Early Electrophysiological Activity of the Visual Cortex Does Not Reflect Access to Visual Awareness

Marc M. Lauffs
Diploma thesis (MSc)

University of Twente, Enschede, The Netherlands

June, 1st 2012

Supervisors: R. H. J. van der Lubbe & M. L. Noordzij
Department: Cognitive Psychology and Ergonomics

Abstract

Current models of visual awareness emphasize the role of the fronto-parietal cortex in the emergence of reportable visual awareness. However, these models are unclear about whether the strength of early visual cortex activity is of importance for visual awareness once a minimum threshold is exceeded. Electrophysiological investigations of this matter have produced differing results.

The current study investigated whether the amplitude of the two earliest components of the visual event-related potential (C1, P1) correlates with the level of visual awareness. Symbolic pre-cues were used to control the focus of visuo-spatial attention. Identical visual stimuli were briefly flashed on a screen and subsequently masked using metacontrast. Subjects indicated the experienced visibility of the stimuli in a two-alternative forced-choice task after each stimulus presentation, allowing for conclusions concerning their level of visual awareness.

The level of visual awareness did not significantly affect the amplitude of the C1 and P1 components. In line with current models of visual awareness, this finding suggests that early responding of the visual cortex is inessential for introspective access to visual awareness once a minimum threshold of activity is exceeded. It can be hypothesized, however, that C1 and P1 might be of importance to processes preceding the access stage.

Keywords: ERP, C1, P1, visual awareness, access consciousness, attention

Samenvatting

Hedendaagse modellen van visueel bewustzijn leggen veel nadruk op de rol van fronto-pariëtale hersengebieden in het ontstaan van rapporteerbar visueel bewustzijn. Er bestaat echter onduidelijkheid of de sterkte van vroege activering van de visuele cortex nog van belang is voor het ontstaan van bewustzijn als een minimaal benodigde mate aan activering al gegeven is. Elektrofysiologische onderzoeken naar dit vraagstuk hebben tegenstrijdige resultaten opgeleverd.

De hier gepresenteerde studie heeft onderzocht of de amplitude van de twee vroegste componenten van de visueel opgewekte event-related potentials (C1, P1) correleren met het level van visueel bewustzijn. Symbolische pre-cues zijn gebruikt om de focus van visuo-spatiale aandacht te manipuleren. Identieke visuele stimuli werden heel kort op een computerscherm aangeboden en korte tijd later met behulp van metacontrast gemaskeerd. De proefpersonen gaven na elke trial aan of ze de target stimulus duidelijk gezien hebben of niet, wat conclusies ten aanzien van het level van hun visueel bewustzijn toelaat.

Het level van visueel bewustzijn had geen significant effect op de amplitude van de C1 en P1 componenten. In overeenkomst met de hedendaagse modellen van visueel bewustzijn suggereren de resultaten dat de vroege responsen van de visuele cortex niet van essentieel belang zijn voor de introspectieve toegankelijkheid van visueel bewustzijn, zodra een minimaal benodigde mate van activering gegeven is.

Table of Contents

Appendix

Functional magnetic resonance imaging (fMRI) and the deduction of event-related potentials (ERPs) from the electroencephalogram (EEG) are now commonly used techniques to relate the activity of specific parts of the brain to mental functioning. Recently, a great part of this research has focused on the identification of the neural processes underlying conscious, or aware[1], visual perception.

The most commonly taken approach in this trend was inspired by Francis Crick and Christoph Koch, who suggested to search for the *neural correlates of consciousness* (NCC): "The minimal set of neuronal events that gives rise to a specific aspect of a conscious percept" (Crick & Koch, 2003). This definition stresses the notion of the minimal, so the NCC is defined as the set of neural events that is both necessary and sufficient for a given conscious percept. For instance, the firing of retinal cells does not constitute part of the NCC, because conscious visual percepts can also occur when the retina is not stimulated and its cells do not fire (as, for example, in visual dreaming) and vice versa. Hence, although the firing of retinal cells is often observed in correlation with visual awareness, it is not part of the minimal NCC as defined above.

One of the major challenges in the search for the NCC is that some standard for comparison must be defined to separate conscious from unconscious processing (assuming there is such a sharp difference at all; cf. Sergent & Dehaene, 2004; Overgaard, Rote, Mouridsen, & Ramsøy, 2006). For any neural correlate to be meaningful, it must first be known what it is to correlate *with*. Here a problem arises: How can one know whether another person (or animal, or object, or machine) has a conscious experience or not? Conscious experience is inherently private, meaning that it is observable from a first-person perspective only. It seems as if the only way to study it from the outside is by inferring some inner state from an observable behavior, action, or report (however, see Lamme, 2006). However, this method is not without problems. As far as perception is concerned, it seems reasonable to accept that when a person confidently indicates to be conscious of a given stimulus this statement is likely to be correct. The information pertaining to the percept seems to be

---

[1] The terms consciousness and awareness will here be treated as equivalent and used interchangeably.

buffered in some mental store, where it is open to the person’s introspection and, hence, available for speech and action. However, in some cases an individual might display behavior that suggests that a given stimulation was well perceived, but yet deny any form of conscious experience. Consider the case of “blindsight”, a neurological condition that can occur following wide-ranging lesioning of the primary visual cortex. Patients suffering from blindsight usually deny consciously perceiving stimulation in the contralesional visual hemifield. Yet, when asked to guess at the color, orientation, movement, or other attributes of a contralesional stimulus in a forced-choice situation, blindsight patients respond correctly significantly more often than would be predicted by chance (Weiskrantz, 2007). Similar results can be obtained from healthy individuals using visual masking. For example, in metacontrast masking identical visual stimuli are briefly flashed on a screen and followed by a trailing, non-overlapping second stimulus (the mask) after a variable delay (Alpern, 1953; Enns & Di Lollo, 2000). When the delay is either very long or very short, perception of the first stimulus (the target) is not or only slightly hampered. Subjects indicate to consciously perceive the target and can accurately discriminate its attributes in a forced-choice situation. However, at intermediate delays (around 30 ms) the subject less often indicates conscious perception of the target stimulus, but forced-choice discrimination performance remains high (Lau & Passingham, 2006; Schwiedrzik, Singer, & Melloni, 2011).

Recapitulating, we are confronted with a dissociation of two behavioral reports that have been proposed to mark the prevalence of consciousness: The capability to correctly discriminate various stimulus features indicates that the information pertaining to the stimulation must have been processed to a high degree. At the same time, this information is not accessible by introspection, causing the perceiving individual not to “feel” conscious of the stimulation. Whether information in such a state is indeed conscious or not is a highly debated issue that, naturally, has profound implications for the neural correlates that are proposed to be involved (cf. Block, 2007).

Current Theories of Visual Awareness

Philosopher Ned Block (2005, 2007) explicitly treats conscious perception and the introspective access of this information as separable. He assumes that we are aware of much more information than we can access at any given moment. Hence, what appears conscious to the perceiving individual is but a fraction of what one is actually aware of at that time. Block (2005) introduced the useful terminology of *phenomenal consciousness* and *access consciousness* to differentiate between the two. He suggests to reserve the latter term for percepts that can be deliberately accessed by introspection and, by consequence, can be reported (at least in normal, healthy human subjects). Access consciousness therefore matches the intuitional definition of consciousness, and it is access consciousness that prevails when one “feels” conscious of a given percept. However, in Block’s theory not everything that is inaccessible is necessarily unconscious: Block suggests to refer to stimulation that is processed to a high degree, but yet is not accessible, as phenomenally conscious (or phenomenal). Block (2007) uses the classic Sperling iconic memory test paradigm to explain this counterintuitive form of awareness: Sperling (1960) briefly flashed matrices of alphanumerical items on a screen and asked subjects to report as many of these items as possible. Usually, subjects could accurately report about four items at a time – the items they had cognitive access to. However, when cued shortly after offset of the matrix to report a specific row of items, subjects could report all, or almost all, items of a three-by-four item matrix (i.e., twelve items in total). According to Block, this shows that in fact all items were represented in phenomenal consciousness and that the bottleneck lies at the access stage[2]. Both forms of awareness are separable from *subliminality*. As implied by the name, subliminal activity refers to activity that possesses insufficient strength to cross the threshold to consciousness. For example, if an even bigger matrix were used in a Sperling-like paradigm, some items are likely not to be processed

---

[2] Please refer to the original paper of Block (2007) for information on the proposed relation between phenomenal and access awareness, and iconic and working memory.

sufficiently to be accessible when cued for report after stimulus offset. So while Block assumes that we have a richer consciousness than it appears, we still are not conscious of everything.

Block's ideas are supported by Lamme (2003, 2006, 2010), who adds a neuroscientific perspective to the argument: Lamme argues that feed-forward activation of neurons is insufficient for conscious experience and is, hence, subliminal. He postulates that (visual) phenomenal consciousness arises from recurrent processing in the visual areas of the occipital lobe. However, for the percept to become available to introspection and report (a state equivalent to Block's access consciousness), recurrent processing between neurons in the visual areas and fronto-parietal areas is necessary.

Dehaene and colleagues agree that occipital processing alone is insufficient for reportable consciousness to arise (Deahene, Changeux, Naccache, Sackur, &, Sergent, 2006). Similar to Lamme, they posit that visual information must reach a state of global availability in a neural workspace that involves fronto-parietal areas to be reportable. However, they disagree on the mere possibility of a state of consciousness that is not open to introspection. Hence, they suggest a *pre-conscious* state to explain behaviors that Block and Lamme propose to reflect phenomenal consciousness. Pre-conscious information is suggested to be reflected in the occipital areas of the cortex (which is again in accordance with the suggested neural basis of phenomenal consciousness). Unlike subliminal information, pre-conscious information can be readily made available to introspection, but remains unconscious until it is attended. Subliminal activity results from stimulation that is initially too weak as to be sufficiently enhanced by attention to reach consciousness.

Lau (2011) agrees that propositions of a conscious state that does not appear conscious to the perceiving individual is not useful to explain the subjectivity of experience. He therefore rejects the notion of phenomenal awareness and the inclusion of the visual areas in the NCC. For Lau, fronto-parietal areas that allow for higher-order thoughts about the visual information processed in the occipital areas are the most likely candidate for the NCC.

