Consciousness and Cognition 20 (2011) 972–983

Contents lists available at ScienceDirect

Consciousness and Cognition

journal homepage: www.elsevier.com/locate/concog

Review

# Tracking the processes behind conscious perception: A review of event-related potential correlates of visual consciousness

Henry Railo [a,b,*], Mika Koivisto [a,b], Antti Revonsuo [a,b,c]

[a] Department of Psychology, University of Turku, 20014 Turku, Finland
[b] Centre for Cognitive Neuroscience, University of Turku, Turku, Finland
[c] School of Humanities and Informatics, University of Skövde, Skövde, Sweden

A R T I C L E  I N F O

*Article history:*
Received 8 March 2010
Available online 8 April 2011

*Keywords:*
ERP
Visual
Consciousness
Awareness
Attention

A B S T R A C T

Event-related potential (ERP) studies have attempted to discover the processes that underlie conscious visual perception by contrasting ERPs produced by stimuli that are consciously perceived with those that are not. Variability of the proposed ERP correlates of consciousness is considerable: the earliest proposed ERP correlate of consciousness (P1) coincides with sensory processes and the last one (P3) marks postperceptual processes. A negative difference wave called visual awareness negativity (VAN), typically observed around 200 ms after stimulus onset in occipitotemporal sites, gains strong support for reflecting the processes that correlate with, and possibly enable, aware visual perception. Research suggests that the early parts of conscious processing can proceed independently of top-down attention, although top-down attention may modulate visual processing even before consciousness. Evidence implies that the contents of consciousness are provided by interactions in the ventral stream, but indispensable contributions from dorsal regions influence already low-level visual responses.

## 1. Introduction

Cognitive neuroscience highlights that visual processing is distributed to a hierarchy of areas in which the analysis of visual information proceeds both serially and in parallel (Felleman & Van Essen, 1991). Yet, although we now understand the cognitive and neural mechanisms of visual perception better than ever before, the most fundamental question of visual processing remains elusive: when does incoming visual information enter consciousness, that is, result in subjective experience of seeing? The visual system can analyze a visual scene extremely rapidly, in under 150 ms (Thorpe, Fize, & Marlot, 1996), but does conscious perception develop and emerge together with these visual analyses, or does the construction of visual consciousness require additional processes? The event-related potential (ERP) technique provides an excellent tool to examine this question. ERPs reflect with a millisecond resolution the temporal evolution of the brain's average electrical response to specific sensory events such as a stimulus appearing in the visual field (Luck, 2005). A typical visual ERP waveform, shown in Fig. 1, consists of predictable peaks that are labeled according to their polarity and timing. For example, the first positive amplitude ERP wave is referred to as the P1 component. By comparing ERPs associated with unconscious vs. conscious visual perception, the aim of ERP studies of visual consciousness is to track the timing and scalp topography of the neuroelectrical processes that specifically correlate with, and perhaps enable, the construction of subjective visual experience.

Consciousness can be studied as a global state that characterizes the subject (unconscious state as under anaesthesia vs. conscious state as in wakefulness) or as a feature that describes whether specific information is consciously experienced by

---

[*] Corresponding author at: Department of Psychology, University of Turku, 20014 Turku, Finland. Fax: +358 2 333 6270.
*E-mail address:* henry.railo@utu.fi (H. Railo).

1053-8100/$ - see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.concog.2011.03.019

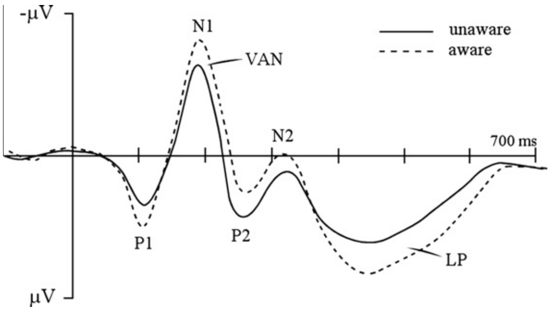

**Fig. 1.** An example of a typical ERP waveform and the three proposed correlates of consciousness. The dashed line represents the ERP produced by stimuli that were consciously perceived, and the solid line the ERP produced by stimuli that were not consciously perceived. The first positive ERP component (P1) is the earliest reported correlate of consciousness. VAN (visual awareness negativity) is a negative amplitude difference that is typically observed around 200 ms, and LP (late positivity) a later positive amplitude difference.

the subject. Interactions between sub-cortical and cortical structures are believed to constitute a vital part of the neural correlate of a general conscious state. More specifically, the modulation of frontoparietal cortical network via brainstem and thalamic nuclei has been identified as crucial for consciousness as a state (e.g. Cavanna & Monaco, 2009; Llinás, Ribary, Contreras, & Pedroarena, 1998; Parvizi & Damasio, 2001). When a subject is in a conscious state, information—say a visual stimulus—can be processed so that it enters consciousness and is experienced by the subject as a specific content of consciousness. This review focuses on the ERP correlates of the contents of visual consciousness.

In the study of the neural correlates of consciousness, stimulus visibility must somehow be manipulated to produce conditions that differ with respect to conscious perception. In visual masking a target stimulus is under certain conditions rendered unconscious by another visual stimulus (the mask), usually presented after the target stimulus. Conscious processing can also be compromised by manipulating attention (e.g. change blindness or attentional blink paradigms). A potential problem for some manipulations of consciousness is that the two experimental conditions are not physically identical. Thus, differences in the ERPs might portray this physical difference, not the difference in the processes that construct subjective stimulus visibility. This problem can be handled with control conditions but another possibility is to use methods with invariant conditions: Masked or low-contrast stimuli that are presented at the threshold of consciousness are only detected consciously on about half of the trials, ambiguous figures can be seen in different mutually exclusive ways (e.g. Rubin's vase), and in binocular rivalry a different stimulus is presented to each eye, producing an alternating conscious percept. Note that although many ERP studies have compared a condition where a stimulus was consciously perceived with a condition where the stimulus was not consciously seen (although presented), some studies have compared two different perceptual experiences in visual consciousness while keeping stimulation constant (e.g. studies utilizing ambiguous figures). It is important to recognize that different methods may emphasize different aspects of visual processing and thus produce different ERPs and perhaps different correlates of consciousness. Arguably the best approach is to employ various methods, each providing a somewhat different perspective to the same problem.

Fig. 1 depicts the three potential ERP signatures of visual consciousness that have emerged repeatedly in different studies. The first ERP component that has been reported to correlate with conscious visual perception is the P1, typically observed right after 100 ms from stimulus onset. Conscious perception has been shown to correlate with enhanced, that is, more positive P1 amplitudes when compared to conditions where the same stimulus is not consciously perceived (e.g. Pins & ffytche, 2003; Roeber, Trujillo-Barreto, Hermann, O'Shea, & Schröger, 2008). Secondly, the results of other studies suggest that a negative amplitude difference around 200 ms after stimulus onset (visual awareness negativity, VAN) is the primary correlate of visual consciousness (e.g. Kaernbach, Schöger, Jacobsen, & Roeber, 1999; Koivisto & Revonsuo, 2008a). Finally, the third ERP amplitude difference that has been associated with visual consciousness is the late positivity (LP), sometimes labeled as P3, and often observed after 300 ms or later (e.g. Babiloni, Vecchio, Miriello, Romani, & Rossini, 2006; Del Cul, Baillet, & Dehaene, 2007).

