the concept of being conscious can be graded in terms of the vividness of one's experience.

Expectations regarding what one is likely to see can also shape one's conscious experience (Summerfield & Egner, 2009). Being on a football field may cause one to perceive a peripherally seen round object as a football, whereas being on a baseball field, may cause one to perceive it as a baseball, even if the sensory stimulation is highly similar. Other sensory modalities may of course also be associated with differences in consciousness and expectations, but for this study, we will use the term “perceptual consciousness” to refer to visual experiences.

To investigate how finely perceptual consciousness can be divided, one can use subjective scales to let participants rate the clarity of their experiences. For example, Sergent & Dehaene (2004) argued, based on an attentional blink task that perceptual consciousness is dichotomous such that a stimulus is either “seen” or “not seen”. The attentional blink (Raymond, Shapiro, & Arnell, 1992) is a phenomenon that occurs when 2 target stimuli, T1 and T2, are presented briefly among a series of rapidly presented distractors. As long as one is only required to respond to one of the targets, one almost never misses that target. However, when responses are required to both targets, T2 is often not consciously perceived, presumably due to attention being directed towards T1. Any claim as to how finely perceptual consciousness can be divided faces a potential concern, namely, the question of how many points should be used for the rating scale. This is not a trivial question since the number of points and the descriptions associated with them may influence how participants rate their perceptions. Sergent & Dehaene (2004) used a 21-point scale with 0 % and 100 % visibility at each end and steps of 5 % in between. Nieuwenhuis & de Kleijn (2011) performed an experiment similar to that of Sergent & Dehaene (2004), but had participants use a 7-point scale to rate perceptual consciousness. Reducing the number of scale points was based on the arguments of Overgaard, Rote, Mouridsen & Ramsøy (2006) that participants are unlikely to be able to meaningfully categorize their experiences into 21 discrete ratings. Using a reduced number of scale points, they found a more graded distribution of perceptual consciousness ratings than Sergent & Dehaene did. They also tested how the task influenced ratings of perceptual consciousness. When the task on T1 was made harder, participants had to indicate which of 8 different digits was shown, the ratings on the 7-point scale were distributed in an even more graded fashion, where all scale points were used. The gradedness of subjective ratings of perceptual consciousness thus seems to depend on both the rating scale used and the difficulty of the task, perhaps reflecting the number of potential targets. In the present study, we investigated how differences in top-down expectations might influence ratings of perceptual consciousness and objective performance, and we expected that less distinct expectations would result in more graded perception. What this means more precisely will be explicated below.

We decided to use the Perceptual Awareness Scale (PAS: Ramsøy & Overgaard, 2004), which has 4 categorically different ratings: No Experience (NE), Weak Glimpse (WG), Almost Clear Experience (ACE) and Clear Experience (CE) (Table 1) .

The PAS scale (Sandberg, Timmermans, Overgaard, & Cleeremans, 2010) has been shown to provide better fits to participant performance in terms of being more *exhaustive* and *sensitive* than both confidence ratings and post-decision wagering (Koch & Preuschoff, 2007) and also to provide better fits than dichotomous scales (Overgaard et al., 2006). For a scale to be exhaustive, the scale must provide evidence that when participants claim to have no experience and no knowledge about what was shown (Table 1: No Experience), their performance should not be different from chance-level performance. For a scale to be sensitive, the scale must provide points such that when participants claim to have (some) experience and (some) knowledge (Table 1: Weak Glimpse, Almost Clear Experience and Clear Experience), their performance should correlate with the clarity of the experience and amount of knowledge. This means that whatever difference participants claim to feel should be reflected by a real difference in objective performance.

**Table 1:** The Perceptual Awareness Scale (PAS)

| Label | Description (from Ramsøy and Overgaard 2004) |
|---|---|
| (1) No Experience (NE) | No impression of the stimulus. All answers are seen as mere guesses |
| (2) Weak Glimpse (WG) | A feeling that something has been shown. Not characterized by any content, and this cannot be specified any further |
| (3) Almost Clear Experience (ACE) | Ambiguous experience of the stimulus. Some stimulus aspects are experienced more vividly than others. A feeling of almost being certain about one's answer |
| (4) Clear Experience (CE) | Non-ambiguous experience of the stimulus. No doubt in one's answer |

Note: Scale steps and their descriptions

A goal of this study was to assess whether PAS was exhaustive and sensitive (Dienes, 2007) even across internal differences in top-down expectations and external differences in sensory saliency. Based on the results of Nieuwenhuis & de Kleijn (2011) and on the notion that top-down expectations can shape our perception (Summerfield & Egner, 2009), we expected that the more vague one's expectations towards prospective stimuli were, the more graded the distribution of PAS ratings would be. We operationalized gradedness as the prevalence of non-extreme ratings, i.e. Weak Glimpses and Almost Clear Experiences (Table 1).

Finally, because expectations are known to speed up response times (Doherty, Rao, Mesulam, & Nobre, 2005; Posner, 1980), we also included an analysis of response times as a further test of our predictions.

## Methods

### Participants

29 participants, 18 women and 11 men, with normal or corrected-to-normal vision, provided informed written consent, and the study took place under the approval of the Institutional Review Board of Vanderbilt University. 6 participants were excluded from the analyses: 2 due to instability issues of the experimental programme, 2 due to failing to use the full range of possible subjective reports and finally, 2 due to shifts in their criterion in the midst of the experiment. In the latter case, both participants only started using the Clear Experience rating about halfway into the experiment.

### Stimuli and procedure

Participants were seated 45 cm from a CRT-monitor running with a resolution of 1024 × 768 pixels and a refresh rate of 85 Hz. Target stimuli consisted of Arabic numerals ranging from 2-9, presented using the “digital-k” font (Fig. 1)  (http://gnome-look.org/content/show.php/DigiTalk-mono+%5Bdigital+clock+font%5D?content=132902, [date last accessed: 31 July 2015]). Participants were instructed to report the parity of the target stimulus, i.e. whether the target digit was even or odd. Task difficulty was manipulated by varying the interstimulus interval between the target digit and the subsequent visual mask.

All stimuli were presented in greyscale. The background was grey (RGB 128, 31.0 cd/m$^2$). Each trial (Fig. 1) began with a white (RGB 255, 115 cd/m$^2$) cue, indicating which digits could be shown during the trial. This cue was always valid. The cue always consisted of an equal amount of even and odd digits. The number of alternatives (NoA) cued consisted of either 8, 4 or 2 digits. The cues were presented in a blocked fashion such that the same cue condition would repeat 12 times before a new cue condition was presented. This was done to keep top-down expectations stable over a series of trials and to strengthen them. Whenever a new cue appeared, it was accompanied by a high-pitch tone to inform participants that a new block of cues was coming up. Trials were self-paced, and each trial was initiated when participants pressed the space-bar.