Zeki (2003) argued that consciousness is best thought of as consisting of different *micro-consciousnesses*. With micro-consciousnesses, Zeki refers to the awareness of different attributes of a stimulus (like its color, direction of movement, etc.), which precedes the compound awareness of the stimulus as a whole (*macro-consciousness*). As different stimulus attributes have been shown to be processed in distributed parts of the visual cortex and in a temporal hierarchy, Zeki assumes heightened activity in these areas to lie at the heart of visual consciousness. However, he acknowledges that the binding of micro-consciousnesses to a macro-consciousness is yet to be explained, and that different supporting systems might be needed for consciousness to arise.

Summarizing, most current theories of awareness allow for (at least) three levels of visual consciousness: First, a subliminal state, in which the activation of the cortex is too weak to produce a lasting effect on the cognitive system and produce a conscious percept. Second, an intermediate state, in which visual information is highly analyzed in the specialized cortical areas of the occipital lobe but, yet, is unavailable to introspection and, hence, does not seem to be aware. And third, a state of full awareness in which the visual information is communicated back and forth between the occipital visual areas and fronto-parietal networks, making it available for introspection, reasoning, and report.

Disagreement among these theories revolves primarily around the intermediate state, and whether it is more accurately described as conscious or unconscious. Naturally, this debate produces varying suggestions as to what might count as neural correlates of consciousness. Theories that reject ideas of consciousness in the absence of accessibility (e.g., Dehaene et al., 2006; Lau, 2011) emphasize the role of fronto-parietal areas, as activity in the occipital areas must be read out by some higher process to be conscious. On the other hand, for theories that allow for the existence of consciousness in the absence of introspective reportability (e.g., Lamme, 2006; Block, 2007; Zeki, 2003) processing in the visual areas of the occipital cortex is already the first crucial process in awareness, and hence part of the NCC.

Early Electrophysiological Markers of Visual Awareness

Whether or not the initial responding of the cortex to visual stimulation can be assumed to correlate with the level of visual awareness is unclear from these models. As mentioned, Dehaene et al. (2006) pose that a given bottom-up strength of stimulation is a prerequisite to qualify for pre-consciousness and consciousness. Once this threshold is exceeded, attentional enhancement is described as the gatekeeper to consciousness, and the role of the initial strength of the activation is somewhat neglected in this discussion. Likewise, Lamme (2003) predicts that consciousness is absent during the feed-forward sweep of activation from the visual to higher areas, whatever its strength might be. Lamme, too, deems attentional selection as important to select (phenomenally conscious) information for access and report. For Lau (2011) the strength of occipital cortex responding reflects the possible level of task performance, which according to him must be separated from visual awareness (cf. Lau & Passingham, 2006, for a suggested method). Importantly, however, the claim that higher processes determine whether a stimulus reaches a state where it is open to introspection and report does not preclude that early bottom-up activation might covary with later reportability, or might even be necessary for further processing to take place (cf. de Graaf, Hsieh, & Sack, 2011; Aru, Bachmann, Singer, Melloni, 2012; van Boxtel, Tsuchiya, & Koch, 2010). Last but not least, Zeki (2003) predicts that the degree of activation in a visual area determines whether a micro-consciousness emerges. But again, the prediction is purely focused on the localization of processing in the cortex and has little to say about its timing.

Electrophysiological studies have capitalized on the supreme temporal resolution of magnetoencephalographic (MEG) and ERP recordings to shed light on this issue. The earliest visual responses that are detectable from the scalp are the C1 and P1 ERP components and their MEG equivalents. Usually, C1 can be observed at posterior midline electrode sites, with onsets of 40 to 60 ms, and peaks around 80 to 100 ms after stimulus onset (Luck, 2005). Source reconstructions (Clark, Fan, & Hillyard, 1995) and fMR imaging (Clark & Hillyard, 1996; Di Russo, Martinez, & Hillyard, 2003) have indicated its source to lie in striate cortex, also known as primary visual cortex, or area V1.

Being the earliest component both timely and anatomically, C1 is thought to signal the arrival of visual information in the cortex (Di Russo et al., 2003; Clark et al., 1995). The slightly later P1 component already reflects responding of extrastriate activities (Di Russo et al., 2003; Clark et al., 1995). It is most strongly reflected at lateral occipital electrode sites, with onsets of 60 to 90 ms and peaks between roughly 100 to 130 ms poststimulus. Latency of P1 is, however, largely dependent on stimulus contrast, with low-contrast stimuli delaying its appearance (Luck, 2005).

Both C1 and P1 are assumed to be mostly stimulus-driven, in that they reflect various attributes of the stimulation (e.g., contrast, spatial frequency, etc.) and are quite a bit smaller in amplitude than later endogenous components (Luck, 2005). Other than P1, the C1 component is additionally sensitive to the spatial location of the stimulation (as will be elaborated upon later). However, both components are not purely exogenous: The amplitude of P1 has been shown to be enhanced for top-down attended as compared to unattended stimuli (e.g., Luck, Woodman, & Vogel, 2000; Hillyard & Anllo-Vento, 1998; Hillyard, Vogel, Luck, 1998). Over the recent years a growing number of studies has also shown C1 amplitudes to be subject to attentional manipulations (Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009; Poghosyan & Ioannides, 2008; Proverbio, Zotto, & Zani, 2007, 2010; Karns & Knight, 2009; Khoe, Mitchell, Reynold, & Hillyard, 2005). Top-down attention effects on C1 amplitude have only recently been reported, however, and were absent in many earlier studies (e.g., Kanwisher & Wojciulijk, 2000; Luck et al., 2000; Hillyard et al., 1998).

Most electrophysiological studies that used masking or stimulus contrast reductions to vary the level of visual awareness have not shown C1 and P1 and their MEG equivalents to correlate with these variations, regardless which behavioral markers were used (e.g., van Aalderen-Smeets, Oostenveld, & Schwarzbach, 2006; Koivisto et al., 2008; Railo & Koivisto, 2009; for comprehensive reviews, see, Railo, Koivisto, & Revonsuo, 2011, and Koivisto & Revonsuo, 2010). Only a handful of studies reported P1 amplitudes to covary with the level of visual awareness: Pins and ffytche (2003) measured detection rates in response to low-contrast stimuli presented at fixation. The presentation duration of the targets was continuously adjusted to achieve a balanced ratio of detected and undetected targets. Detected targets evoked significantly stronger P1 responses than undetected targets. This finding has been replicated by Mathewson, Gratton, Fabiani, Beck, and Ro (2009) using metacontrast, and Boehler, Schoenfeld, Heinze, and Hopf (2008) using object-substitution masking (cf. Enns & Di Lollo, 2000).

Koivisto and Revonsuo (2010) critique the interpretation of this early amplitude difference as a correlate of awareness. Instead they suggest that "the enhanced P1 might reflect a greater engagement of attentional resources at an early pre-conscious stage of processing, which does not directly indicate the appearance of the sensory event in awareness. Rather, it may reflect successful allocation of attentional resources to the stimulus and sufficient amplification of the signal to cross the threshold to consciousness." But studies in which this proposition was tested, by varying both the level of visual awareness and attention, are scarce. Koivisto, Revonsuo and colleagues (Koivisto, Revonsuo, & Salminen, 2005; Koivisto & Revonsuo, 2007; Koivisto, Revonsuo, & Lehtonen, 2006; Koivsito, Kainulainen, & Revonsuo, 2009) consistently report an attention-independent difference between unmasked and masked trials, between roughly 120 to 300 ms, as the earliest electrophysiological correlate of awareness (the visual awareness negativity, or VAN). In their studies, effects on P1 by variations in visual awareness were observed only sporadically in interaction with other factors, and could not be further located in post-hoc tests. Koivisto and colleagues therefore discredited P1 as correlate of visual awareness (e.g., Koivisto et al., 2008). However, their VAN is critiqued by others as occurring too late to qualify as a direct correlate of consciousness (Bachmann, 2009). In line with this critique, analyses in the time-frequency domain found attention-independent effects of awareness at an early latency that matches the time-range of P1 (Wyart, Dehaene, & Tallon-Baudry, 2012).

Amplitudes in the C1 time-range have not been reported to vary as a function of visual awareness. However, some peculiarities apply to the measurement of the C1, which might potentially explain the absence of effects in earlier studies (cf. Kelly et al., 2008). First, C1 has very small amplitudes compared to later components and background EEG noise in particular. Compared to later components, a much larger amount of trials is needed per experimental cell to allow for the cancellation of random noise to occur in averaging and changes in C1 activity to be detectable. If the number of repetitions is not planned accordingly, C1 amplitude variations are unlikely to show in the data. Second, the striate cortex, from which C1 originates, is situated in and around the calcarine fissure (Clark & Hillyard, 1996; Di Russo et al., 2003). Also, the striate cortex is retinotopically organized, meaning that a given part of the visual field is processed in a corresponding part of the striate cortex. Consequently, some part of the visual field is processed in the upper and some other part in the lower bank of the fissure. In studies specifically designed to map how these anatomical properties translate to ERP scalp topographies (Jeffreys & Axford, 1972; Clark et al., 1995), it has been found that electrophysiological signals recorded from the scalp reverse in polarity at (approximately) the horizontal median of the visual field. Stimuli in the upper hemifield usually produce negative C1 amplitudes, as they are processed in the lower bank. Stimuli in the lower hemifield usually produce positive C1 amplitudes, as they are mainly processed in the upper bank. However, the exact stimulus elevation at which the amplitude reversal occurs is subject to inter-individual differences (cf. Proverbio et al., 2007; Kelly et al., 2008). Slight variations in anatomy might already have great impact on the orientation of the C1 component's source and, hence, at which scalp electrode it is best detectable, and with which polarity.

Kelly and colleagues (2008) suggested that taking into account this inter-individual variability might considerably improve the signal-to-noise ratio of the recording and hence allow for the detection of C1 amplitude variations that had gone undetected in earlier studies (also see Proverbio et al., 2007). In a pretest session, Kelly et al. probed different stimulus positions on a computer screen to find the two stimulus locations that produced the best detectable activity in the C1 range for each subject individually. The earliest foci of opposing polarity were then identified in the scalp topographies for upper versus lower hemifield stimuli. Finally, the electrodes closest to these foci were selected for analysis of the experimental data. Using this procedure, Kelly et al. (2008) were among the first to demonstrate the susceptibility of C1 amplitudes top-down to attentional enhancement. Their findings supported their proposition that compensating for individual anatomical differences in striate cortex anatomy can grandly improve the power of electrophysiological studies to detect amplitude differences of the C1 component.