The ERP waves that have been suggested to correlate with conscious perception differ from each other not only in their timing, but also in their magnitude, polarity, and scalp topography, demonstrating that they are based on anatomically and functionally different sources in the brain. The ERP waves and the underlying brain processes that have been suggested to be correlates of visual consciousness are thus very different from each other. Whereas some of the models see visual consciousness arising rapidly as a consequence of localized sensory processes in the visual system, others consider consciousness as a later phase of integrative, "postperceptual" processing. Thus, which one of these waveforms is identified as the correlate of visual consciousness has important consequences for theories of the neural correlates of consciousness in general, and for models of the neural basis of visual consciousness in particular. The disagreements concerning the ERP correlates of visual consciousness also signify differences in the background assumptions and definitions of consciousness.

Two senses of the term 'consciousness' (or awareness) are often differentiated from each other: phenomenal consciousness and reflective/access consciousness (Block, 2007; Lamme, 2004; Revonsuo, 2006). Other similar distinctions have also been made (Damasio, 1998; Edelman, 1989; Farthing, 1992). *Phenomenal consciousness* refers to immediate, fleeting, nonverbal subjective experiences. The contents of phenomenal consciousness, it is often proposed, can vary in clarity. The contents you focus on are the clearest, whereas other sensations might be vaguer, at the fringe of consciousness (James, 1890). The contents of phenomenal consciousness that are chosen to further perusal by selective attention become part of *reflective consciousness*, which is a higher-order form of consciousness and portrays the ability to reflect and manipulate the contents of phenomenal consciousness, and access a range of cognitive output systems. The conceptual and functional distinction between phenomenal and reflective consciousness implies that they may also have distinct neural correlates that can be dissociated from each other and investigated separately, for example, using ERPs. As later discussed, other views would not separate phenomenal and reflective consciousness, but assert that all conscious contents reach the cognitive output stage (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006).

Next, we briefly discuss some of the current models and hypotheses concerning the neural correlates of visual consciousness. We then review findings concerning each of the three major ERP deflections that have been observed to correlate with visual consciousness, and discuss the conclusions implied by the evidence.

## 2. Current hypotheses of the neural basis of visual consciousness

The majority of visual signals reach the cortex via the lateral geniculate nucleus of thalamus, although other pathways also exist. In the cortex, visual information is projected to dorsal and ventral visual areas, which, although not being completely separate and independent of each other, mediate different visual functions (Milner & Goodale, 2006). The dorsal visual stream converges on parietal areas and can perhaps be best characterized as supporting visuomotor functions and egocentric spatial coding. The ventral visual stream projects to the temporal cortical areas which code allocentric spatial relations, and enable visual functions such as object recognition.

A substantial amount of evidence implies that activity along the ventral visual stream is closely associated with and necessary for visual consciousness (Logothetis, 1998; Milner & Goodale, 2006; Sheinberg & Logothetis, 1997; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Vanni, Revonsuo, Saarinen, & Hari, 1996). According to Lamme's (2004, 2010) model, phenomenal visual awareness is generated in the ventral visual stream by local recurrent interactions between higher and lower ventral visual areas. The initial sensory-driven volley of activity spreading towards higher visual areas (i.e. feedforward activity) is unconscious (Lamme, 2010; Lamme & Roelfsema, 2000). Reflective consciousness emerges as the local recurrent interactions spread out further, connecting frontal and parietal areas with the sensory cortices (Lamme, 2010). Data supporting the role of feedback activity in visual awareness has come especially from studies showing that neural activity occurring after feedforward signals correlates with subjective perception of the stimulus (e.g. Supèr, Spekreijse, & Lamme, 2001). Transcranial magnetic stimulation (TMS) studies have shown that early visual areas contribute to visual perception both before and after the contributions of higher visual areas (e.g. Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011; Silvanto, Lavie, & Walsh, 2005). Other researchers have argued that momentary feedforward bursts of activity correlate with conscious perception—recurrent interactions only serve a modulatory purpose (Macknik & Martinez-Conde, 2007). Both views, however, share the idea that the correlates of visual consciousness reside primarily within the visual cortex (see also Zeki (2003), for a similar view).

Although few would question the claim that ventral cortical areas are essential for visual consciousness, it is typically recognized that activity in specific visual areas, although correlating with awareness, is not itself sufficient for aware perception (e.g. Dehaene et al., 2001; Moutoussis & Zeki, 2002, 2006). The role of primary visual cortex (V1) is more controversial. In neurologically healthy humans V1 is a crucial part of the visual system, and damage to it usually leads to evident deficits in visual consciousness (Lamme, Supèr, Landman, Roelfsema, & Spekreijse, 2000; Silvanto, Cowey, Lavie, & Walsh, 2005; Tong, 2003). Yet, subtle conscious visual contents may be present even if V1 is damaged, implying that V1 is not necessary for subjective visual experiences (ffytche & Zeki, 2011, see also Tse, Martinez-Conde, Schlegel, & Macknik, 2005). The role of extrasensory areas is another controversial issue. The results of various studies suggest that visual awareness is accompanied, not only by activity in the visual system, but also by activity in the prefrontal, anterior cingulate, and parietal regions (Beck, Rees, Frith, & Lavie, 2001; Genetti, Khateb, Heinzer, Michel, & Pegna, 2009; Haynes, Driver, & Rees, 2005; Kouider, Dehaene, Jobert, & Le Bihan, 2007). Indeed, some theories propose that consciousness emerges as a result of synchronous activity over distributed cortical areas (Crick & Koch, 1990; Dehaene et al., 2006; Edelman, Gally, & Baars, 2011; Engel & Singer, 2001). Others emphasize the role of synchronous activity between the cortex and thalamus in generating conscious perception (Llinás et al., 1998).