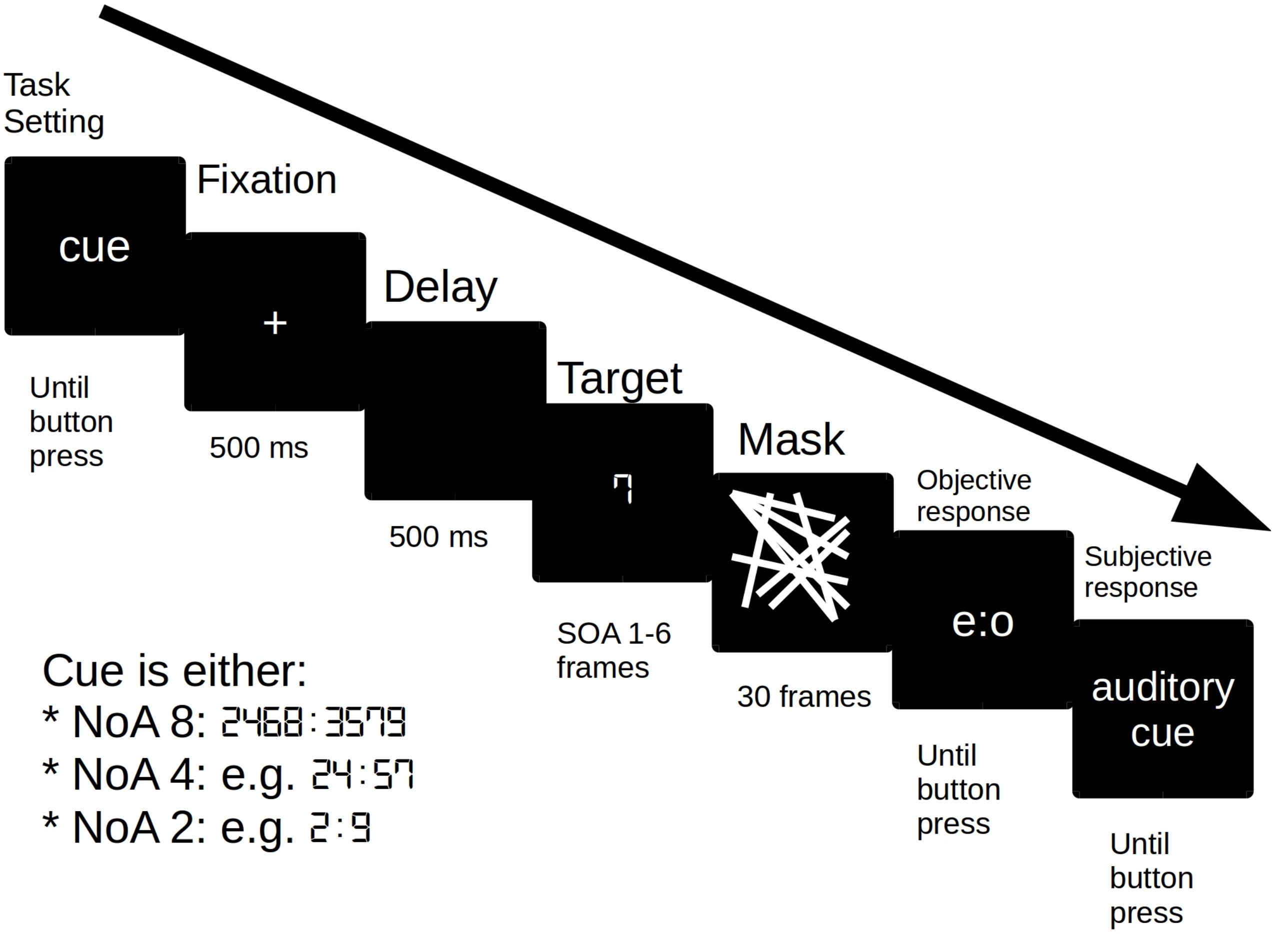


**Figure 1:** Experimental paradigm. A cue was presented, creating a top-down expectation as to which digits could be presented. The Number of Alternatives was one of 3 levels (2, 4 or 8 alternatives). A cue was repeated for 12 trials and was then changed. A high-pitched sound alerted participants whenever the cue changed. A fixation cross (500 ms) was followed by a delay, to avoid forward masking. A target digit (in a digital font) was then presented between 1 and 6 frames (frame = 11.8 ms), which was followed by a backward mask made of random lines presented for 30 frames. An objective response was prompted as to whether the presented digit was even, *e*, or odd, *o.* Finally, following an auditory cue, signalling that the objective response had been made, participants reported perceptual consciousness of the target by pressing one of the buttons 1-4.

A black (RGB 0, 1.77 cd /$m^2$) fixation cross appeared for 500 ms, followed by an empty screen for 500 ms, then a grey (RGB 140, 36.5 cd/$m^2$) low-contrast target digit, brighter than the background, was then presented for a duration of 1-6 frames (11.8-70.6 ms). A slight jitter was applied to the position of the target digit, randomly drawn from a uniform distribution that fell within ±0.5 ° of the fixation point. The target digit was followed by a backward pattern mask, which was randomly generated on each trial, consisting of 250 white (RGB 255, 115 cd/$m^2$) lines whose endpoints were randomly chosen from a Gaussian distribution centred at fixation with a standard deviation of 6 ° of visual angle in both the *x*- and *y*-directions. The mask was presented for 353 ms (30 frames). This was followed by a visual prompt, indicating that the participant should press either *e*, for even, or *o*, for odd, as quickly and as accurately as possible. An auditory signal indicated that the response had been made and signalled that participants should rate their subjective experience using the Perceptual Awareness Scale (Table 1) (Ramsøy & Overgaard, 2004). This was done using the buttons 1-4 (upper-left corner). Each participant performed a total of 864 experimental trials. PsychoPy 1.81.03 (Peirce, 2009) was used to run the experiment. Before the actual experiment was run, 18 practice trials were run with representative target durations, and participants were instructed to use the same criterion for rating perceptual consciousness throughout the experiment.

## Psychometric curves

We modelled performance and average PAS Rating by using a sigmoid function (Sandberg et al., 2010; Windey, Gevers, & Cleeremans, 2013).

Equation 1: $$f(x) = a + \frac{b-a}{1+e^{\frac{c-x}{d}}}$$

The 4 free parameters of this function represent the following: *a* is the lower asymptote, *b* is the upper asymptote, *c* is the inflexion point of the sigmoid function, or threshold, and *d* is a measure of the steepness of the curve at the point of inflection. When *d* goes towards infinity, the function goes towards a linear function, and when *d* goes towards 0, the function goes towards a step function. A unique function was fitted for each participant and for each of the 3 levels of Number of Alternatives (NoA: 2, 4 or 8). Mixed model analyses (McCulloch & Neuhaus, 2005) were applied to investigate how top-down expectations (NoA) affected perceptual consciousness and objective performance. We analysed results around the perceptual thresholds estimated (Equation 1) because this is where the greatest variation in perceptual consciousness is expected.