Summarizing, two main questions arise from the literature with respect to the early neurophysiological correlates of visual awareness: First, can top-down effects on C1 amplitude be demonstrated when individual anatomical differences are taken into account? And if so: Can the effect be dissociated from attentional mechanisms and related to the access of visual consciousness? Second, can the finding of a P1 correlate of visual awareness (as reported by, e.g., Pinns & ffytche, 2003) be confirmed when attention effects are controlled for?

The Current Study

In the current study, the protocol of Kelly et al. (2008) was followed to increase sensitivity to the C1 component. It was reasoned that if it can be shown that the method is suited to detect slight variations in C1 amplitude caused by attention, it should also be able to detect C1 variations caused by other cognitive functions, provided they are of similar magnitude. Therefore, sensitivity of the procedure to early striate cortex activity was to be demonstrated by a replication of the earlier reported attentional C1 amplitude variations (e.g., Kelly et al., 2008).

Kelly et al.'s visuo-spatial attention task was combined with a metacontrast masking paradigm. By varying spatial attention and the level of visual awareness in a full-factorial design, the relative contribution of (top-down) attention to the signal can be disseminated from changes due to variations in the level of visual awareness. Three limitations of earlier studies are thereby overcome: First, the methodology is specifically tuned to the detection of early activity of striate cortical origin (i.e., the C1 component). Second, the influences of top-down attention are adequately controlled (cf. Koivisto & Revonsuo, 2010). Lastly, by restricting the focus of the analyses to these early components, which are usually observed before 200 ms, eventual overlap of target and mask related activity can be controlled for statistically, obviating the use of mathematical manipulations of the data (e.g., subtraction of an individually assessed mask response from "target-plus-mask" activity). As will be discussed in the following section, this procedure thus lends an unaltered and, hence, more objective data-set for analysis than was the case in earlier studies.

Most earlier studies used mere detection of stimulus presence as behavioral marker of the level of visual awareness. This is of special relevance in those studies that reported P1 variations (e.g., Pins & ffytche, 2003; Mathewson et al., 2009; Wyart et al., 2012), since detection of a single stimulus feature (i.e., a single micro-consciousness) or mere facilitation of a motor response might suffice to reach high detection rates. High forced-choice detection rates should also be observable in blindsight patients, who lack introspective access to the stimulation (cf. Bachmann, 2009). Hence, not all current frameworks would agree that detection of the stimulus necessarily reflects conscious perception. This makes it difficult to set eventually observed neurophysiological differences in relation to the current frameworks of visual awareness and their interpretation of the NCC. We therefore chose to use subjective visibility as behavioral marker of the level of awareness. The current frameworks would all agree that an introspective report ("Yes, I clearly saw the stimulus.") signals "full" awareness, in the sense that some highly analyzed mental reflection of the stimulation is accessed by the systems needed for introspective report. On the other hand, reports of unclear visibility suggest that this state was not reached.

Participants observed identical visual stimuli at two diagonally opposite stimulation sites on a computer screen, which had been probed for optimal early responding in a pre-session. Before presentation of a stimulus the subjects were urged by a central cue to covertly shift their attention to one of the two locations, while maintaining central fixation. A square, rotated by either 0° or 45° degrees with equal probability from trial to trial, was then presented at either the attended or the unattended location. Metacontrast masks were presented at both locations shortly afterwards. Masking strength was varied by an automated staircase procedure that adjusted the asynchrony between target and mask onset on a trial-by-trial basis. This procedure ensured that the physical stimulation was identical across subjects and trials, necessitating neither the adjustment of stimulus presentation duration nor its contrast to vary the level of visual awareness. Eventual changes in the early components thus could not be explained by their sensitivity to changing bottom-up stimulus attributes (cf. Verleger, 2010).

The automatic adjustment of masking strength was programmed to establish a balanced proportion of clearly visible and less visible (or invisible) targets. Subjects provided the necessary input for this classification by rating the experienced visibility of the target on a dichotomous scale after each trial. Specifically, subjects first performed a two alternative forced-choice discrimination of target orientation. Subsequently they were asked whether they had “clearly seen” the target stimulus or had to guess at target orientation. Visibility ratings like these probe the participant’s subjective experience of the target stimulus, which requires introspection to be reportable (Lau, 2011; Lau & Passingham, 2006). As mentioned earlier, ratings of clear visibility can be assumed to signal full awareness of the target stimulus independent of the theoretical framework chosen (i.e., macro-consciousness, access-awareness, etc.). On the other hand, when subjects indicate to have guessed at the target discrimination task it can be assumed that information pertaining to the target stimulus did not reach a state of fully reportable visual awareness, but resides in some lower state of awareness. Specifically, targets that are not rated to be clearly perceived might either be only subliminally processed, or prevail in some pre-conscious or phenomenally conscious state that is not accessible by introspection.

In line with earlier findings it was hypothesized that enhanced amplitudes of the C1 and P1 components would be found for validly as compared to invalidly cued targets, reflecting attentional enhancement of the neural responding. This finding would demonstrate the method’s general sensitivity to amplitude variations of the earliest visual components, including C1. Since this is the first study to employ masking in a paradigm that can potentially be demonstrated to possess such sensitivity, our hypotheses were open to the question as to whether C1 amplitude variations would occur in dependence of the level of visual awareness. Given the ongoing discussion in the literature, potential effects of effective masking on P1 amplitude were likewise approached exploratively.

Method

Participants

Seventeen students of the University of Twente participated in the experiment for course credits. The experiment spanned a separate pretest and experimental session with an approximate duration of respectively two and three hours including preparation and debriefing. All participants had normal or corrected to normal vision and reported no psychological or neurological anomalies. Ultimately, the data-sets of 10 of the initial 17 subjects were retained for analysis after data pre-processing (see below). The average age of these subjects was 22.5 years (range 19 – 27, three females). Eight participants were right-handed, one was left-handed, and one ambidextrous, as assessed with the Annett Handedness Inventory (Annett, 1970). Each retained data set included 90 % of the original trials or more (min *N* = 1178 trials; data loss: *M* = 3.8 %, *SD* = 3.3, max = 10.0 %). All participants gave written informed consent prior to the study, which was approved of by an ethics board of the University of Twente.

Apparatus

Participants were seated in a darkened room behind a desk with a generic QWERTY keyboard and a 17 inch CRT monitor (1024 x 768 pixels resolution, 60 Hz refresh rate, 16.7 ms per video frame) at a distance of approximately 60 cm. To reduce muscle artifacts, no head restrain was used, therefore all stimulus sizes reported below are approximate. Stimuli were presented using Neurobehavioral Systems Presentation software 11.0 (www.neurobs.com) on a Windows XP personal computer (single core 3 GHz CPU, 1 GB RAM, onboard video card). Auditory feedback was played from standard stereo computer speakers.

The EEG was continuously recorded from 61 sintered Ag/AgCl electrodes fixed to an EasyCap electrode cap, with electrode nomenclature corresponding to the international 10-10 system (www.easycap.de). Bipolar electrodes above and below the left eye and on the outer canthi were used to record the vertical and horizontal electroencephalogram (EOG), respectively. The EEG and EOG signals were amplified in a QuickAmp amplifier and recorded on a second computer running BrainVision Recorder 1.03 (www.brainproducts.com). Impedances were kept below 10 kΩ. Data were recorded with a mean reference at a sampling rate of 1000 Hz, using a high-cutoff filter at 280 Hz and a notch filter at 50 Hz. An additional high-cutoff filter at 30 Hz and a low-cutoff filter with time-constant 1 s (both 24 db/Oct. roll-off) were applied after the recording in BrainVision Analyzer 2.01 (www.brainproducts.com).

Stimuli

Size and positioning of the stimuli were modeled after Kelly et al. (2008). However, different stimuli had to be used to allow for backward masking. Two identical shapes, differing merely by their orientation, were used to minimize differences in the physical properties between the targets: Square shaped stimuli were 1.1° x 1.1° in size, with a line of 0.064° in width and light grey color. Diamond shaped stimuli were identical but rotated by 45°, thus having equal dimensions except for negligible inaccuracies due to the square shape of screen pixels.

Eight possible stimulus positions were aligned circularly around a central fixation cross (size 0.58° x 0.58°, line width 0.064°, grey color), with one position lying in each visual octant (see Figure 1). Being numbered as on a clock face, their approximate Cartesian (x/y) coordinates in degrees of visual angle from the fixation point were: #1 (2.32°, 3.09°); #2 (3.57°, 1.71°); #3 (3.57°, -1.71°); #4 (2.32°, -3.09°); positions #5 through #8 lay at corresponding positions mirrored on the y-axis.

In the main-experiment only two diagonally opposite stimulus positions were used, which had been individually selected for each subject in the pretest (see below). These positions were permanently indicated on the screen by four grey dots (0.16° x 0.16°), denoting a square area of 1.64° x 1.64°, in which the stimuli would appear centrally. Cues consisted of two isosceles triangles, one blue, one yellow, adjoining at their hypotenuses (length 0.71°), each pointing at one of the two stimulus positions. Which color was to be interpreted as the relevant pointer was balanced across subjects. To keep the physical image constant across trials, both triangles were presented for all subjects and in all trials. Metacontrast masks consisted of an overlapping square and diamond shape and were sized to trail, but not overlap the contours of the target stimuli. Like the target stimuli, the masks had a line width of 0.064° and were of the same gray color.

Task and Procedure

Pretest. A pretest session, preceding the experimental session by at least 24h, was conducted to identify the two diagonally opposite stimulus locations to be used in the main-experiment. To this end, stimuli were randomly presented one at a time and with equal probability at each of the eight possible positions, while subjects maintained central fixation. Stimuli were presented for the duration of two video frames (33.4 ms), with a fixed stimulus onset asynchrony (SOA) of 1500 ms. Square-shaped stimuli were presented on 90% of the trials. To ensure that subjects monitored the events on the screen closely, diamond shaped stimuli were randomly presented as imperative targets on 10% of the trials. Targets had to be reacted upon by pressing the space-bar of the keyboard as quickly as possible. If the response key was pressed following presentation of a non-target (square, *false positive*), or no response was given within 800 ms from target onset (*miss*), an auditory feedback signal and text specifying the nature of the fault were presented. Presentation of imperative targets was used for online control of task compliance only, and therefore not further analyzed.