A hallmark of the models that highlight the importance of global, widespread neural activity as necessary for consciousness is that they focus on the functional and cognitive aspects of consciousness, especially the availability of conscious information to output systems and verbal reporting. According to the "global neuronal workspace model", harmonious global interaction of separate individual processors is the signature trait of the conscious brain (Dehaene & Naccache, 2001; Dehaene et al., 2006; see Baars (1997) or (2002) for a similar cognitive model). Information in the visual cortex, for example, only reaches consciousness after it has been selected into the widespread neuronal network that enables it to influence cognitive and motor systems. The model also stresses the importance of top-down attention for consciousness: attention is seen as a necessary (but not sufficient) prerequisite for conscious perception (Dehaene & Naccache, 2001; Dehaene et al., 2006). This is in line with numerous findings showing the importance of attention for visual consciousness (e.g. Mack & Rock, 1998; Merikle & Joordens, 1997). Others, however, have attempted to differentiate attention from consciousness (e.g. Fernandez-Duque, Grossi, Thornton, & Neville, 2003; Koivisto & Revonsuo, 2008a; Lamme, 2003), proposing that even if attention is tightly linked with consciousness, some features of consciousness might still prove to be independent of attention. It is now becoming evident that voluntary top-down attention is neither sufficient nor necessary for visual consciousness (van Boxtel, Tsuchiya, & Koch, 2010). Still, as discussed below, the relationship between attention and consciousness is one of the central puzzles in the search for the neural events that correlate with conscious perception. A point that is often overlooked in discussions of the relationship between attention and consciousness is that attention is a broad concept which can be divided into separate processes, such as alertness, spatial attention, and feature-based attention. Attention can also be directed voluntarily (top-down), or it can be stimulus-driven (bottom-up). Hence, there is no simple answer to the relationship between attention and consciousness. There are different types of attention and different types of consciousness, and they do not all relate to each other in the same way.

To summarize, current models of awareness disagree substantially on whether activity in the visual cortical areas suffices to generate visual consciousness, or whether widespread cortical activity is necessary for consciousness. As the latter view stresses the importance of large-scale neural interactions, it has associated consciousness with a late, centrally and parietally localized ERP deflection (P3/LP; e.g. Del Cul et al., 2007; Sergent, Baillet, & Dehaene, 2005). By contrast, the opposing view predicts that visual awareness should manifest itself earlier in occipitotemporal electrode sites as visual consciousness is expected to emerge from interactions within the ventral visual cortical areas.

## 3. Early positive correlates of consciousness (P1)

Studies that have used low-contrast stimuli (e.g. Pins & ffytche, 2003), binocular rivalry (e.g. Roeber, Trujillo-Barreto, Hermann, O'Shea, & Schröger, 2008), ambiguous figures (e.g. Kornmeier & Bach, 2005), or metacontrast masking (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009) have observed that enhancement of P1 wave correlates with conscious visual perception. Dipole modeling results suggest that the P1, observed about 100 ms after stimulus onset, originates in extrastriate visual areas (Di Russo, Martínez, & Hillyard, 2003). A component labeled the C1 is considered to mark the earliest cortical stimulus-related signals in striate and extrastriate areas (Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2001; Foxe & Simpson, 2002; Foxe et al., 2008). The C1 emerges about 50 ms and peaks before 100 ms after stimulus onset over parieto-occipital sites. It may be either positive or negative, and can only be observed under specific stimulation conditions (Foxe et al., 2008). Research on humans (Baseler & Sutter, 1997; Boehler, Schoenfeld, Heinze, & Hopf, 2008; Foxe & Simpson, 2002; Vanni, Tanskanen, Seppä, Uutela, & Hari, 2001; Wilson, Babb, Halgren, & Crandall, 1983) and monkeys (Schmolesky et al., 1998; Schroeder, Mehta, & Givre, 1998) suggest that the V1 is activated as quickly as 40–70 ms after stimulus onset. Because local cortical feedback signals have been shown to influence lower-order areas rapidly (Boehler et al., 2008; Hupe et al., 2001), the P1 correlates of consciousness might already reflect the earliest feedback interactions between early visual cortical areas.

Studies that have reported the P1 to correlate with conscious visual perception are faced with a problem of possible interference from attention and arousal as they have manipulated awareness using methods that are vulnerable to attentional confounds. This is usually acknowledged in the studies that have reported the P1 to correlate with consciousness. Pins and ffytche (2003) presented participants with stimuli near the threshold of subjective visibility, and reported that P1 amplitude correlated with the subjective visibility of the stimulus. A closer look at the ERP-waveform shows that no P1 was observed when the participants did not detect the target, suggesting a failure in the attentional selection of the target. Importantly, the P1 is known to be enhanced by spatial attention (Hillyard & Anllo-Vento, 1998), feature-based attention (Zhang & Luck, 2009), and arousal levels (Vogel & Luck, 2000). One subsequent ERP study utilizing perceptually complex low-contrast stimuli reported the P1 to correlate with consciousness (Wilenius & Revonsuo, 2007), but considered it to reflect fluctuations in the level of attention. Another study (Koivisto et al., 2008) failed to replicate the P1 finding reported by Pins and ffytche (2003). Mathewson et al. (2009) presented subjects with a target followed by a metacontrast mask after a constant delay, and observed a more pronounced P1 during the trials when the target was reported as seen, than when the target was reported as not seen. Since visual stimulation was identical in the "seen" and "unseen" conditions, it can be argued that attentional selection determined whether a target was consciously processed or not. Hence, the P1 might correlate with this selection, rather than processes that produce conscious visibility.

As attentional selection has been shown to play a role in determining the dominance in binocular rivalry (Mitchell, Stoner, & Reynolds, 2004), the enhanced P1 observed in studies employing binocular rivalry (Roeber & Schröger, 2004; Roeber, Trujillo-Barreto, Hermann, O'Shea, & Schröger, 2008; Veser, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008) may be due to confounding differences in attentional processing between the aware and unaware conditions. When a stimulus that is outside awareness during binocular rivalry is changed (i.e. percept-compatible change), it might not reach awareness because input from that eye is at that point suppressed. The fact that percept-compatible changes might not elicit a P1 at all (Veser, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008) is consistent with this. Conversely, when a stimulus that is consciously processed during binocular rivalry is changed (i.e. percept-incompatible change), it is the attended stimulus that changes. This is likely to emphasize the processing of the changed stimulus which can be assumed to enhance the P1. The P1 findings observed in studies employing ambiguous figures (Kornmeier & Bach, 2005, 2006; Pitts, Neger, & Davis, 2007) could also be explained by similar differences in attentional selection.

As we discuss later, ERP studies which have manipulated attention in addition to consciousness have been able to show that their effects may be separable, and at least partly independent of each other (e.g. Koivisto & Revonsuo, 2008a). The neural processes underlying P1 are probably not directly involved in the generation of visual consciousness, but they may reflect preconscious processes of attentional selection that affect what enters consciousness. Other processes than attention may also influence early visual responses, thereby modulating P1, and possibly subsequent contents of consciousness. By using a clever paradigm that allowed them to dissociate subjectively perceived contrast from the physical contrast of the stimulus, Haynes, Roth, Stadler, and Heinze (2003) reported that already P1, peaking 80 ms after the stimulus onset, correlated better with the perceived contrast than with the actual physical contrast of the stimulus. The reduction in perceived contrast, produced by orientation-specific surround suppression, might take place at a processing level outside consciousness, and the P1 modulation may be a sign of this preconscious suppression. Because later processing stages (N1) showed even stronger correlation with perceived contrast than P1, the results support the idea that feedback signals shape the contents of consciousness (Haynes et al., 2003).