### Factors of interest for the near-threshold analyses

The factor Number of Alternatives (NoA) reflected the manipulation of top-down expectations with its 3 levels, 2, 4 and 8. We estimated the perceptual threshold based on Equation 1 below and defined 3 target durations of interest, below threshold, at threshold and above threshold. The final factor in our analyses was perceptual consciousness with 4 levels: No Experience, Weak Glimpse, Almost Clear Experience and Clear Experience.

## Results

### Accuracy

Fits of the sigmoid function to the mean level of performance averaged across all participants suggested that there was not much difference between the functions underlying accuracy (Fig. 2).

Even more so, Bayesian *t*-tests (Rouder, Speckman, Sun, Morey, & Iverson, 2009), revealed that the data supported the null hypothesis that the *c*-parameters were of similar magnitude: Number of Alternatives 2 versus Number of Alternatives 4, $BF_{NULL} = 2.10$ (±0.02 %); Number of Alternatives 2 versus Number of Alternatives 8, $BF_{NULL} = 1.37$ (±0.02 %); Number of Alternatives 4 versus Number of Alternatives 8, $BF_{NULL} = 3.29$ (±0.02 %). The prior for these tests were all Cauchy-distributed with the scale set at $\sqrt{2}/2$ (Morey & Rouder, 2011).

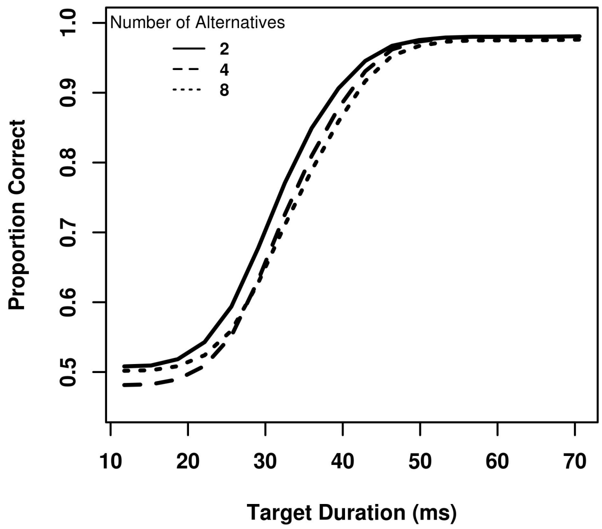


**Figure 2:** Psychometric curves for proportion correct for each of the 3 conditions for top-down expectations. There are no significant differences between lower asymptotes, upper asymptotes, inflexion points or steepness of the curves.

### Average PAS Rating

Judging from the mean sigmoid function calculated across all participants' individual parameters, there was not much difference between the function underlying average PAS Rating across the different number of alternatives used (Fig. 3).

Bayesian *t*-tests revealed that the data again favoured that the *c*-parameters were of similar magnitude: Number of Alternatives 2 versus Number of Alternatives 4, $BF_{NULL}$ = 2.33 (±0.02 %); Number of Alternatives 2 versus Number of Alternatives 8, $BF_{NULL}$ = 2.05 (±0.02 %); Number of Alternatives 4 versus Number of Alternatives 8, $BF_{NULL}$ = 3.34 (±0.02 %). The priors for these tests were all Cauchy-distributed with the scale set at √2/2.

### Differences around threshold

We expected differences to be greatest around the subjective perceptual threshold, estimated by the *c*-parameters (Fig. 3), which we collapsed across the different Numbers of Alternatives because there was evidence they were of similar magnitude ($\mu_{PAS}$ = 2.92 frames, $SD_{PAS}$ = 0.323). We thus analysed 3 target durations more thoroughly, below threshold (2 frames; ~23.5 ms), at threshold (3 frames; ~35.3 ms) and above threshold (4 frames; ~47.1 ms).

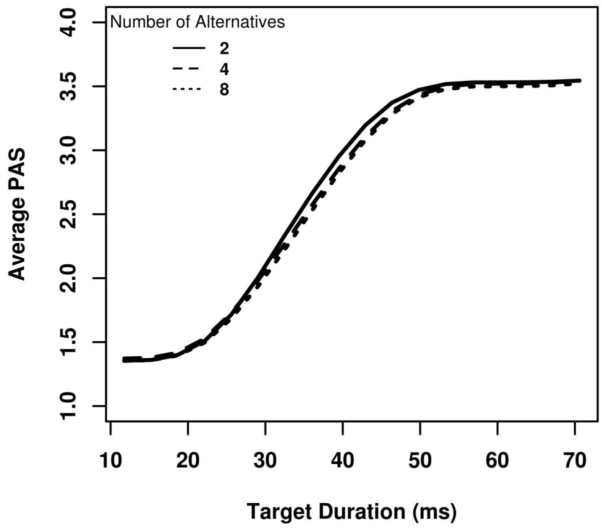


**Figure 3:** Psychometric curves for average rating on the Perceptual Awareness Scale for each of the 3 conditions for top-down expectations. There are no significant differences between lower asymptotes, upper asymptotes, inflexion points or steepness of the curves.

For all of the mixed models below, we aimed at finding the best compromise between an explanatory and a parsimonious model. First, we defined the *full model*, which included all possible interactions and main effects. We removed one term, main effect or interaction, at a time and performed a model comparison by comparing the log-likelihoods of the 2 models. 2 times the ratio between these 2 log-likelihoods approximates a $\chi^2$-distribution whose degrees of freedom is the difference in free parameters between the 2 models. If the observed ratio under the $\chi^2$-distribution was associated with a *p*-value less than 0.05, that term was kept in the model. Subsequently the next term was tested. Thus, only parameters whose removal would result in a significant drop in explanatory power, weighted relative to the number of parameters, were kept in the model. If a term was included in a higher-order interaction, it was not tested but left in the model.

## Distributions of ratings

We modelled the frequency of PAS Ratings using a generalized linear mixed model based on the assumption that the data were Poisson-distributed, because they were count data (Fig. 4). We tested the fixed effects of PAS (4 levels: No Experience, Weak Glimpse, Almost Clear Experience or Clear Experience), Number of Alternatives (3 levels: 2, 4 or 8), Target Duration (3 levels: 2, 3 or 4 frames) and all their interactions. A unique intercept was modelled for each participant. By doing log-likelihood comparisons between models, we found that the optimal model included the 2-way interaction PAS Rating × Target Duration, $\chi^2(6) = 4564$, $p < 0.001$, and the 2-way interaction PAS Rating × Number of Alternatives, $\chi^2(6) = 15.93$, $p = 0.014$. All main effects were thus kept in the model. The 3-way interaction was removed from the model, $\chi^2(12) = 13.92$, $p = 0.31$, and so was the 2-way interaction Target Duration × Number of Alternatives, $\chi^2(4) = 4.446$, $p = 0.35$.