Per subject, a total of 1920 trials was run in three blocks of 640 trials each (about 16 min/block). Subjects could pause between blocks for as long as they desired. Prior to the recording, each subject practiced the task in a practice block of 32 trials, including 8 targets.

Average ERP responses to non-targets were averaged online and plotted for each stimulus position and subject. Individually per subject, the two diagonally opposite stimulus positions eliciting the largest activity between 50 and 100 ms poststimulus at posterior electrode sites, were selected as stimulation positions for the main-experiment. For seven out of ten subjects presentation positions in the upper left and lower right quadrant were selected. For the remaining subjects upper right and lower left positions were used.

Main-experiment. Before each trial, a central cue, shown for about 300 ms, indicated to which of the two positions the subject was to covertly shift her attention (cf. Figure 1). About 1200 ms later a target appeared at one of the two positions for the duration of two video frames (33.4 ms). Both target shape (square/diamond) and position (upper/lower visual half-field) were randomly chosen with equal probability from trial to trial. The cue validly predicted the target location on 70% of the trials; in the remaining trials the target appeared at the uncued location. After a variable delay of 0 – 8 video frames (0 - 133.6 ms) metacontrast masks appeared at both positions for 800 ms. Following mask presentation, the subject was asked to indicate whether a square or a diamond had been presented by pressing the appropriate button (two alternative forced-choice discrimination). The subject subsequently had to indicate whether she had clearly seen the shape of the target or whether her shape discrimination had been based on guesswork (two alternative subjective visibility measure). In both tasks, the “1” and “2” buttons of the keyboard’s Num-pad served as response buttons and could be pressed with whatever hand the subject preferred. Accuracy was emphasized to the subjects and no time constraints for their answers were imposed. The next trial started 400 ms after the second response was given.

Masking strength was varied by an automated staircase procedure, which adjusted the SOA between target and mask based on the subjects’ visibility ratings. Starting at the longest SOA (167 ms), the SOA was shortened in the upcoming trial by one video frame duration (16.7 ms) whenever the subject indicated to have clearly seen the target on two successive trials. On the other hand, whenever the subject indicated on two successive trials she had guessed at the shape of the target, the SOA was prolonged by one frame duration. As a consequence, the staircase was expected to quickly decrease the SOA duration until reaching the subject’s critical SOAs (the SOAs producing strongest masking effects), and subsequently fluctuate around the higher end of that SOAs. Nine SOAs were available for the staircase, ranging from two to ten video frame durations (33.4 – 167 ms). Consequently, target and mask were never presented simultaneously, but mask onset coincided with target offset in the shortest SOA (33.4 ms). Subjects were informed that the delay between target and mask presentation would vary, with the result that the target would be perceived better on some than on other occasions, but were kept in the dark on the precise workings of the procedure, and especially its relation to their visibility reports.

Per subject a total of 1320 trials was run in 11 blocks of 120 trials each (about 12 min/block). Breaks between the blocks could again be terminated by the subject. During the breaks feedback on the percentage of correct shape discriminations was provided as a means of motivation. The first trial of each block was considered a warm-up trial and not taken into account in the analyses. Before the start of the experimental trials, the subjects received written instructions and completed a practice block of 20 trials. After completion of the practice block the instructions were explained again verbally, making use of an exemplary screen-flow paper (similar to Figure 1), to ensure that the task was understood correctly.

Data Processing

Artifact rejection. For the classification of EOG artifacts, epochs of -1500 to +250 ms relative to target onset were derived from the continuous EEG and referenced against the time the central cue was present on the screen (-1500 to -1200 ms relative to target onset). Epochs containing EOG amplitudes exceeding +/-40 µV horizontally and +/-120 µV vertically over the interval of -100 to +200 ms were classified as contaminated and automatically rejected. For the remaining trials new epochs of -100 to +250 ms were defined and a new baseline was set from -100 ms to target onset. An automated artifact detection routine identified and removed epochs containing voltage steps exceeding 100 µV / ms, amplitudes above 100 µV or below -100 µV, or intervals of 50 ms or more in which less than 0.1 µV of activity was recorded.

Six subjects were excluded due to eye-movements on over 20 % of the trials (*M* = 26.1 %, *SD* = 11.2 %). Inspection of their EOG data revealed that for most of these subjects the signal changes were structural: The direction of the cue could reliably predict the polarity of the EOG deviations, showing that eye movements were made in direction of the target location. Another subject was removed for which a balanced ratio of “clearly seen” and “guessed” trials could not be established. This resulted in the use of a restricted range of SOAs (100.2 – 167 ms only) and a mean SOA of more than nine frame durations (a level at which generally little impairment by the mask would be expected).

Statistical control for ERP overlap. Because an automation feature adjusted the SOA rather freely, a likely consequence was that in trials with very short SOAs electrophysiological activity in response to the target would be overlapped by mask evoked activity, thereby preventing an undiluted measure of target processing (van Aalderen-Smeets et al., 2006). As a preliminary test for that kind of overlap, average amplitudes of consecutive 20 ms-windows from stimulus onset to 240 ms afterwards were calculated for electrodes PO7 and PO8. Each time-window was then subjected to a repeated measures analysis of variance (RM ANOVA), with the factors SOA (7), and stimulus position (2; left vs. right hemifield). Only the electrode contralateral to the stimulus presentation position was used. Potential overlap of activity would present itself in a significant effect involving factor SOA. An exclusion criterion of $p < .2$ was used for these preliminary tests. Note, that in the given situation the use of a higher p threshold is more conservative than use of lower significance levels since the hypothesis that the amplitude is identical across SOAs (and thus free of overlap) is rejected more readily.

The two longest SOAs were not included in this test for overlap as the data of three subjects would have automatically been excluded due to empty cells in these SOAs. Overlap of activity is much more likely to occur when the stimuli are presented in quick succession than when their onsets are delayed. Therefore, the exclusion of the two longest SOAs most likely does not affect the conclusions drawn from this procedure and is preferable to the loss of a considerable amount of data sets. One subject did not perform trials in the shortest SOA. This SOA was retained in the analysis, however, as it is most likely to produce overlap. Consequently, overlap testing was based on nine out of ten subjects and seven SOAs of 33.4 to 133.6 ms.

This procedure indicated the data to be free of overlap until 180 ms after stimulus onset (Greenhouse-Geisser corrected *p*s ≥ .213 for all windows and effects involving factor SOA). Since the components of interest are expected earlier than 180 ms, no trials had to be dropped.

Note, that others have dealt with overlapping target- and mask-related activity by assessing the time-course of mask-related activity in a separate mask-only condition and subtract it from all trials containing both target and mask (e.g., Mathewson et al., 2009; Del Cul, Baillet, & Deahene, 2007), or by confirming that in the absence of a target the mask does not evoke activity in the time-window of interest (e.g., Koivisto & Revonsuo, 2007). Both these techniques inevitably rely on the questionable assumption that mask-evoked activity is constant across experimental conditions (e.g., SOA variations) and adds up linearly with target-evoked activity (cf. Bachmann, 2009). These pre-assumptions do not necessarily hold true: For example, Del Cul et al. (2007) observed amplitude variations in mask-evoked components as a function of target-mask onset asynchrony. Complete isolation of the target-evoked response from overlapping mask-evoked activity, using subtraction of a mask-evoked response in a mask-only condition, was therefore not possible. The here performed exclusion of data containing overlap is conceptually less problematic, as it relies on much fewer pre-assumptions and prevents the necessity to alter the original data by means of subtraction.

Behavioral data. Forced-choice performance and subjective visibility ratings were preprocessed in Matlab (The MathWorks, Inc.) using the event and response markers recorded alongside the EEG. Trials that were dismissed from the ERP analysis were also excluded from the behavioral analyses.

Forced-choice shape discrimination performance was analyzed using signal detection theory (SDT; e.g., Abdi, 2007). Responses were categorized based on the presence or absence of a diamond shaped target stimulus: Subjects' reports of a diamond were considered hits when a diamond had in fact been presented; reports of a diamond, while in fact a square had been presented, were considered false-alarms. In order to buffer extreme false-alarm and hit rates and prevent infinite *z*-scores, 0.5 was added to the hit and false alarm counts in all cells, and 1 was added to the total number of signal and noise trials (i.e., the number of diamonds and squares that were presented). This so called log-linear correction has been shown to result in less biased estimates of *d′* than other corrections and has the property of reliably underestimating the value of *d′*, instead of producing over- and underestimations interchangeably (Hautus, 1995). Bias estimate *c* was calculated in parallel to *d′* to assess the presence and extent of response preferences. Since differing sensitivity between conditions was hypothesized, *c* is to be preferred above β and likelihood ratios as a bias statistic (Macmillan & Creelman, 2005). As no catch trials (i.e., trials in which no target stimulus is presented) were included in the current study, the subjective visibility ratings could not be classified in SDT. Subjective visibility will therefore be discussed in terms of the proportion of trials rated "clearly seen".

Discrimination performance (*d′*) and subjective visibility were analyzed separately in RM ANOVAs with the factors SOA (7; 33.4 – 133.6 ms) and attention (2; attended vs. unattended). Two subjects indicated clear visibility of the target in all trials of SOA 8 (133.6 ms), causing the staircase procedure to shorten the SOA duration on the next trial. Consequently, these subjects did not perform any trials in the two longest SOAs (150.3 and 167 ms; cf. Figure 4). Another subject did not perform any trials in the longest SOA for the same reason. As RM ANOVAs cope with empty cells by eliminating the respective subject from the analysis, we chose not to include these SOAs in the analysis of discrimination performance and visibility. Masking is assumed to be very weak or even absent at these SOAs (e.g., Enns & Di Lollo, 1997, 2000). The amount of relevant information lost can therefore be assumed to be restricted. Given the small subject population the loss of these SOAs is therefore preferable to the loss of statistical power due to the exclusion of participants.

Since our staircase procedure was designed to prolong the SOA duration at approximately the SOA where masking is strongest the *d′*-by-SOA and visibility-by-SOA functions were expected to describe only the continuously increasing right branch of the U-curve masking function, that is typically reported in the metacontrast masking literature (e.g., Enns & Di Lollo, 1997, 2000). Perception was expected to be strongly affected by masking at the shorter and less so at the longer SOAs, which would show up in a significant main-effect of factor SOA for both behavioral measures. Attention was assumed to facilitate processing, which would show in higher behavioral performance in validly than invalidly cued trials.