Marzi et al. recorded ERPs while a patient suffering from visual extinction symptoms (right temporoparietal damage) was performing a visual detection task with targets appearing either unilaterally or bilaterally (Marzi, Girelli, Miniussi, Smania, & Maravita, 2000). The results showed that although the ERPs to accurately identified bilateral and contralesional unilateral targets showed clear P1 and N1 waves, these components were absent during visual extinction (i.e. when a contralesional stimulus was not perceived during bilateral stimulation). Another case-study of a visual extinction patient with inferior posterior parietal damage combined functional magnetic resonance imaging (fMRI) and ERPs, and also reported that extinguished contralesional stimuli evoked a reduced P1 (Vuilleumier et al., 2001). Furthermore, although unperceived visual stimuli could activate early visual areas, consciously seen stimuli activated a wider network of sensory and temporo-occipital areas. These results exemplify that visual extinction is caused by defects in the inferior parietal contributions to visual awareness (Karnath, Himmelbach, & Küker, 2003), and suggest that parietal areas modulate relatively early sensory responses. The contribution of parietal areas to bistable perception is also evident in the results of Britz, Landis, and Michel (2009) who reported that prestimulus activity in the right inferior parietal cortex correlated with perceptual reversal in bistable perception.

We propose that the P1 correlates of consciousness stem from preconscious top-down attentional gain control (Hillyard, Vogel, & Luck, 1998), or related factors (e.g. Haynes et al., 2003; Marzi et al., 2000). The evidence does not support the claim that the P1 would reveal the processes that produce visual awareness. It is well known that attention amplifies the P1, and many of the reported P1 correlates of consciousness have been observed using methods that are sensitive to the influences of attention. Moreover, many studies have not found the P1 to correlate with consciousness (e.g. Koivisto & Revonsuo, 2008a; Lamy, Salti, & Bar-Haim, 2009; Sergent et al., 2005).

## 4. Visual awareness negativity

Numerous studies using a variety of methods for manipulating visual awareness, such as visual masking (Genetti et al., 2009; Koivisto, Kainulainen, & Revonsuo, 2009, 2007, 2008a; Koivisto, Revonsuo, & Lehtonen, 2006; Koivisto, Revonsuo, & Salminen, 2005; Railo & Koivisto, 2009; Vanni et al., 1996), low-contrast stimuli (Ojanen, Revonsuo, & Sams, 2003; Wilenius & Revonsuo, 2007; Wilenius-Emet, Revonsuo, & Ojanen, 2004), change blindness (Busch, Fründ, & Herrmann, 2010; Koivisto & Revonsuo, 2003; Schankin & Wascher, 2007), attentional blink (Koivisto & Revonsuo, 2008b), and binocular rivalry (Kaernbach et al., 1999), have reported that increased negativity around 200 ms poststimulus in the occipitotemporal sites correlates with consciousness. This negative amplitude difference between aware and unaware conditions has been termed visual awareness negativity (VAN), and unlike the P1 effects discussed above, it is not tied to a specific component, but it appears typically in the N1–N2 latency range. Some studies that have reported a P1 effect have also reported VAN (Pins & ffytche, 2003; Wilenius & Revonsuo, 2007), and usually VAN is followed by a positive amplitude enhancement in the P3 latency range (the late positivity, discussed in the next section). Studies which have investigated the ERP correlates of perceptual reversals of ambiguous figures have repeatedly reported a negative amplitude difference (reversal negativity, RN) that resembles VAN (e.g. Kornmeier & Bach, 2005; Pitts et al., 2007). However, a recent study suggested that RN does not consistently correlate with consciousness (Intaitė, Koivisto, Rukšėnas, & Revonsuo, 2010), and hence it is not yet clear whether or not RN is related to consciousness or to some other more specific perceptual function.

As the enhanced negativity around 200 ms in the occipitotemporal sites is similar to selection negativity (SN), a well known correlate of non-spatial attentional selection (Hillyard & Anllo-Vento, 1998), the possibility that VAN would simply reflect the same attentional mechanisms as SN has been examined. In a study by Koivisto and Revonsuo (2008a) participants attended to different combinations of spatial frequency and orientation. The participants' awareness of the stimulus was manipulated by presenting a mask after a short (unconscious) or a long (conscious perception of stimulus) stimulus onset asynchrony. The results, shown in Fig. 2, indicated that while the ERPs elicited by consciously seen and unseen stimuli started to differ after 100 ms (VAN), the effects of attention emerged after 200 ms (SN). Thus, at least the early part of VAN (100–200 ms) showed independence of non-spatial attention. Other studies that have manipulated non-spatial attention and awareness have yielded similar results (Koivisto & Revonsuo, 2005, 2007; Koivisto et al., 2005, 2006, 2009). Importantly, VAN has been observed during passive viewing (Koivisto & Revonsuo, 2008a) or in response to nontargets that required no motor responses (Koivisto et al., 2005), also suggesting independence from attentional factors.

Although the results reviewed above show that VAN emerges independently of attention to stimulus features, VAN might nevertheless show dependence of spatial attention as it is well known that stimuli presented to unattended spatial locations are often not consciously perceived (e.g. Mack & Rock, 1998; Shapiro, Arnell, & Raymond, 1997; Simons & Levin, 1997). To investigate this, Koivisto et al. (2009) presented a letter stimulus simultaneously to two spatial locations, but participants were asked only to attend to one of these locations and to respond whenever a pre-specified letter was presented in this location. Because the participants were not required to respond to any stimulus presented at the unattended location, they were safe to completely ignore the stimuli presented to this location. Visual awareness of the stimuli was manipulated using masking. The results showed that VAN only emerged to stimuli presented to the attended location, suggesting that spatial attention is a prerequisite of conscious perception. As in previous studies, attention to target features (letter identity) modified later ERP responses (SN) independently of visual awareness (VAN). These results disagree with the findings of an earlier study (Koivisto & Revonsuo, 2007) in which unmasked stimuli presented to the unattended location produced VAN, when compared with masked stimuli. However, as this study (Koivisto & Revonsuo, 2007) employed single target stimuli, attention was probably reflexively captured by the presented stimulus, whether or not it appeared in the attended or unattended location. The results of Chica, Lasaponara, Lupiáñez, Doricchi, and Bartolomeo (2010) also suggest that successful selection by spatial attention, measured by P1 amplitude modulation, is crucial for conscious perception.