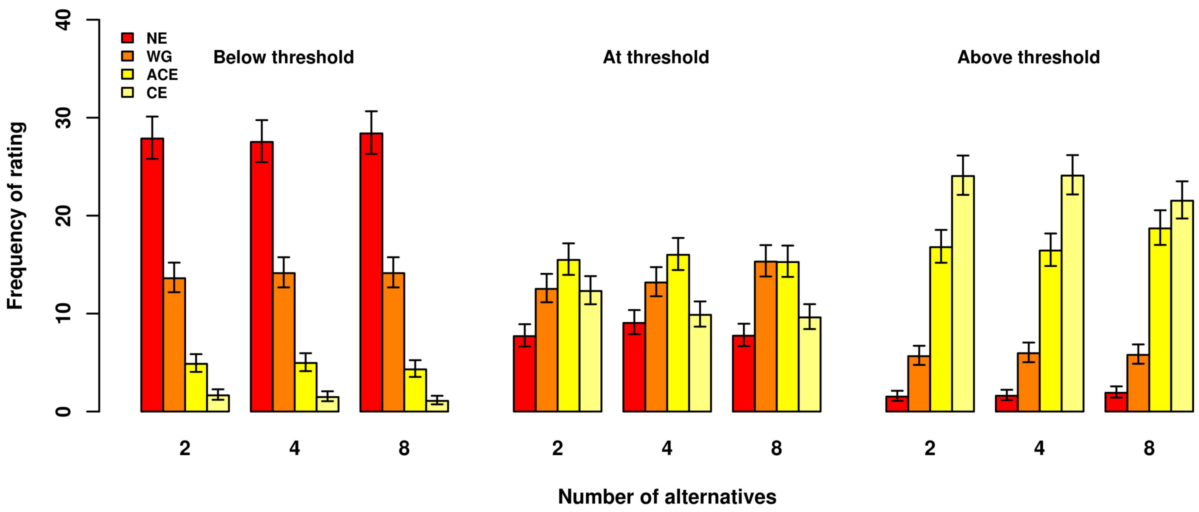


**Figure 4:** Mean number of times each rating on the Perceptual Awareness Scale (Table 1) was used below threshold, at threshold, 3 frames, and above threshold for each of the 3 conditions of top-down expectations (Number of alternatives). Error bars are 95 % confidence intervals. Model comparisons and statistical testing revealed that 8 alternatives was associated with fewer Clear Experiences (CE) and more Weak Glimpses (WG) than 2 alternatives. Below threshold participants rated most trials as No Experiences (NE) or Weak Glimpses, while above threshold this shifted to them rating most trials as Almost Clear Experiences (ACE) or Clear Experiences. At threshold, participants used all gradations of the scale.

The PAS Rating × Target Duration interaction indicated that the frequency of PAS Ratings differed between Target Durations, with low ratings, No Experience and Weak Glimpse, being most frequent below threshold and high ratings, Almost Clear Experience and Clear Experience, being most frequent above threshold. At the subjective threshold, middle ratings, Weak Glimpse and Almost Clear Experience, were the most frequent (Fig. 4). This corroborated that the threshold is around a target duration of 3 frames.

More interestingly, Number of Alternatives also interacted with PAS Rating, indicating that participants rated perceptual consciousness differently dependent on the number of alternative stimuli that could have been shown. Subsequent tests revealed that this interaction effect was primarily driven by participants reporting fewer Clear Experiences when Number of Alternatives was 8 compared to when Number of Alternatives was 2, $z = 3.31$, $p < 0.001$, and also by participants reporting more Weak Glimpses when the Number of Alternatives was 8 compared to when Number of Alternatives was 2, $z = 2.01$, $p = 0.044$. These results provide evidence for our expectation that vague, (Number of Alternatives: 8), top-down expectations should result in more graded distributions of PAS ratings compared to more distinct expectations, (Number of Alternatives: 2).

### Accuracy

We modelled accuracy based on the same fixed and random effects as above, but assumed that the data were binomially distributed (Fig. 5). We found that the optimal model included the 2-way interaction PAS Rating × Target Duration, $\chi^2(6) = 117$, $p < 0.001$, and thus the main effects of PAS Rating and Target Duration. The 3-way interaction was removed from the model, $\chi^2(12) = 10.6$, $p = 0.56$, so was the 2-way interaction PAS Rating × Number of Alternatives, $\chi^2(6) = 4.69$, $p = 0.58$, the 2-way interaction Number of Alternatives × Target Duration, $\chi^2(4) = 2.99$, $p = 0.56$, and the main effect of Number of Alternatives, $\chi^2(2) = 5.44$, $p = 0.066$.

Thus, the shifts in the gradedness of distributions of PAS ratings could not be explained by significant differences in accuracy between different top-down expectations.

The PAS Rating × Target Duration interaction was driven by significant differences in accuracy for Weak Glimpse, Almost Clear Experience and Clear Experience between Target Durations. For these 3 ratings, a Target Duration of 4 frames resulted in a significantly higher accuracy than a Target Duration of 3 frames, which in turn resulted in a significantly higher accuracy than a Target Duration of 2 frames did, all $z$'s > 4.31, all $p$'s < 0.001. For No Experience, there were no significant differences, all $z$'s < 1.25, all $p$'s > 0.21.

The finding that accuracy for No Experience was not different from chance in any of the conditions (Fig. 5) supports the proposal that the Perceptual Awareness Scale is exhaustive (Dienes, 2007).