C1 analysis. From the pretest data, each individual subject's average ERP response to upper and lower hemifield stimuli was calculated for the positions that were selected for use in the main-experiment[3]. Kelly et al. (2008) had been able to identify early foci of opposing polarity for upper versus lower hemifield stimuli, reflecting the characteristic polarity reversal of C1 (cf. Introduction). The electrodes nearest to the center of these foci were then used for C1 analysis. Adoption of this method proved infeasible in the current study, as only a single subject showed clear early foci of opposing polarity for upper versus lower hemifield stimuli. The inspection of individual channels confirmed this impression: For most subjects no contralateral or central amplitude variations could be identified that markedly exceeded the extent of baseline fluctuations and seemed separable from P1. However, averaging of the pre-test data was based on roughly 200 trials per stimulus position, compared to roughly 500 trials in Kelly et al. (2008). It is not unlikely that 200 trials are insufficient to

---

[3] The same artifact and EOG rejection criteria as for the main-experiment data were applied to the pretest data, except that the baseline against which EOG deviations were evaluated was set from -100 to 0 ms, as no pre-cue was presented in the pretest.

single out the small-amplitude C1 component from the background noise. Therefore, the data from the main-experiment, containing over 600 trials per stimulus position and subject, were inspected following the same procedure. Again, we were unable to locate early foci of opposing polarity at contralateral or central posterior electrode sites in all but one subject. If not overall absent, early components that preceded P1 were found at individual channels for either upper or lower hemifield stimuli, but not both.

Earlier studies reported observations of C1 at a single central electrode (e.g., Di Russo et al., 2003) or symmetrical pairs of electrodes (e.g., Proverbio et al., 2007), which were identical for all subjects. As explained earlier, this is not optimal due to individual anatomical variations and is especially problematic in the present study, given that different stimulus presentation positions have been used across participants. However, the present data provided no sound basis for the determination of electrodes for C1 analysis at the individual level. We therefore relented to the use of a collective central electrode for analysis. Grand average data were plotted for upper versus lower hemifield stimuli. A C1-characteristic amplitude difference with an early onset of 60 ms poststimulus was found at central posterior electrodes, which was most pronounced at occipito-central electrode Oz within 70 to 100 ms poststimulus (cf. Figure 2). The procedure for the detection of overlap between target and mask evoked activity (see above) indicated this time-range to be free of overlap at electrode Oz, $F(6, 48) = 2.31$, $p = .120$, $\varepsilon = .397$[4]. Average amplitudes of the selected time-range were exported for testing in a RM-ANOVA with the factors stimulus position (2; upper vs. lower hemifield), cue-validity (2; valid vs. invalid), and visibility (2; “clearly seen” vs. “guessed”).

P1 analysis. Electrodes and time window for analysis of the P1 component were determined by identification of the first large positivity from approximately 90 ms onwards in the grand average waveforms for stimuli in the left and right hemifield, respectively (Figure 3). P1 was found to be most

---

[4] In this test, upper and lower visual hemifield were used as the levels of factor stimulus position to accommodate the polarity reversal of C1.

pronounced at electrodes PO7 and PO8 and between 125 to 165 ms poststimulus. The overlap detection procedure confirmed this time-range to be free of overlapping activity, $F(6, 48) = 1.08$, $p = .361$, $\varepsilon = .325$. Only the electrode contralateral to target presentation was used in the testing for overlap and the later testing for experimental effects (i.e., PO7 for targets in the right visual field and PO8 for targets in the left visual field). Average amplitudes in the selected time-range were exported for testing in a RM ANOVA with the factors stimulus position (2; left vs. right hemifield), cue-validity (2; valid vs. invalid), and visibility (2; “clearly seen” vs. “guessed”).

Results

Greenhouse-Geisser corrections were applied to the degrees of freedom wherever Mauchly's test of sphericity indicated the sphericity assumption to be unjustified ($p \leq .05$). In that case ε-values are reported along with the test statistics. Post-hoc tests were performed using Bonferroni corrections for multiple comparisons. Unless stated otherwise, two-tailed, uncorrected *p*-values are reported. In indications of effect sizes, standard deviations are given in parentheses.

Averaged across subjects, the proportion of trials performed per SOA described a bell-shaped distribution and was highest in SOAs 66.8 to 100.2 ms (Figure 4). This trend was statistically insignificant, however, due to substantial individual variability (cf. Figure 4), RM ANOVA, $F(8, 72) = 2.16$, $p = .147$, $\varepsilon = .240$. A paired-samples *t*-test indicated that the staircase procedure had established an even proportion of "clearly seen" and "guessed" trials, $t(9) = -1.39$, $p = .198$.

Behavioral Data

Measures of subjective visibility and discrimination performance confirmed that mask presentation had impaired target perception as intended: The proportion of targets rated "clearly seen" increased linearly with SOA (Figure 5), $F(6, 54) = 17.8$, $p \leq .001$, $\varepsilon = .278$. Likewise, discrimination performance increased linearly with SOA duration (Figure 6), $F(6, 54) = 19.2$, $p \leq .001$, $\varepsilon = .435$. Significant response bias in the discrimination task was absent except for a slight preference towards reporting the presence of diamond shaped stimuli in invalidly cued trials with an SOA of 83.5 ms, one-sample *t*-test against zero, $t(9) = -2.74$, $p = .023$, $c = -0.12$.

Cue-validity did not significantly affect the subjective visibility ratings, nor discrimination performance, $F(1, 9) = 0.01$, $p = .933$, and $F(1, 9) = 1.61$, $p = .237$, respectively. Also, there were no interactions of cue-validity and SOA (*p*s ≥ .546).

Electrophysiological Data

C1 (70-100 ms). The amplitude difference that had served as criterion for the selection of the electrode and time-window for C1 analysis was reflected in a significant effect of stimulus position, $F(1, 9) = 7.83$, $p = .021$. Upper hemifield stimuli produced a positive component of on average 0.9 µV, while lower hemifield stimuli were on average slightly negative -0.2 µV (cf. Figure 2). Note, that Clark et al. (1995) described positive C1 amplitudes for lower field and negative amplitudes for upper field stimuli. However, a reversal of this relation is not necessarily unusual and can be explained by individual differences (Proverbio et al., 2007).

Neither cue-validity nor rated visibility significantly affected the average C1 amplitude, $F(1, 9) = 2.12$, $p = .174$, and $F(1, 9) = 0.08$, $p = .783$, respectively. Also, cue-validity and visibility did not interact overall, $F(1, 9) = 0.01$, $p = .931$, nor in interaction with stimulus position, $F(1, 9) = 2.59$, $p = .142$.

P1 (125-165 ms). The analysis of mean P1 amplitude indicated no significant effects. Rated visibility did not influence the average P1 amplitude (Figure 3), $F(1, 9) = 0.27$, $p = .617$. Also cue-validity did not affect the strength of P1 and both factors did not interact, $F(1, 9) = 0.13$, $p = .727$, and $F(1, 9) = 0.30$, $p = .600$, respectively. An effect of stimulus position approached significance, with stimuli in the right visual field eliciting somewhat more negative amplitudes than stimuli in the left visual field, $F(1, 9) = 4.46$, $p = .064$, $\Delta_{\text{left – right}} = -0.60$ µV. All other interactions were insignificant ($ps \geq .091$).

Discussion

The current study investigated whether enhanced early responding of the striate and extrastriate cortex to visual stimulation, as reflected in higher amplitudes of the C1 and P1 ERP components, would be found when a reportable level of visual awareness was reached (compared to when this level is not reached). To this end, peripheral visual stimuli were presented and masked shortly afterwards using metacontrast. Subjects indicated whether they had clearly seen the stimuli or not, allowing for conclusions concerning their experienced level of visual awareness. An automated staircase procedure adjusted the masking strength to achieve a balanced proportion of clearly seen targets. Additionally, symbolic pre-cues were used to manipulate the locus of visuo-spatial attention and allow for the dissection of attention-related enhancement from the signal. Further, the protocol of an earlier study was followed to compensate for individual differences in striate cortex anatomy and thereby increase sensitivity to small C1 amplitude changes (Kelly et al., 2008).

It was found that neither the C1 nor the P1 component were enhanced when subjects reported clear visibility of a target stimulus, a behavioral marker used here to indicate whether introspectively available visual awareness was reached or not. The majority of earlier electrophysiological studies of visual awareness have produced similar results (see the reviews of Railo et al., 2011, and Koivisto & Revonsuo, 2010). Earlier studies that did find a relation of the level of visual awareness and P1 amplitude used detection rates (e.g., Pins & ffytche, 2003; Mathewson et al., 2009; Wyart et al., 2012) or forced-choice discriminations of a single stimulus attribute (Boehler et al., 2008) as behavioral markers of awareness. For reasons explained earlier, it is possible that these markers signal a state that differs from, and is reached earlier than fully accessible perception. Our results therefore leave room for the hypothesis that C1 and P1, while not crucial to the access of visual awareness, have an important role to play in earlier processes related to visual awareness, which would explain the findings of P1 effects in earlier studies.

Since the current study probed access to visual awareness to define the conditions for comparison, the here presented results are in line with contemporary theories of visual awareness that assume a crucial role of the fronto-parietal cortex in reportable visual awareness (e.g., Dehaene et al., 2006; Lamme, 2003; Lau, 2011). These theories generally posit that a minimum bottom-up strength of stimulation is needed for visual awareness. Once this threshold is exceeded, attention selects information for amplification in feedback-loops between cortical regions, which determines the depth of processing: If activity reaches a state of widespread activation including fronto-parietal areas, the stimulation will be open to introspection and will hence be experienced as aware and "clearly seen". Our findings generally support this proposition, as the amplitude of the two earliest components did not correlate with reported visibility. Whether or not the stimulation appeared conscious to the subject has thus likely been determined at a later stage, which might well involve recurrent processing, a specific fronto-parietal network, or widespread cortical activation.

The current findings can also be reconciled with the model of Zeki (2003), who poses that the amount of processing in the visual areas determines whether visual awareness emerges. Zeki assumes that individual stimulus attributes, like the orientation of the here presented stimuli, become aware separately before they are bound into a (macro-)conscious percept of the whole stimulus somewhat later. Assuming that subjects would not indicate clear perception of a target when only a single or some of its attributes are perceived, it can be argued that the here observed neural responses occurred too early to correlate with macro-consciousness. Instead they might or might not have contributed to the (micro-)consciousness of individual attributes of the target. These were, however, not probed in the current study[5]. In the same line of reasoning, it cannot be stated whether early activity in the visual areas might play a crucial role in the emergence of an earlier form

---

[5] As explained earlier, correct forced-choice shape discriminations do not necessarily reflect conscious perception.

of awareness that is inaccessible by introspection (like Block's phenomenal awareness, cf. Block, 2007).