Based on the estimated latency of re-entrant cortical activity (e.g. Di Russo et al., 2001; Lamme & Roelfsema, 2000), it has been proposed that recurrent interactions within the visual system might underlie VAN (Koivisto et al., 2006; Wilenius & Revonsuo, 2007; see also Fahrenfort, Scholte, & Lamme, 2007). However, there is considerable variability in the latency of VAN in different stimulation conditions. At earliest, VAN has been observed to begin soon after 100 ms (the P1 time-window; e.g. Koivisto & Revonsuo, 2008a; Koivisto et al., 2005, 2009), but some studies using low-contrast or otherwise challenging stimuli have reported VAN to emerge relatively late, at 300–400 ms (Ojanen et al., 2003; Railo & Koivisto, 2009; Wilenius & Revonsuo, 2007). Two of the studies that have reported a delayed VAN (Ojanen et al., 2003: VAN "peaked" at ~460 ms; Wilenius & Revonsuo, 2007: VAN "peaked" at ~400 ms) presented the subjects with low-contrast stimuli, and hypothesized that prolonged recurrent processing was needed to resolve the low-contrast stimuli. Although the proposition is plausible, Pins and ffytche (2003), who also used low-contrast stimuli, reported negativity around 250 ms after stimulus onset (in addition to a P1 correlate). As shown in Fig. 3, Railo and Koivisto (2009) compared ERPs elicited by metacontrast masked stimuli with stimuli masked, or "pseudomasked", to a lesser extent, and observed a delayed VAN (onset after 300 ms). As the metacontrast masked stimuli (reduced subjective visibility) were compared with stimuli whose visibility was reduced to a lesser degree (pseudomasked), and not with perfectly visible stimuli, it was proposed that the finding reflected the latter, more attention dependent part of VAN. In other words, considerable attentional processing was needed to resolve the pseudomasked target.

The variability and span of VAN latencies, as well as the selective influences of feature-based attention on the later parts of VAN, suggest that VAN does not reflect a single time-locked process, but a set of different processes associated with conscious perception. In the same way, initially processed visual features are typically thought to be bound and enhanced by attention in later processing stages to form coherent and detailed conscious percepts (Carrasco, Ling, & Read, 2004; Treisman, 1996; Treisman & Gelade, 1980; Wolfe, 1999). A recent change blindness ERP experiment by Busch and colleagues (2010) sheds light on these interactions between attention and awareness. Busch et al. showed that when participants detected or sensed a change in a visual display without identifying what changed, a negative difference similar to VAN was observed. It can be argued that this detecting and sensing, which was coupled with VAN, shows that the participants were

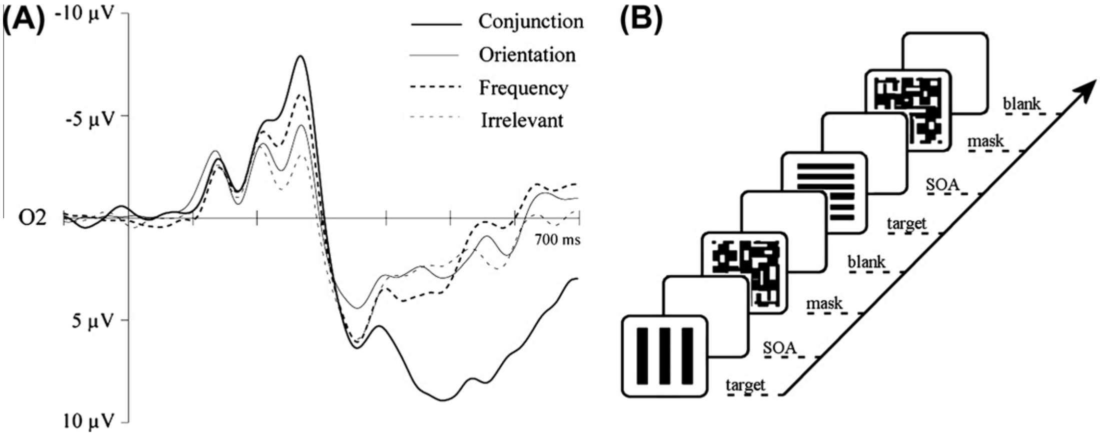

**Fig. 2.** (A) Difference waves (aware – unaware condition) in different attention conditions. (B) Example of the stimulus sequence. Awareness was manipulated by masking (long vs. short stimulus onset asynchrony, SOA). The target stimuli were horizontal or vertical square-wave gratings that had either a high or low spatial frequency. The participants were asked to attend and respond to a specified *conjunction* of spatial frequency and orientation (e.g. high spatial frequency and vertical orientation). In each trial the target's orientation and frequency, spatial frequency, orientation, or neither of them corresponded with the attended features. The correspondence of the presented stimulus to the attended features is indicated by line type (e.g. orientation: the orientation, but not the spatial frequency corresponded with the attended features). The ERPs to consciously perceived stimuli start to differ from unperceived stimuli after 100 ms (VAN: more *negative* P1 amplitudes), but the different attention conditions start to differ only after 200 ms (selection negativity). VAN is followed by late positivity (LP). Adapted from Koivisto and Revonsuo (2008a).

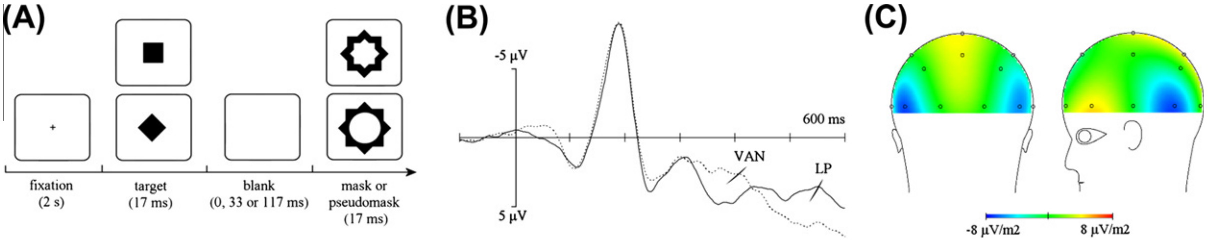

**Fig. 3.** (A) A schematic presentation of the stimulus sequence. A target was presented for 17 ms and followed by either a metacontrast mask (above) or a pseudomask (below) after a variable delay. The metacontrast mask greatly reduced the visibility of the target when the stimuli were separated by a 33 ms blank screen, whereas the pseudomask suppressed target visibility only weakly in the same condition. (B) ERPs to metacontrast masked (solid line) or pseudomasked (dashed line) targets in the 33 ms blank condition. The data is from temporal electrodes T5 and T6 pooled together. The difference between consciously perceived (pseudomasked) and unperceived (masked) targets is first reflected as negative amplitude difference (VAN), which is followed by the late positivity (LP). Note that both VAN and LP are somewhat delayed. (C) The scalp distribution of VAN shows that it localizes to the temporal electrode sites. Adapted from Railo and Koivisto (2009).

faintly phenomenally conscious of the change. Identified (not just detected) changes elicited a larger VAN and also an N2pc (a posterior negativity contralateral to the target in N2 time-range), which is usually taken as evidence for a shift in the locus of attention (Eimer, 1996; Hopf et al., 2006). Busch et al. (2010) proposed that when the participants sensed a change without identifying it, the change engaged feature-selective attentional processes, but only unbound visual features were perceived and thus the object could not be identified. The change could be identified only when the attentional locus was focused on the relevant location (N2pc), enabling visual features to be bound to form coherent object representations. Thus, successful attentional selection enhanced the visibility of the object which was also reflected as enhanced VAN.