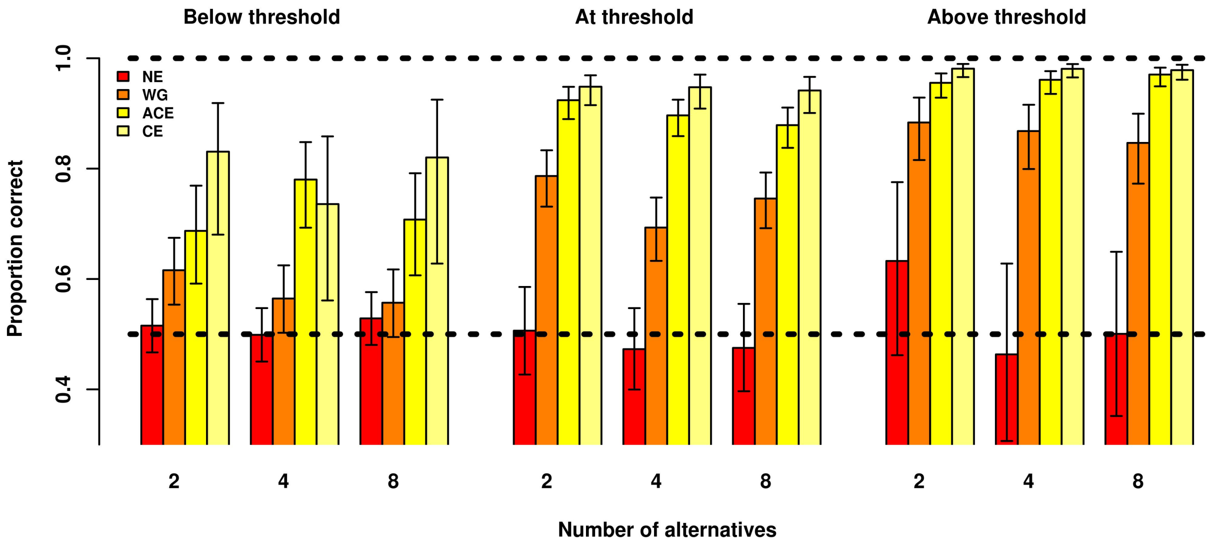


**Figure 5:** Mean proportion correct for each rating on the Perceptual Awareness Scale (Table 1) shown below threshold, at threshold, 3 frames, and above threshold for each of the 3 conditions of top-down expectations (Number of alternatives). Error bars are 95 % confidence intervals. Model comparisons and statistical testing revealed that proportions correct for Weak Glimpses (WG), Almost Clear Experiences (ACE) and Clear Experiences (CE) interacted with objective differences in stimuli, i.e. whether the stimulus was presented below, at or above threshold. No Experiences (NE) did not interact however and was not significantly different from chance as judged by the confidence intervals. No significant effects or interactions were found for differences in top-down expectations (Number of Alternatives).

## Null hypothesis testing of accuracy for No Experience

In this study, we were not able to find any evidence of No Experiences being affected by differences in top-down expectations or sensory saliency, but as the old adage goes: “absence of evidence is not evidence of absence”, thus we used Bayesian testing to test the null hypotheses that accuracy for No Experiences was equal across all differences.

We found some evidence for accuracy being equal across Number of Alternatives: Number of Alternatives 2 versus Number of Alternatives 4: $BF_{NULL} = 2.77$; Number of Alternatives 4 versus Number of Alternatives 8: $BF_{NULL} = 2.85$; and Number of Alternatives 2 versus Number of Alternatives 8: $BF_{NULL} = 4.57$.

We also found evidence for accuracy being equal across differences in sensory saliency: below threshold versus at threshold: $BF_{NULL} = 2.31$; below threshold versus above threshold: $BF_{NULL} = 4.39$; and at threshold versus above threshold: $BF_{NULL} = 3.25$.

For all the analyses above, we used a Cauchy distribution as the prior distribution with a scale parameter of $\sqrt{2}/2$ (Morey & Rouder, 2011).

These analyses support that the accuracy of responses based on No Experiences is independent of both sensory saliency and top-down expectations.

## Response times

An analysis of response times was included as a further check that our manipulation of top-down expectations really did work (Doherty et al., 2005; Posner, 1980).

We log transformed the response times of participants and modelled them the same we did accuracy and frequency of PAS Ratings, but assumed that they were normally distributed (Fig. 6). We found that the optimal model included the 2-way interaction PAS Rating × Target Duration, $\chi^2(12) = 33.5$, $p < 0.001$, and the 2-way interaction PAS Rating × Number of Alternatives, $\chi^2(6) = 20.2$, $p = 0.0025$. All main effects were thus included in the model. The 3-way interaction was removed, $\chi^2(12) = 17.7$, $p = 0.12$, and so was the 2-way interaction Number of Alternatives × Target Duration, $\chi^2(4) = 3.76$, $p = 0.44$.

The PAS Rating × Number of Alternatives interaction was driven by response times for Weak

Glimpse being faster for 2 alternatives: Number of Alternatives 2 versus 4, $z = 3.75$, $p < 0.001$, and Number of Alternatives 2 versus 8, $z = 2.27$, $p = 0.023$. The same was the case for Almost Clear Experience: Number of Alternatives 2 versus 4: $z = 3.78$, $p < 0.001$; Number of Alternatives 2 versus 8: $z = 2.00$, $p = 0.046$; and for Clear Experience, Number of Alternatives 2 versus 4: $z = 2.86$, $p = 0.0042$; Number of Alternatives 2 versus 8: $z = 4.28$, $p < 0.001$. These effects provided evidence that top-down expectations sped up response times the more distinct they were, indicating that our manipulation of top-down expectations worked as intended (Doherty et al., 2005; Posner, 1980). Interestingly, however, top-down expectations only sped up response times for Weak Glimpse, Almost Clear Experience and Clear Experience.

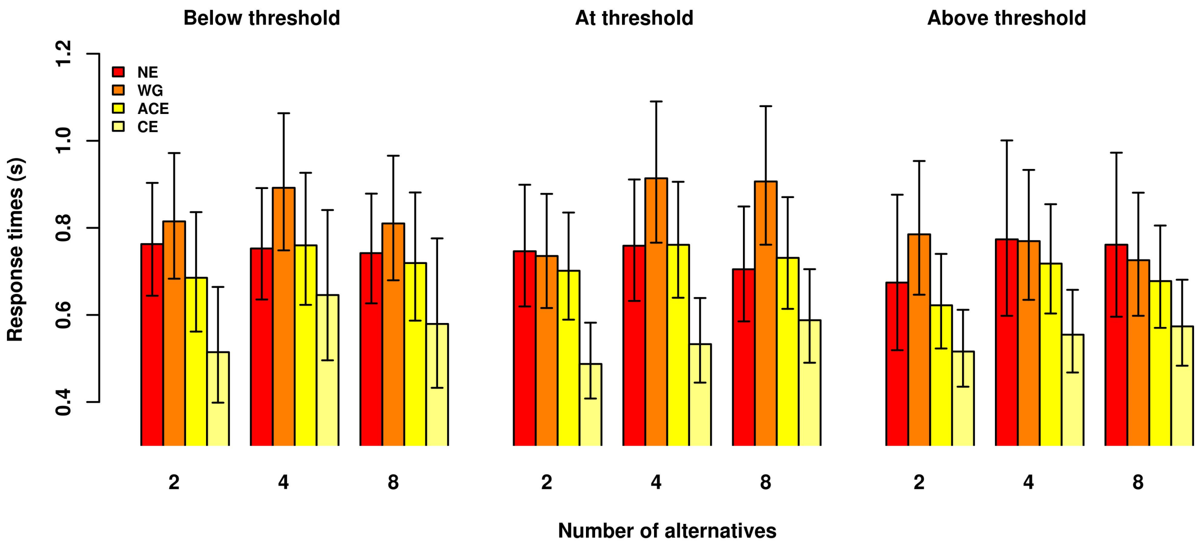


**Figure 6:** Mean response times for each rating on the Perceptual Awareness Scale (Table 1) shown below threshold, at threshold, 3 frames, and above threshold for each of the 3 conditions of top-down expectations (Number of alternatives). Error bars are 95 % confidence intervals. Model comparisons and statistical testing revealed that response times for Weak Glimpses (WG), Almost Clear Experiences (ACE) and Clear Experiences (CE) interacted both with objective differences in stimuli, i.e. whether the stimulus was presented below, at or above threshold and differences in top-down expectations (Number of alternatives). No Experiences (NE) did not interact however and was not significantly different from chance as judged by the confidence intervals.