Limitations

Cue-validity effects were found in neither the behavioral nor the electrophysiological data. Control over the focus of the participants' visuo-spatial attention could, hence, not be demonstrated. Usually, faster or more accurate behavioral responding can be observed if the location of the target stimulus is attended, an effect that has been demonstrated in a variety of paradigms, including metacontrast masking (e.g., Posner, Snyder, & Davidson, 1980; Tata, 2002). Likewise, enhanced P1 amplitudes are usually observed to co-occur with this enhancement (Luck et al., 2000; Hillyard & Anllo-Vento, 1998; Hillyard et al., 1998). The overall absence of cue-validity effects in the current study could suggest that top-down spatial attention did not markedly affect the processing of the here presented stimuli. Concurrently, the absence of cue-validity effects may point to a failed manipulation of top-down attention. Covertly shifting one's attention in the cued direction requires a certain amount of effort and concentration, especially when done repeatedly over a long time. Informal conversation with our participants yielded the impression that the task was experienced as tedious and extremely boring. At the same time, the staircase procedure caused the target to be experienced as "seen" on only 50 % of the trials, irrespective of the level of attention. The subjects thus were deprived of some of the rewarding experience of better perceiving the target when using the cue. It is not unlikely that the study's duration in combination with the lack of "reward" caused at least part of the subjects to neglect the instruction to shift their attention to the cued location, at least in part of the trials. Support for this suggestion lies in the finding that the subjects that had to be excluded for excessive eye-movements made eye-movements mostly in direction of the cue, and thus not necessarily in direction of the target stimulus. This indicates that their eye-movements were no automatic orientation response to the stimulus, but reflect deliberate neglect of the instruction to remain focused on the center of the screen.. Future studies should be cautious of this potential problem and take steps to increase involvement of the participants (e.g., a combination of a monetary reward system and an online control for cue-validity effects).

Sensitivity to amplitude changes in the C1 component was to be improved by selecting presentation and recording sites individually per subject (as originally suggested by Kelly et al., 2008). However, the individual identification of recording sites per subject failed due to unclear reflections of C1 at the single-subject level. Instead, C1 was analyzed collectively from a single occipito-central electrode for both upper and lower hemifield stimuli, as was done in earlier studies (e.g., Di Russo et al., 2003). This strategy allowed for the detection of a component that matches earlier descriptions of C1, based on its timing and differing polarity for upper versus lower hemifield stimuli. However, earlier studies' potential lack of sensitivity due to insufficient compensation for individual anatomical differences was largely paralleled in the current study, since an individual selection of electrodes was not possible (cf. Kelly et al., 2008). It thus remains disputable whether the absence of significant effects on C1 amplitude results from a mere lack of sensitivity or indeed reflects their absence.

Differences between the current study and Kelly et al. (2008) potentially explain the failed identification of C1 in individual subjects' data. In the current study, uncorrected pre-test trials were visually inspected for early activity in an approximate C1 time-range following online averaging. A thorough offline analysis of the data, as done by Kelly et al. (2008), might allow for a better informed choice of stimulation sites and, hence, clearer reflections of C1 in the experimental session. Further, only 200 trials were performed per stimulus position in the pre-test to the here reported experiment, opposed to 500 in the study of Kelly and colleagues. The rationale was the desire to restrict the total duration of the experiment and the assumption that the more numerous experimental trials could be used for electrode selection. This assumption turned out to be problematic. Potentially the experimental manipulations themselves introduced variations in C1 latency that diluted the component's peak when averaged across conditions, rendering it indistinguishable from the background noise. A waveform obtained from uniform pre-test trials, as done by Kelly and colleagues, might be better suited for visual identification of early components such as C1 and the selection of electrodes for analysis.

Concomitantly, Kelly et al.'s choice of stimuli was not restricted by masking affordances. Relatively large black-and-white gratings were presented for 100 ms. These stimuli can be assumed to evoke stronger bottom-up responses in the early visual areas than the stimuli used here (cf. Luck, 2005). These responses are accordingly easier to detect visually as they stand out more from the baseline fluctuations. For future studies the use of stronger stimuli therefore seems advisable. A first step can be the use of opaque versions of the stimuli used here, as was done by Railo and Koivisto (2009) and Albrecht, Klapötke, and Mattler (2010). The thereby increased contrast against the background might be sufficient to enhance the initial responding of the striate cortex while metacontrast masking is still possible. Checkered versions of the current stimuli might evoke even stronger responses, but it would have to be shown that they are still usable for metacontrast masking (cf. Wyart et al., 2012). As a disadvantage of the use of stronger stimuli, an increase of the rate of irrepressible eye-movements must be expected. However, we think that the expected increase in sensitivity is worth the effort of examining some additional participants to compensate for the potentially resulting exclusion of data-sets. If structural differences between participants are suspected, excluded participants might be re-invited to perform additional trials.

Last but not least, it must be noted that the absence of effects in the electrophysiological signal does not "prove" the absence of effects in general. Like with any other imaging instrument, there are limitations as to what can be recorded using EEG. Specifically, the EEG can only detect the synchronous firing of a large number of neighboring neurons, and only if they are organized in an open-field configuration (cf. Luck, 2005). It cannot be excluded that there are cell populations in the early visual areas that are differently organized and contribute to visual awareness or the access thereof. Also, the activity of very small or distributed populations of cells does not show in the recording, since their signal is hidden in the background noise. Finally, different analyses can be applied to electrophysiological data than the here performed average amplitude comparisons.

Recent studies have shown early awareness-dependent effects in specific gamma-band frequencies (e.g., Wyart, Dehaene, & Tallon-Baudry, 2012). This suggests that analyses in the time-frequency domain can provide insights that might be missed when using more traditional approaches, like the one used here.

Conclusion

The current findings suggest that, above a minimum threshold, access to visual consciousness does not crucially rely on the strength of early striate and extrastriate cortex responding. This finding is in line with current frameworks of the neural correlates of visual awareness that emphasize the role of fronto-parietal networks in the access of phenomenal information. It cannot be excluded, however, that the strength of early visual cortex responding is of crucial importance to the processes providing the contents of phenomenal experience. New, ingenious paradigms and behavioral markers are needed to clarify this relationship in future studies.

References

Abdi, H. (2007). Signal detection theory. In N. Salkind (Ed.), *Encyclopedia of Measurement and Statistics.* Thousand Oaks, CA: Sage.

Albrecht, T., Klapötke, S., & Mattler, U. (2010). Individual differences in metacontrast masking are enhanced by perceptual learning. *Consciousness and Cognition, 19*, 656-666.

Alpern, M. (1953). Metacontrast. *Journal of the Optical Society of America, 43*, 648-657.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 67*, 303-321.

Aru, J., Bachmann, T., Singer, W., & Melloni, L. (2012). Distilling the neural correlates of consciousness. *Neuroscience and Biobehavioral Reviews, 36*, 737-746.

Bachmann, T. (2009). Using ERP-signatures of target awareness: Puzzle persists because of experimental co-variation of the objective and subjective variables. *Consciousness and Cognition, 18*, 804-808.

Bachmann, T. (2010). Individual differences in metacontrast: An impetus for clearly specified new research objectives in studying masking and perceptual awareness? *Consciousness and Cognition, 19*, 667-671.

Block, N. (2005). Two neural correlates of consciousness. *Trends in Cognitive Sciences, 9*, 46-52.

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behavioral and brain Sciences, 30*, 481-548.

Boehler, C. N., Schoenfeld, M. A., Heinze, H.-J., & Hopf, J.-M. (2008). Rapid recurrent processing gates awareness in primary visual cortex. *Proceedings of the National Academy of Sciences U.S.A., 105*, 8742-8747.

Clark, V. P., Fan, S., & Hillyard, S. A. (1995). Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Human Brain Mapping, 2*, 170-187.

Clark, V. P., & Hillyard, S. A. (1996). Spatial selective attention affects early extrastriate but not striate components of the visual evoked potential. *Journal of Cognitive Neuroscience, 8*, 387-402.

Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience, 6*, 119-1

De Graaf, T. A., Hsieh, P.-J., Sack, A. T. (2012). The “correlates” in neural correlates of consciousness. *Neuroscience and Biobehavioral Reviews, 36*, 191-197.

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*, 204-211.

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *Public Library of Science: Biology, 5*, 2408-2423.

Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*, 489-499.

Enns, J. T., & Di Lollo, V. (1997). Object substitution: A new form of visual masking in unattended visual locations. *Psychological Science, 8*, 135-139.

Enns, J. T., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Neuroscience, 4*, 345-352.

Hautus, M. J. (1995). Corrections for extreme proportions and their biasing effects on estimated values of *d'*. *Behavior Research Methods, Instruments, & Computers, 27*, 46-51.

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences U.S.A., 95*, 781-787.

Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: electro-physiological and neuroimaging evidence. *Philosophical Transactions of the Royal Academy of London, 353*, pp. 1257-1270.

Jeffreys, D. A., & Axford, J. G. (1972). Source locations of pattern-specific components of human visual evoked potentials. I. Components of striate cortical origin. *Experimental Brain Research, 16*, 1-21.

Kanwisher, N., & Wojciulik, E. (2000). Visual attention: Insights form brain imaging. *Nature Reviews Neuroscience, 1*, 91-100.

Karns, C. M., & Knight, R. T. (2009). Intermodal auditory, visual, and tactile attention modulates early stages of neural processing. *Journal of Cognitive Neuroscience, 21,* 669-683.

Kelly, S. P., Gomez-Ramirez, M., & Foxe, J. J. (2008). Spatial attention modulates initial afferent activity in human primary visual cortex. *Cerebral Cortex*, *18*, 2629-2636.

Khoe, W., Mitchell, J. F., Reynolds, J. H., & Hillyard, S. A. (2005). Exogenous attentional selection of transparent superimposed surfaces modulates early event-related potentials. *Vision Research, 45*, 3004-3014.

Kiesel, A., Kunde, W., & Hoffmann, J. (2007). Mechanisms of subliminal response priming. *Advances in Cognitive Psychology, 3*, 307-315.