## 5. Late positivity

The third deflection that has been associated with consciousness is the late positivity (LP), localizing predominantly to the parietal and central electrode sites, and typically beginning between 300 and 400 ms after stimulus presentation (Del Cul et al., 2007; Koivisto & Revonsuo, 2008a; Turatto, Angrilli, Mazza, Umilta, & Driver, 2002; Vogel, Luck, & Shapiro, 1998). While VAN has been suggested to mark the neural interactions underlying phenomenal consciousness, LP has been associated with reflective consciousness (e.g. Koivisto & Revonsuo, 2008a). According to this interpretation, LP is not a direct correlate of phenomenal consciousness, but rather a sign of post-phenomenal cognitive processes during which the phenomenally conscious information enters working memory where it is conceptualized, named, transformed, and enabled to access output mechanisms such as verbal reporting of the content. This interpretation of LP emphasizes that conscious *perception as such* should not be confused with further processes that enable the manipulation of perceptual contents (e.g. report). However, there is also a competing interpretation. The global neuronal workspace model denies the existence of purely phenomenal consciousness and regards widespread cortical activation and top-down attention as necessary for consciousness. According to this view, LP is the primary correlate of visual consciousness (Del Cul et al., 2007; Sergent et al., 2005). The disagreement between the two opposing views is not purely empirical (i.e. what the data shows) but partly depends on what we take “visual consciousness” or “conscious perception” to consist of.

Some studies have observed only the LP when comparing consciously perceived stimuli with unperceived stimuli (Babiloni et al., 2006[1]; Chica et al., 2010[1]; Fernandez-Duque et al., 2003; Lamy et al., 2009; Niedeggen, Wichmann, & Storeig, 2001; van Aalderen-Smeets, Oostenveld, & Schwarzbach, 2006). This may be due to the fact that LP is a large deflection which is easier to detect than the earlier ones. However, as shown in Figs. 2 and 3, the LP is often observed after earlier ERP correlates of consciousness (e.g. Del Cul et al., 2007; Pourtois, De Pretto, Hauert, & Vuilleumier, 2006; Schankin & Wascher, 2007; Sergent et al., 2005). Consequently, it is difficult to decide which of the ERP correlates reflect the entry of the stimulus information into consciousness. One of the predictions made by the global neuronal workspace view seems to provide an interesting tool to examine this question. The theory predicts that the shift from unconscious to conscious processing is dichotomous and nonlinear (Sergent & Dehaene, 2004). That is, because the key feature of conscious contents is assumed to be their accessibility, a stimulus either reaches awareness or remains subliminal—there are no intermediate steps, although some information might be preconscious, in other words, right below the threshold to consciousness (Dehaene et al., 2006). Two studies have concluded that the P3 (i.e. LP) is the first deflection that exhibits a nonlinear modulation similar to what was observed in behavioral results of the same studies (Del Cul et al., 2007; Sergent et al., 2005). Both studies also reported earlier deflections that correlated with the visibility of the target stimulus, but as these deflections (e.g. VAN) did not show nonlinear modulation, they were interpreted as unconscious (or preconscious) processes. The problem is that it is not at all clear that the requirement of nonlinearity is valid. Evidence supporting the all-or-none variation comes from the attentional blink paradigm which might have artificially

---

[1] Unfortunately, Babiloni et al. (2006) and Chica et al. (2010) only report comparisons of P3 (i.e. LP) amplitudes between target seen and unseen conditions, so it remains unclear whether prior deflections correlated with consciousness. Inspection of their figures (Fig. 4 in Babiloni et al. (2006), and Fig. 4D in Chica et al. (2010)) imply that consciously seen targets elicited more negative ERPs than unseen targets around 200 ms after stimulus onset (i.e. VAN).

dichotomized the response profile (Overgaard, Rote, Mouridsen, & Ramsøy, 2006). Del Cul and colleagues (2007) employed visual masking, but floor and ceiling effects distort the pattern of the results, leading to a nonlinear profile. In other words, the conscious visibility of a stimulus might be better characterized as a continuum with intermediate stages linking the two extremes (Bar et al., 2001; Christensen, Ramsøy, Lund, Madsen, & Rowe, 2006; Genetti et al., 2009; Overgaard et al., 2006).

Some results also suggest that consciousness might be dissociable from the LP, so that even when a stimulus is consciously perceived, no LP is necessarily observed when aware and unaware conditions are compared. For example, Koivisto and colleagues (2006) contrasted aware (unmasked) and unaware (masked) conditions during attention to local or global features of a target. The results showed that when comparing consciously perceived and unperceived targets, LP was reduced or even absent when attention was directed to local features, although it was observed in the condition where attention was deployed to global features. Awareness was found to correlate with VAN in both attention conditions. Similarly, negativity around 200 ms (VAN), but not LP, was observed when comparing consciously recognized repeated targets with unrecognized repeated targets (repetition blindness; Koivisto & Revonsuo, 2008b). Eimer and Mazza (2005) have proposed that the LP reveals differences in confidence ratings rather than consciousness. Taken together, these findings suggest that LP does not directly correlate with conscious perception, but might reflect postperceptual operations (e.g. Donchin & Coles, 1988).

## 6. Conclusions

P1 is the earliest ERP component that correlates with visual consciousness, but the overall evidence concerning P1 as a correlate of processes that generate any type of consciousness, whether phenomenal or reflective, is rather weak. Our interpretation is that the effects of conscious perception on P1 most likely reflect preconscious modulation of stimulus features. The earliest ERP difference that reliably correlates with consciousness in a large number of different studies using a variety of methods, and also shows independence from non-spatial attention, is a negative amplitude shift with an onset at earliest right after 100 ms (VAN) and typically peaking 200–250 ms from stimulus onset. It is this ERP deflection that most likely reflects the neural interactions that underlie the emergence of conscious visual percepts. Late positivity (LP), the third ERP deflection often observed to correlate with conscious perception, is not caused by neural activity directly underlying the onset of phenomenal visual awareness of the stimuli, but later cognitive manipulation and processing of the contents of conscious perception. What do these findings tell us about the course of neural processes that construct conscious visual perception?