The PAS Rating × Target Duration interaction was driven by response times for Weak Glimpse being faster for Target Durations of 4 frames than response times for Weak Glimpse for both Target

Durations of 3 frames, $z = 2.63$, $p = 0.0086$, and Target Durations of 2 frames, $z = 3.09$, $p = 0.0020$ and by faster response times for Almost Clear Experience for Target Durations of 4 frames than response times for Almost Clear Experience of 3 frames, $z = 3.24$, $p = 0.0012$, but not significantly faster than response times for Almost Clear Experience of 2 frames, $z = 1.80$, $p = 0.071$. These effects provided evidence that response times for graded responses, Weak Glimpse and Almost Clear Experience, speed up as sensory saliency increased.

In general, these results provide evidence for top-down expectations and sensory saliency affecting response times when perceptual consciousness is rated as Weak Glimpse or clearer.

The absence of significant effects on No Experience in terms of objective performance prompted a further Bayesian investigation into whether there was evidence of response times being similar for No Experience independently of Target Duration and Number of Alternatives, which would show that top-down expectations and sensory saliency *only* affect response time when perceptual consciousness is rated as Weak Glimpse or clearer.

### Null hypothesis testing of response times for No Experience

For all the analyses below, we used a Cauchy distribution as the prior distribution with a scale parameter of $\sqrt{2}/2$ (Morey & Rouder, 2011).

For No Experience, we found evidence for the null hypothesis that response times did not differ across Target Durations: below versus at threshold: $BF_{NULL} = 3.75$; below versus above threshold: $BF_{NULL} = 4.36$; at versus above threshold: $BF_{NULL} = 4.57$.

For No Experience, we also found evidence for the null hypothesis across Number of Alternatives: Number of Alternatives 2 versus 4: $BF_{NULL} = 4.57$; Number of Alternatives 4 versus 8: $BF_{NULL} = 3.19$ and Number of Alternatives 2 versus 8: $BF_{NULL} = 3.14$.

These results expand on the earlier tests and provide evidence that expectations and sensory saliency *only* affect response times when perceptual consciousness is rated as Weak Glimpse or clearer.

### Bayesian follow-up on the effect of Number of Alternatives when modelling accuracy

Because the *p*-value for removing the main effect of Number of Alternatives in the accuracy model (Fig. 5) was close to the pre-defined $\alpha$-value, we decided to do a follow-up test of effect of task on accuracy. The priors for these tests were all Cauchy-distributed with the scale set at $\sqrt{2}/2$ (Morey & Rouder, 2011). We found evidence suggesting that Number of Alternatives 4 and Number of Alternatives 8 might be associated with lower accuracy than Number of Alternatives 2: Number of Alternatives 2 versus Number of Alternatives 4: $BF_{ALTERNATIVE} = 3.14$; Number of Alternatives 2 versus Number of Alternatives 8: $BF_{ALTERNATIVE} = 1.93$; Number of Alternatives 4 versus Number of Alternatives 8: $BF_{ALTERNATIVE} = 0.640$.

## Discussion

In this study, we tested the effect that top-down expectations had on performance in terms of accuracy, response times and ratings of perceptual consciousness.

We did not find any differences based on the individually estimated parameters based on the non-linear function (Equation 1) (Figs. 2 & 3). These analyses, however, made it possible to estimate the thresholds for both objective performance and perceptual consciousness. Around the threshold for perceptual consciousness, perceptual consciousness became more graded as expectations towards prospective stimuli became more vague (Fig. 4). Interestingly, these differences in gradedness based on the distinctness of expectations were not accompanied by significant differences in objective accuracy, as found in memory tasks (Rademaker, Tredway, & Tong, 2012). Expectations about prospective stimuli thus seem capable of influencing subjective experience without significantly influencing objective accuracy. Accuracy for No Experiences did not significantly correlate with differences in top-down expectations or with differences in sensory saliency (Fig. 5). This is evidence of the Perceptual Awareness Scale being exhaustive (Dienes, 2007). If a scale is *exhaustive*, then when participants claim no perceptual consciousness, there should be no (significant) correlation between stimulus strength and accuracy. These data indicate that this is the case even when participants have strong expectations towards what can be seen.

Interestingly, top-down expectations did not have a significant effect on objective accuracy, indicating that expectations can have an effect on the perceived clarity of one's experiences without affecting objective performance. We thus have provided evidence that differences in top-down expectations around the subjective threshold have an effect on subsequent ratings of perceptual consciousness, while having no statistically significant effect on accuracy. This suggests that the bimodal distributions of perceptual ratings that have been implicated by some studies (Del Cul, Baillet, & Dehaene, 2007; Sergent & Dehaene, 2004) are partly dependent on the top-down expectations participants may have towards what will be shown, independent of the difficulty of the task. In other words, the bimodal distributions reported in these studies may be one end of the extreme, where distinct expectations, among other factors, make perceptional consciousness appear more bimodal than more vague expectations would have.

One potential concern about the conclusion that top-down expectations affect perceptual consciousness (Fig. 4), but not objective performance in terms of accuracy, was that we might have committed a type-II error. We investigated the non-significant main effect of expectations (Fig. 5) further with the use of Bayesian statistics to make certain that we did not overstate our findings. There was some suggestive evidence for higher accuracy when there were only 2 potential stimuli versus when there were 4 potential stimuli, but importantly the evidence for higher accuracy for 2 potential stimuli versus 8 potential stimuli was less conclusive. This contrast, between 2 and 8 potential stimuli, was where the differences in how top-down expectations affected reported perceptual consciousness were the greatest (Fig. 4), so any effect that expectations may have on accuracy is not likely to be caused by simple performance differences.

Another interesting finding of this study was the qualitative distinction between No Experiences on one side, and Weak Glimpses, Almost Clear Experiences and Clear Experiences on the other side.

Accuracy and response times for No Experiences were independent of both top-down expectations and sensory saliency, while accuracy and response times for the 3 other ratings were dependent on sensory saliency (Figs. 5 & 6), with response times furthermore dependent on top-down expectations (Fig. 6).