Koivisto, M., Kainulainen, P., & Revonsuo, A. (2009). The relationship between awareness and attention: Evidence from ERP responses. *Neuropsychologia, 47*, 2891-2899.

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*, 91-103.

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. *Neuroscience and Biobehavioral Reviews, 34*, 922-934.

Koivisto, M., Revonsuo, A., & Lehtonen, M. (2006). Independence of visual awareness from the scope of attention: An electrophysiological study. *Cerebral Cortex, 16*, 415-424.

Koivisto, M., Revonsuo, A., & Salminen, N. (2005). Independence of visual awareness from attention at early processing stages. *NeuroReport, 16*, 817-821.

Lachter, J., Durgin, F., & Washington, T. (2000). Disappearing percepts: Evidence for retention failure in metacontrast masking. *Visual Cognition, 7*, 269-279.

Lamme, V. A. F. (2003), Why visual attention and awareness are different. *Trends in Cognitive Sciences, 7*, 12-18.

Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences, 10*, 494-501.

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience, 1,* 204-220.

Lau, H. C. (2011). Theoretical motivations for investigating the neural correlates of consciousness. *WIREs Cognitive Science, 2*, 1-7.

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 U.S.A., 103*, 18763-18768.

Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.

Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences, 4*, 432-440.

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

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus alpha phase predicts visual awareness. *The Journal of Neurosciene, 29*, 2725-2732.

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*, 700-708.

Pins, D., & ffytche, D. (2003). The neural correlates of conscious vision. *Cerebral Cortex, 13*, 461-474.

Poghosyan, V., & Ioannides, A. A. (2008). Attention modulates earliest responses in the primary auditory and visual cortices. *Neuron, 58*, 802-813.

Proverbio, A. M., Del Zotto, M., & Zani, A. (2007). Inter-individual differences in the polarity of early visual responses and attention effects. *Neuroscience Letters, 419*, 131-136.

Proverbio, A. M., Del Zotto, M., & Zani, A. (2010). Electrical neuroimaging evidence that spatial frequency-based selective attention affects V1 activity as early as 40-60 ms in humans. *BMC Neuroscience, 11*, 1-13.

Railo, H., & Koivisto, M. (2009). The electrophysiological correlates of stimulus visibility and metacontrast masking. *Consciousness and Cognition, 18*, 794-803.

Railo, H., Koivisto, M., & Revonsuo, A. (2011). Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness. *Consciousness and Cognition, 20*, 972-983.

Rauss, K. S., Pourtois, G., Vuillemier, P., & Schwartz, S. (2009). Attentional load modifies early activity in human primary visual cortex. *Human Brain Mapping, 30*, 1723-1733.

Schwiedrzik, C. M., Singer, W., & Melloni, L. (2011). Subjective and objective learning effects dissociate in space and time. *Proceedings of the National Academy of Sciences U.S.A., 108*, 4506-4511.

Sergent, C., & Dehaene, S. (2004). Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychological Science, 15*, 720-728.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied, 74*, 1-29.

Tata, M. S. (2002). Attend to it now or lose it forever: Selective attention, metacontrast masking, and object substitution. *Perception & Psychophysics, 64*, 1028-1038.

Van Aalderen-Smeets, S. I., Oostenveld, R., & Schwarzbach, J. (2006). Investigating neurophysiological correlates of metacontrast masking with magnetoencephalography. *Advances in Cognitive Psychology, 2*, 21-35.

Van Boxtel, J. A., Tsuchiya, N., & Koch, C. (2010). Consciousness and attention: On sufficiency and necessity. *Frontiers in Psychology, 1*, 1-13.

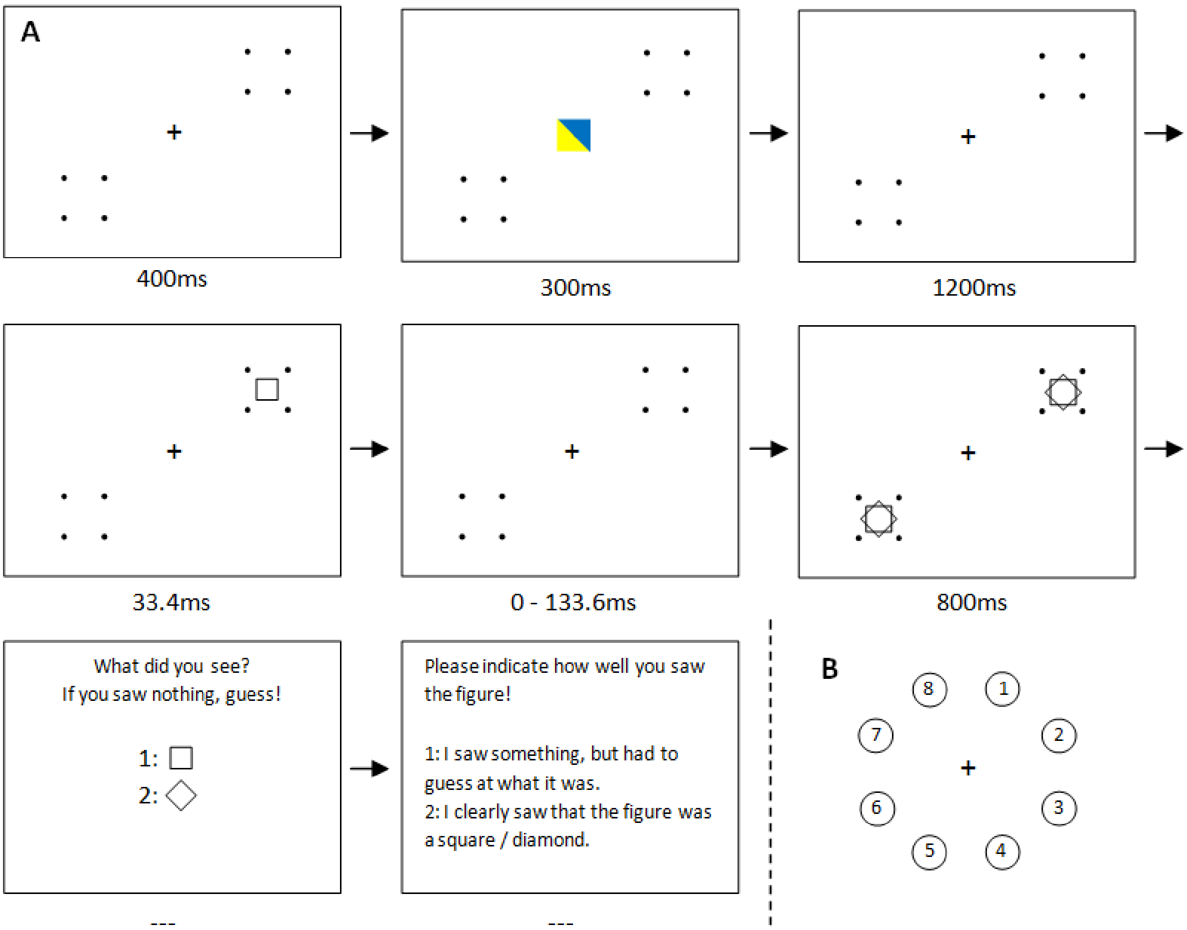
Verleger, R. (2010). Markers of awareness? EEG potentials evoked by faint and masked events, with special reference to the “attentional blink”. In I. Czigler & I. Winkler (Eds.), *Unconscious memory representations in perception: Processes and mechanisms in the brain* (pp. 37 – 70). Amsterdam, Netherlands: John Benjamins B.V.

Weiskrantz, L. (2007). Blindsight. *Scholarpedia, 2*, 3047, revision #91068.

Wyart, V., Dehaene, S., & Tallon-Baudry, C. (2012). Early dissociation between neural signatures of endogeneous spatial attention and perceptual awareness during visual masking. *Frontiers in Human Neuroscience, 6*, 1-14.

Zeki, S. (2003). The disunity of consciousness. *Trends in Cognitive Sciences, 8*, 214-218.

Figure 1. A) Exemplary screenflow for an experimental trial: After 400 ms from trial onset an imperative cue is presented centrally for about 300 ms. 1200 ms from cue offset, a target appears at the cued (70%) or the uncued (30%) location for the duration of two frames (33.4 ms). After a variable delay of 0 to 133.6 ms, a metacontrast mask is presented at both locations for 800 ms. Two questions have to be answered without time constraint before the program proceeds to the next trial. B) Exemplary map of stimulus positioning (adapted from Kelly et al., 2008).



What did you see?
If you saw nothing, guess!

1: □
2: ◇

Please indicate how well you saw the figure!

1: I saw something, but had to guess at what it was.
2: I clearly saw that the figure was a square / diamond.

Figure 2. Grand average waveforms from occipito-central electrode Oz showing the characteristic polarity reversal of component C1 for stimuli in the upper versus lower hemifield. Upper hemifield stimuli produced a positive-going C1 that overlapped the ascending phase of P1. Lower hemifield stimuli produced a component of opposite direction with slightly positive amplitudes. Differences between “clearly seen” and “guessed” amplitudes are insignificant. Scalp topography maps are shown with a range of +/- 1 µV.