The timing and the occipitotemporal topography of VAN suggests that the processes that correlate with conscious visual perception take place within the ventral visual stream, and do not require widespread activation over the whole cortex. Yet, VAN does not seem to be a sign of a single neural process, but a set of events that underlie conscious vision. The earliest parts of VAN (~100 ms poststimulus) might coincide with feedforward activity (e.g. Di Russo et al., 2001; Macknik & Martinez-Conde, 2007; Sack, van der Mark, Schumann, Schwarzbach, & Goebel, 2009), although a substantial amount of stimulus-related bottom-up signals reach the cortex earlier (e.g. Foxe & Simpson, 2002; Wilson et al., 1983). Some estimates of the timing of feedback signals (Boehler et al., 2008; Hupe et al., 2001), support the idea that feedback activity might contribute already to the earliest parts of VAN. TMS studies have indicated that activity in the early visual areas about 60–100 ms after stimulus presentation is crucial for conscious visual perception (Amassian et al., 1989; Kammer, Puls, Strasburger, Hill, & Wichmann, 2005; Railo & Koivisto, 2011), so the typical suppressive time window of TMS, when applied to early visual areas, is earlier than the average VAN latencies. A likely reason for this is that TMS of early visual areas can disrupt the unconscious feedforward response, or the very beginning of the electrophysiological processes that underlie consciousness, but is inefficient at suppressing awareness completely once these processes have built up to a certain level. More delayed TMS pulses to early visual areas can nevertheless degrade the quality of conscious perception (e.g. Koivisto et al., 2011). The later part of VAN occurs too late to reflect purely bottom-up stimulus-related activity. VAN may therefore reflect reverberating feedback activity within the ventral visual stream (e.g. Fahrenfort et al., 2007; Koivisto et al., 2006; Wilenius & Revonsuo, 2007). It is, of course, too simplistic to assume that feedback activity as such would be specific to awareness. Feedback is likely to be involved in a number of processes, including low-level visual functions (Ringach, Hawken, & Shapley, 1997), and even unconscious perception (Koivisto, Mäntylä, & Silvanto, 2010). Feedback activity is also considered as the mechanism of top-down attentional control (Di Russo et al., 2003; Olson, Chun, & Allison, 2001).

ERP studies imply that awareness of objects may arise independently of voluntary feature-based attention. The later interaction between feature-based attention and VAN might be a sign of binding visual features together (Treisman, 1996), or enhancing the contents of consciousness (Carrasco et al., 2004). Sometimes this top-down attentional modulation might be essential to amplify the neural representation to make it cross the threshold to consciousness, which might also explain the variability of VAN latencies in different stimulation conditions (Railo & Koivisto, 2009). Perceptual demands might also explain the inconsistent findings concerning the role of prefrontal areas in conscious vision (Eriksson, Larsson, & Nyberg, 2008). Indeed, it has been shown that already the C1 ERP component, observed before any of the proposed correlates of consciousness, can be modulated by voluntary feature-based attention (Proverbio, Del Zotto, & Zani, 2010), implying that visual cortical processing is shaped by attention from the earliest stages. This preconscious modulation can be later reflected in the contents of consciousness. In fact, already prestimulus neural fluctuations predict whether a subsequent visual stimulus is perceived (Mathewson et al., 2009; Wyart & Tallon-Baudry, 2009).

Even though ERP studies imply that the earliest phases of aware processing evolve independently of feature-based attention, they also show that the resources provided by spatial attention might be necessary for aware perception, although salient stimuli which lead to reflexive bottom-up attentional capture can penetrate consciousness (Koivisto et al., 2009). Because the distribution of attentional resources is known to be dependent on perceptual demands (Lavie, 2006), top-down spatial attention is likely to determine which contents enter consciousness especially during high attentional loads. Under lower attentional loads, subjects may also be conscious of the more peripheral, task-irrelevant sensory information. These peripheral, vaguer conscious contents should produce VAN, although it might be smaller in magnitude when compared to VAN produced by clear, attended conscious contents. By using fMRI it has been verified that the sensory processing of irrelevant peripheral stimuli is reduced when a competing central task assumes substantial attentional resources (Scwartz et al., 2005), and parietal areas have been identified as the mediators of this load dependent modulation (Vuilleumier et al., 2008). Thus, as suggested by ERP (Di Russo, Aprile, Spitoni, & Spinelli, 2008; Marzi et al., 2000; Vuilleumier et al., 2001) and fMRI (Vuilleumier et al., 2001) studies on neglect and visual extinction patients, parietal lesions disturb already relatively early visual processing, not merely late, high-level spatial representations or attentional processes. This supports the view that the loss of perceptual awareness in spatial neglect and visual extinction compromises phenomenal consciousness, not just reflective consciousness as Lamme (2010) has proposed. The same might not always be true for change blindness, or related attentional manipulations. The results of Busch et al. (2010) showed that barely detected, but unidentified, changes elicited a small VAN but no LP, suggesting that the change was registered at phenomenal level. Identified changes generated a large VAN and LP; the participants had a clear conscious percept (VAN), and could retrieve and report the identity of the object (LP).

Therefore, although the ERP data suggests that the neural interactions underlying aware perception take place within the occipitotemporal regions (ventral stream), some of the resources provided by parietal areas (dorsal stream) are necessary for conscious perception, just as Milner and Goodale (2006) have proposed. The specific contributions of parietal areas to conscious perception are not yet well understood. In addition to the processes of attention, parietal areas have been proposed to provide the necessary spatial representation into which the contents of consciousness are embedded (Deouell, 2002; Driver, Vuilleumier, Eimer, & Rees, 2001; Milner & Goodale, 2006; Revonsuo, 2006). Moreover, parietal areas are known to interact, not only with sensory cortices, but also with frontal cortical areas. For example, spatial (Kastner & Ungerleider, 2000) and non-spatial attention (Egner et al., 2008; Peelen & Mruczek, 2008) are mediated through a frontoparietal cortical network, and a network of subcortically driven frontoparietal cortical areas has been found to be involved in generating a default conscious mode (Cavanna & Monaco, 2009; Gusnard & Raichle, 2001). A recent study examining the phase synchrony of neuroelectrical processes associated with visual consciousness showed that transient synchronous reverberations between occipital, parietal and frontal sites correlated with conscious perception already around 100 ms after stimulus onset (Melloni et al., 2007). In the same study, an ERP component resembling the P3 (i.e. LP) emerged after this early phase synchrony, suggesting that a frontoparietal network might contribute to conscious visual perception even before the LP. This finding is consistent with the view that VAN portrays the neural processes underlying conscious visual perception, whereas sustained access and transformation of the contents of conscious perception is reflected in the LP.

To sum up, a negative amplitude difference (VAN) unfolding around 200 ms after stimulus onset in ERPs has consistently been observed to correlate with visual consciousness. At least in situations that are not particularly attention demanding, the early parts of conscious visual perception can emerge independently of voluntary feature-based attention, right after 100 ms after stimulus onset in occipitotemporal regions. Soon after the beginning of VAN, however, top-down attention interacts with conscious processing (Koivisto & Revonsuo, 2008a), and during this period neural interactions have evolved to the point that object discrimination, for example, is possible (Koivisto et al., 2011; Thorpe et al., 1996). It is tempting to associate the early stages of VAN with phenomenal consciousness. Later access and manipulation of the conscious contents in working memory (reflective consciousness) results roughly after 300 ms after stimulus presentation (Sergent et al., 2005), and is coupled with sustained brainwide processing. Hence, the evidence does not support the proposal (Dehaene et al., 2006) that sustained widespread frontoparietal activation underlies conscious perception. Nevertheless, a central issue for future studies of neural correlates of consciousness is to clarify the exact roles of frontal and parietal cortical areas in conscious perception.