Based on these results, we suggest that a distinction is made between uninformative states, No Experiences, and informative states, Weak Glimpses, Almost Clear Experiences and Clear Experiences. Uninformative states result in random responses, which is what No Experiences did (Fig. 5). The response times in the current experiment may be taken as providing evidence that the cognition that leads to a random response is similar independently of top-down expectations and differences in sensory saliency (Fig. 6). We propose that uninformative states should be characterized by being *cognitively independent* of both external differences, e.g. differences in sensory saliency, and internal differences, e.g. differences in top-down expectations. In other words, that the cognition involved in assessing that one has no evidence for one or the other response should be independent of expectations and differences in sensory saliency, which would result in similar response times as here.

Informative states, on the other hand, may be expected to interact with differences in top-down expectations, which have been found to speed motor responses (Doherty et al., 2005; Posner, 1980), and differences in sensory saliency, which have been found to speed motor responses (Eriksen & Hoffman, 1972) and to increase accuracy (Sandberg et al., 2010). This is exactly what we found evidence of in this study (Figs. 5 & 6). Theoretically speaking, making a decision between responding “even” or “odd” may be seen as accumulating evidence for one or the other response. When accumulated evidence has crossed a threshold, a response is made (Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006). Expectations may help resolve or bias what response should be made, therefore the decrease in response time. But only when participants are in an informative state can expectations hasten or speed up that response. They cannot, so to say, speed up the accumulation process when there is nothing to accumulate.

All in all, this study raises some interesting questions. If the distinction between informative states and uninformative states is valid, uninformative states should also be *cognitively independent* of other external and internal differences, such as priming (Tulving & Schacter, 1990) and working memory load (Lavie, Beck, & Konstantinou, 2014).

There is also reason to expect neural signatures corresponding to both informative and uninformative states. In particular, the event-related potential P3 (Doherty et al., 2005; Polich, 2003) may be of interest here, as its latency and amplitude have been associated with closure of cognitive processes. As we argued earlier, expectations may bias or resolve what response should be made, but only if the state is informative. Thus, one may expect that interaction between expectations and informativeness may be neurally realized by the P3. This leads to the question of whether top-down expectations may interact with neural signatures of consciousness, because the P3 has been implicated as a neural correlate of consciousness (Dehaene, 2014), and whether this is dependent on the informativeness of the state (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011).

## Conclusions

The gradedness of the distribution of perceptual ratings is dependent on top-down expectations, even when accuracy did not differ significantly across different expectation conditions. Thus, bimodal distributions reported in other studies may be one end of the extreme, where distinct expectations, among other factors, can make perceptional consciousness appear more bimodal than more vague expectations would have.

The findings also provided evidence for the exhaustiveness of the Perceptual Awareness Scale, with participants being able to accurately report when they had no experience and no knowledge about the correct response even across differences in sensory saliency and top-down expectations.

We propose the idea that one can distinguish between uninformative and informative perceptual states. Responses based on uninformative states are *cognitively independent* of both internal and external differences, exemplified by the independence from top-down expectations and sensory saliency reported in this study.

Responses based on informative states, on the other hand, are characterized by correlating with both external and internal differences, exemplified by the reduction of response times by distinct expectations and increased sensory saliency reported here. It is also exemplified by the increased accuracy by increased sensory saliency reported here.

It remains to be investigated whether the proposed *cognitive independence* of uninformative states extends to other external and internal differences, such as priming and working memory load. Also, the neural underpinnings of informative and uninformative states are a field that seems open to inquiry based on the interactions revealed in this study between informativeness and expectations. Especially the P3 may be interesting to investigate.

## References

Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006). The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological Review*, *113*(4), 700–765. http://doi.org/10.1037/0033-295X.113.4.700

Dehaene, S. (2014). *Consciousness and the Brain: Deciphering How the Brain Codes Our Thoughts*. NY, USA: Penguin.

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology*, *5*(10), e260. http://doi.org/10.1371/journal.pbio.0050260

Dienes, Z. (2007). Subjective measures of unconscious knowledge. In R. B. and B. K. Chakrabarti (Ed.), *Progress in Brain Research* (Vol. 168, pp. 49–269). Elsevier. Retrieved from http://www.sciencedirect.com/science/article/pii/S0079612307680054

Doherty, J. R., Rao, A., Mesulam, M. M., & Nobre, A. C. (2005). Synergistic Effect of Combined Temporal and Spatial Expectations on Visual Attention. *The Journal of Neuroscience*, *25*(36), 8259–8266. http://doi.org/10.1523/JNEUROSCI.1821-05.2005

Eriksen, C. W., & Hoffman, J. E. (1972). Temporal and spatial characteristics of selective encoding from visual displays. *Perception & Psychophysics*, *12*(2), 201–204. http://doi.org/10.3758/BF03212870

Koch, C., & Preuschoff, K. (2007). Betting the house on consciousness. *Nature Neuroscience*, *10*(2), 140–141. http://doi.org/10.1038/nn0207-140

Lavie, N., Beck, D. M., & Konstantinou, N. (2014). Blinded by the load: attention, awareness and the role of perceptual load. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641), 20130205. http://doi.org/10.1098/rstb.2013.0205

McCulloch, C. E., & Neuhaus, J. M. (2005). Generalized Linear Mixed Models. In *Encyclopedia of Biostatistics*. John Wiley & Sons, Ltd. Retrieved from http://onlinelibrary.wiley.com/doi/10.1002/0470011815.b2a10021/abstract

Melloni, L., Schwiedrzik, C. M., Müller, N., Rodriguez, E., & Singer, W. (2011). Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *31*(4), 1386–96. http://doi.org/10.1523/JNEUROSCI.4570-10.2011

Morey, R. D., & Rouder, J. N. (2011). Bayes factor approaches for testing interval null hypotheses. *Psychological Methods*, *16*(4), 406–419. http://doi.org/10.1037/a0024377

Nieuwenhuis, S., & de Kleijn, R. (2011). Consciousness of targets during the attentional blink: a gradual or all-or-none dimension? *Attention, Perception & Psychophysics*, *73*(2), 364–73. http://doi.org/10.3758/s13414-010-0026-1

Overgaard, M., Rote, J., Mouridsen, K., & Ramsøy, T. Z. (2006). Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task. *Consciousness and Cognition*, *15*(4), 700–708. http://doi.org/10.1016/j.concog.2006.04.002

Peirce, J. W. (2009). Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, *2*, 10. http://doi.org/10.3389/neuro.11.010.2008

Polich, J. (2003). Theoretical Overview of P3a and P3b. In J. Polich (Ed.), *Detection of Change* (pp. 83–98). Springer US. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4615-0294-4_5

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25. http://doi.org/10.1080/00335558008248231