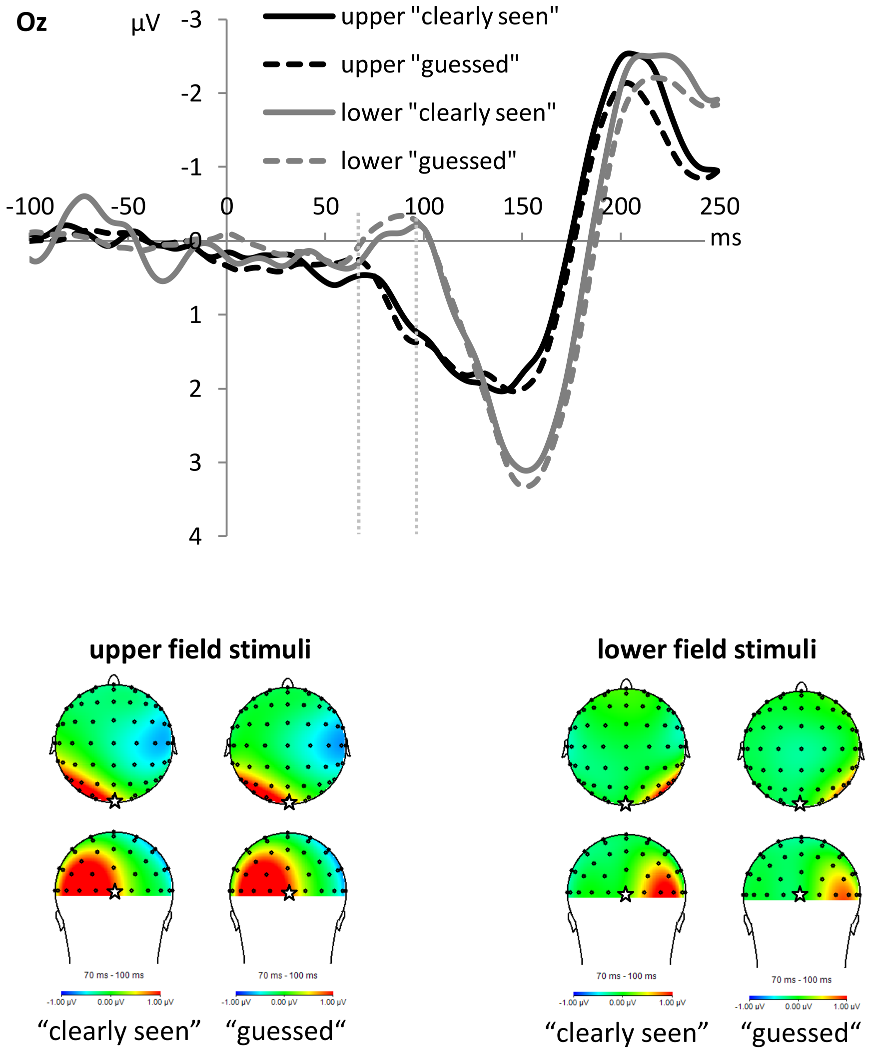


Figure 3. Grand average waveforms and scalp topographies for stimuli presented in the left and right visual hemifield. Data are obtained from the respective contralateral electrode PO7 or PO8. The vertical dashed lines indicate the time-window for P1 analysis. Differences between “clearly seen” and “guessed” amplitudes are not significant.

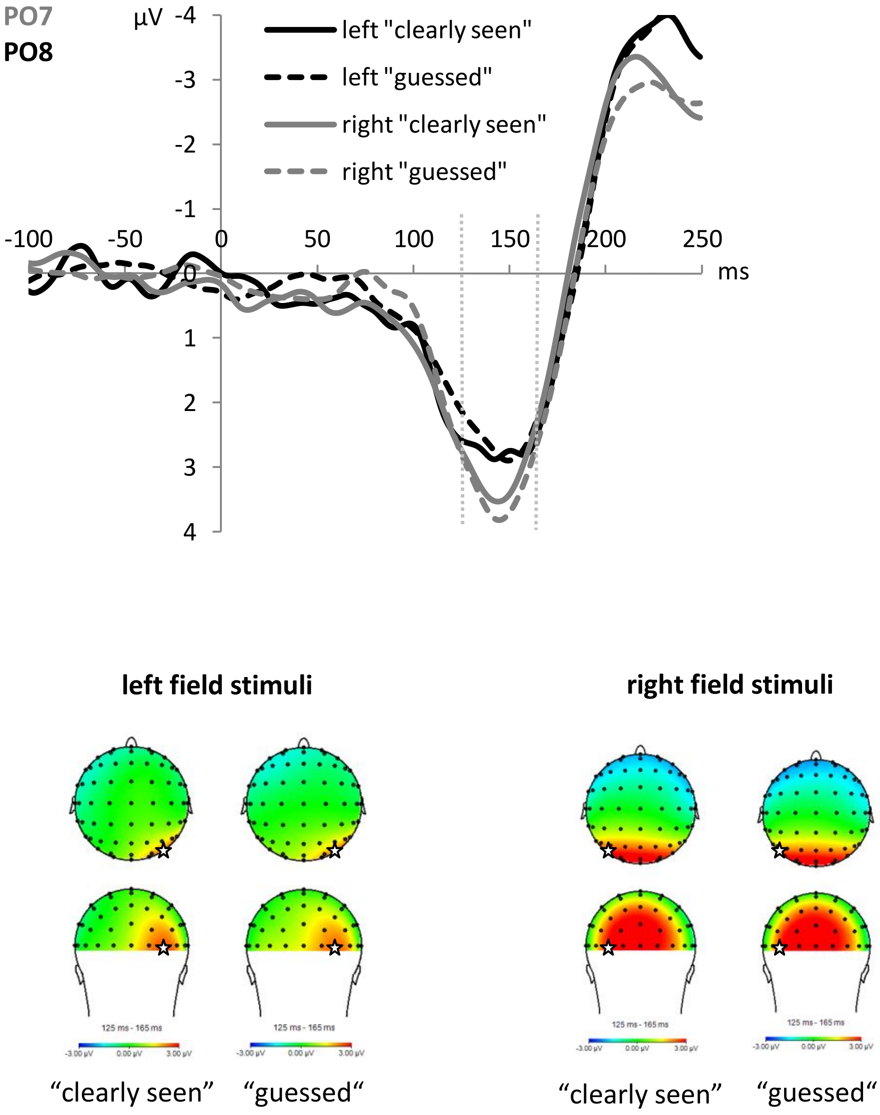


Figure 4. Distribution of trials across SOAs per subject. Error bars indicate the standard error of the mean.

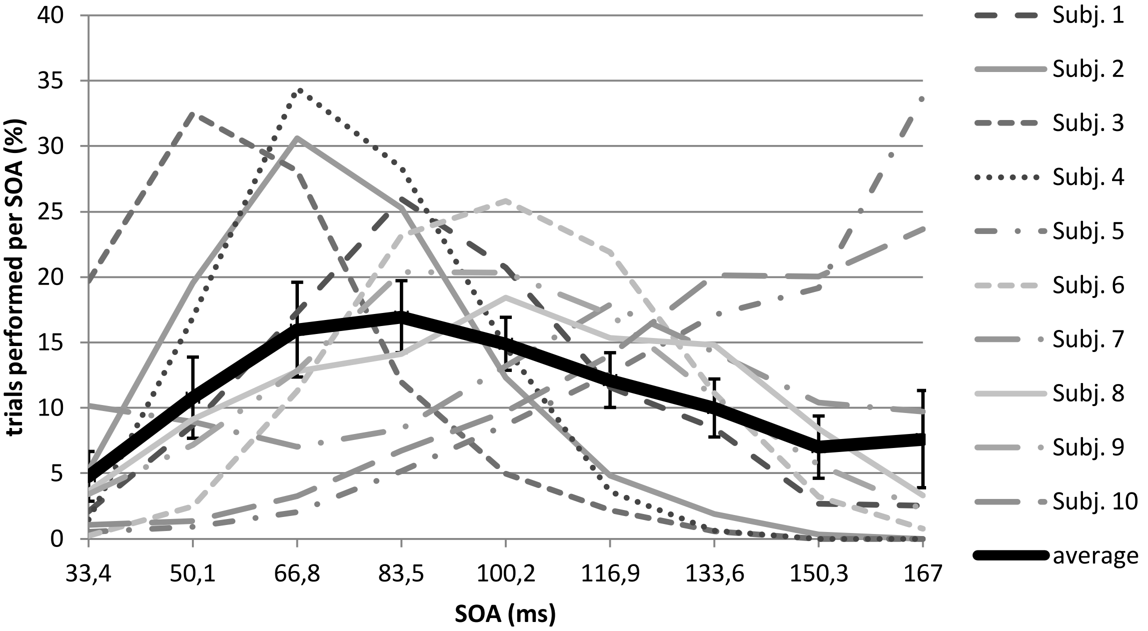


Figure 5. Average fraction of targets rated to be "clearly seen" per SOA and level of cue-validity. Error bars indicate the standard error of the mean.

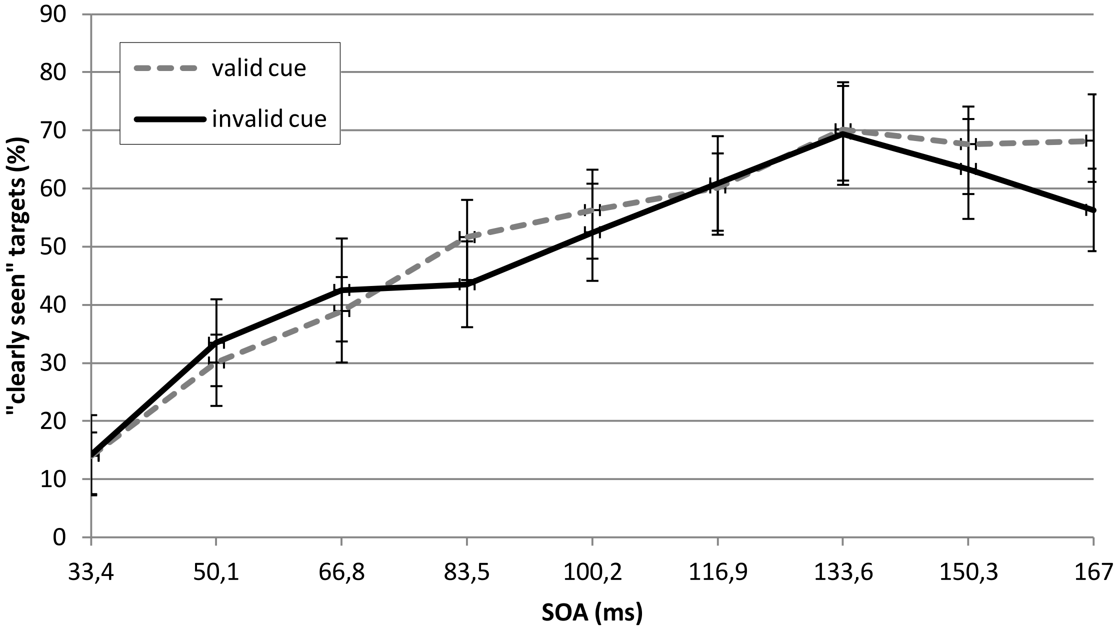


Figure 6. Average shape discrimination performance (*d'*) per SOA dependent on cue-validity. Error bars indicate the standard error of the mean. Note, that *d'* here does not indicate detection sensitivity, but is an estimator of discrimination performance that can be assumed to be free of response preference bias.