Rademaker, R. L., Tredway, C. H., & Tong, F. (2012). Introspective judgments predict the precision and likelihood of successful maintenance of visual working memory. *Journal of Vision*, *12*(13), 21. http://doi.org/10.1167/12.13.21

Ramsøy, T. Z., & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, *3*(1), 1–23. http://doi.org/10.1023/B:PHEN.0000041900.30172.e8

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *18*(3), 849–860. http://doi.org/10.1037/0096-1523.18.3.849

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review*, *16*(2), 225–237. http://doi.org/10.3758/PBR.16.2.225

Sandberg, K., Timmermans, B., Overgaard, M., & Cleeremans, A. (2010). Measuring consciousness: Is one measure better than the other? *Consciousness and Cognition*, *19*(4), 1069–1078. http://doi.org/10.1016/j.concog.2009.12.013

Sergent, C., & Dehaene, S. (2004). Is Consciousness a Gradual Phenomenon? Evidence for an All-or-None Bifurcation During the Attentional Blink. *Psychological Science*, *15*(11), 720–728. http://doi.org/10.1111/j.0956-7976.2004.00748.x

Summerfield, C., & Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences*, *13*(9), 403–409. http://doi.org/10.1016/j.tics.2009.06.003

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science*, *247*(4940), 301–306. http://doi.org/10.1126/science.2296719

Windey, B., Gevers, W., & Cleeremans, A. (2013). Subjective visibility depends on level of processing. *Cognition*, *129*(2), 404–409. http://doi.org/10.1016/j.cognition.2013.07.012

# Appendix V

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## Declaration of co-authorship

Full name of the PhD student: Lau Møller Andersen

This declaration concerns the following article/manuscript:

| | |
|---|---|
| Title: | Top-Down Perceptual Expectations Affect the Gradedness of Perception and the Evidence Weighting of Informative Levels of Perceptions |
| Authors: | Lau M. Andersen, Frank Tong |

The article/manuscript is: Published ☐ Accepted ☐ Submitted ☐ In preparation ☒

If published, state full reference:

If accepted or submitted, state journal:

Has the article/manuscript previously been used in other PhD or doctoral dissertations?

No ☒ Yes ☐ If yes, give details:

The PhD student has contributed to the elements of this article/manuscript as follows:

A. No or little contribution
B. Has contributed (10-30 %)
C. Has contributed considerably (40-60 %)
D. Has done most of the work (70-90 %)
E. Has essentially done all the work

| Element | Extent (A-E) |
|---|---|
| 1. Formulation/identification of the scientific problem | D |
| 2. Planning of the experiments and methodology design and development | D |
| 3. Involvement in the experimental work/clinical studies/data collection | E |
| 4. Interpretation of the results | D |
| 5. Writing of the first draft of the manuscript | E |
| 6. Finalization of the manuscript and submission | |

### Signatures of the co-authors

| Date | Name | Signature |
|---|---|---|
| Aug 20, 2015 | Prof. Frank Tong | Frank Tong |

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In case of further co-authors please attach appendix

Date: 21-08-2015

Signature of the PhD student

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## Declaration of co-authorship

Full name of the PhD student: Lau Møller Andersen

This declaration concerns the following article/manuscript:

| | |
|---|---|
| Title: | Using multivariate decoding to go beyond contrastive analyses in consciousness research |
| Authors: | Kristian Sandberg, Lau M. Andersen and Morten Overgaard |

The article/manuscript is: Published ☒ Accepted ☐ Submitted ☐ In preparation ☐

If published, state full reference: *Frontiers in Psychology*. 2014;5:1250. doi:10.3389/fpsyg.2014.01250.

If accepted or submitted, state journal:

Has the article/manuscript previously been used in other PhD or doctoral dissertations?

No ☒ Yes ☐ If yes, give details:

The PhD student has contributed to the elements of this article/manuscript as follows:

A. No or little contribution
B. Has contributed (10-30 %)
C. Has contributed considerably (40-60 %)
D. Has done most of the work (70-90 %)
E. Has essentially done all the work

| Element | Extent (A-E) |
|---|---|
| 1. Formulation/identification of the scientific problem | B |
| 2. Planning of the experiments and methodology design and development | B |
| 3. Involvement in the experimental work/clinical studies/data collection | C |
| 4. Interpretation of the results | B |
| 5. Writing of the first draft of the manuscript | C |
| 6. Finalization of the manuscript and submission | C |

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In case of further co-authors please attach appendix

Date: 7-9- 2015

Signature of the PhD student

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## Declaration of co-authorship

Full name of the PhD student:

This declaration concerns the following article/manuscript:

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|---|---|
| Title: | Occipital MEG Activity in the Early Time Range (<300 ms) Predicts Graded Changes in Perceptual Consciousness |
| Authors: | Lau M. Andersen, Michael N. Pedersen, Kristian Sandberg, Morten Overgaard |

The article/manuscript is: Published ☒ Accepted ☐ Submitted ☐ In preparation ☐

If published, state full reference: Cerebral Cortex 2015 doi: 10.1093/cercor/bhv108

If accepted or submitted, state journal:

Has the article/manuscript previously been used in other PhD or doctoral dissertations?

No ☒ Yes ☐ If yes, give details:

The PhD student has contributed to the elements of this article/manuscript as follows:

A. No or little contribution
B. Has contributed (10-30 %)
C. Has contributed considerably (40-60 %)
D. Has done most of the work (70-90 %)
E. Has essentially done all the work

| Element | Extent (A-E) |
|---|---|
| 1. Formulation/identification of the scientific problem | D |
| 2. Planning of the experiments and methodology design and development | D |
| 3. Involvement in the experimental work/clinical studies/data collection | D |
| 4. Interpretation of the results | D |
| 5. Writing of the first draft of the manuscript | E |
| 6. Finalization of the manuscript and submission | D |

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In case of further co-authors please attach appendix

Date: 7/9- 2015

Jan Møller Andersen

Signature of the PhD student

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# Declaration of co-authorship

Full name of the PhD student: Lau Møller Andersen

This declaration concerns the following article/manuscript:

| | |
|---|---|
| Title: | Task differences induce differences in magnetoencephalographic correlates of consciousness |
| Authors: | Lau M. Andersen, Mikkel Vinding, Kristian Sandberg and Morten Overgaard |

The article/manuscript is: Published ☐ Accepted ☐ Submitted ☐ In preparation ☒

If published, state full reference:

If accepted or submitted, state journal:

Has the article/manuscript previously been used in other PhD or doctoral dissertations?

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A. No or little contribution
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| Element | Extent (A-E) |
|---|---|
| 1. Formulation/identification of the scientific problem | E |
| 2. Planning of the experiments and methodology design and development | D |
| 3. Involvement in the experimental work/clinical studies/data collection | D |
| 4. Interpretation of the results | D |
| 5. Writing of the first draft of the manuscript | E |
| 6. Finalization of the manuscript and submission | |

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