## References

Amassian, V. E., Cracco, R. Q., Maccabee, P. J., Cracco, J. B., Rudell, A., & Eberle, L. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalography and Clinical Neurophysiology, 74*, 458–462.

Baars, B. (1997). *In the theater of consciousness: The workspace of the mind*. New York: Oxford University Press.

Baars, B. (2002). The conscious access hypothesis: Origins and recent evidence. *Trends in Cognitive Sciences, 6*, 47–52.

Babiloni, C., Vecchio, F., Miriello, M., Romani, G. L., & Rossini, P. M. (2006). Visuo-spatial consciousness and parieto-occipital areas: A high resolution EEG study. *Cerebral Cortex, 16*, 37–46.

Bar, M., Tootell, R. B., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., et al (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron, 29*, 529–535.

Baseler, H. A., & Sutter, E. E. (1997). M and P components of the VEP and their visual field distribution. *Vision Research, 37*, 675–690.

Beck, D. M., Rees, G., Frith, C. D., & Lavie, N. (2001). Neural correlates of change detection and change blindness. *Nature Neuroscience, 4*, 645–650.

Block, N. (2007). Consciousness, accessibility, and the mesh between psychology and neuroscience. *Behavioural & 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 of the USA, 105*, 8742–8747.

Britz, J., Landis, T., & Michel, C. M. (2009). Right parietal brain activity precedes perceptual alternation of bistable stimuli. *Cerebral Cortex, 19*, 55–65.

Busch, N. A., Fründ, I., & Herrmann, C. S. (2010). Electrophysiological evidence for different types of change detection and change blindness. *Journal of Cognitive Neuroscience, 22*, 1852–1869.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience, 7*, 308–313.

Cavanna, A. E., & Monaco, F. (2009). Brain mechanisms of altered conscious states during epilectic seizures. *Nature Reviews Neurology, 5*, 267–276.

Chica, A. B., Lasaponara, S., Lupiáñez, J., Doricchi, F., & Bartolomeo, P. (2010). Exogenous attention can capture perceptual consciousness: ERP and behavioural evidence. *NeuroImage, 51*, 1205–1212.

Christensen, M. S., Ramsøy, T. Z., Lund, T. E., Madsen, K. H., & Rowe, J. B. (2006). An fMRI study of the neural correlates of graded visual perception. *NeuroImage, 31*, 1711–1725.

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

Damasio, A. (1998). Investigating the biology of consciousness. *Philosophical Transactions of the Royal Society B, 353*, 1879–1882.

Dehaene, S., Changeux, J. P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Science, 10*, 204–211.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition, 79*, 1–37.

Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J.-F., Poline, J.-B., et al (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4*, 752–758.

Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology, 5*, 2408–2423.

Deouell, L. Y. (2002). Pre-requisites for conscious awareness: Clues from electrophysiological and behavioral studies of unilateral neglect patients. *Consciousness and Cognition, 11*, 546–567.

Di Russo, F., Aprile, T., Spitoni, G., & Spinelli, D. (2008). Impaired visual processing of contralesional stimuli in neglect patients: A visual-evoked potential study. *Brain, 131*, 842–854.

Di Russo, F., Martínez, A., & Hillyard, S. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*, 486–499.

Di Russo, F., Martínez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. (2001). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95–111.

Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences, 11*, 355–372.

Driver, J., Vuilleumier, P., Eimer, M., & Rees, G. (2001). Functional magnetic imaging and evoked potential correlates of conscious and unconscious vision in parietal extinction patients. *NeuroImage, 14*, S68–S75.

Edelman, G. M. (1989). *The remembered present*. New York: Basic Books.

Edelman, G. M., Gally, J. A., & Baars, B. J. (2011). Biology of consciousness. *Frontiers in Consciousness Research, 2*, 1–7.

Egner, T., Monti, J. M., Trittschuh, E. H., Wieneke, C. A., Hirsch, J., & Mesulam, M. M. (2008). Neural integration of top-down spatial and feature-based information in visual search. *Journal of Neuroscience, 28*, 6141–6151.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology, 99*, 225–234.

Eimer, M., & Mazza, V. (2005). Electrophysiological correlates of change detection. *Psychophysiology, 42*, 328–342.

Engel, A., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. *Trends in Cognitive Sciences, 5*, 16–25.

Eriksson, J., Larsson, A., & Nyberg, L. (2008). Item-specific training reduces prefrontal cortical involvement in perceptual awareness. *Journal of Cognitive Neuroscience, 20*, 1777–1787.

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2007). Masking disrupts re-entrant processing in human visual cortex. *Journal of Cognitive Neuroscience, 19*, 1497–1499.

Farthing, G. W. (1992). *The psychology of consciousness*. New York: Prentice Hall.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchial processing in the primate cerebral cortex. *Cerebral Cortex, 1*, 1–47.

Fernandez-Duque, D., Grossi, G., Thornton, I. M., & Neville, H. J. (2003). Representation of change: Electrophysiological markers of attention, awareness, and implicit processing. *Journal of Cognitive Neuroscience, 15*, 491–507.

ffytche, D. H., & Zeki, S. (2011). The primary visual cortex, and feedback to it, are not necessary for conscious vision. *Brain, 134*, 247–257.

Foxe, J. J., & Simpson, G. V. (2002). Flow of activation from V1 to frontal cortex in humans – A framework for defining "early" visual processing. *Experimental Brain Research, 142*, 139–150.

Foxe, J. J., Strugstad, E. C., Sehatpour, P., Molholm, S., Pasieka, W., Schroeder, C. E., et al (2008). Parvocellular and magnocellular contributions to the initial generators of the visual evoked potential: High-density electrical mapping of the "C1" component. *Brain Topography, 21*, 11–21.

Genetti, M., Khateb, A., Heinzer, S., Michel, C. M., & Pegna, A. J. (2009). Temporal dynamics of awareness for facial identity revealed with ERP. *Brain and Cognition, 69*, 296–305.

Gusnard, D. A., & Raichle, M. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience, 2*, 685–694.

Haynes, J. D., Driver, J., & Rees, G. (2005). Visibility reflects dynamic changes of effective connectivity between V1 and fusiform cortex. *Neuron, 46*, 811–821.

Haynes, J. D., Roth, G., Stadler, M., & Heinze, H. J. (2003). Neuromagnetic correlates of perceived contrast in primary visual cortex. *Journal of Neurophysiology, 89*, 2655–2666.

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 of the USA, 95*, 781–787.

Hillyard, S. A., Vogel, E. K., & Luck, S. L. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 353*, 1257–1270.

Hopf, J.-M., Luck, S. J., Boelmans, K., Schoenfeld, M. A., Boehler, C. N., Rieger, J., et al (2006). The neural site of attention matches the spatial scale of perception. *Journal of Neuroscience, 26*, 3532–3540.

Hupe, J. M., James, A. C., Girard, P., Lomber, S. G., Payne, B. R., & Bullier, J. (2001). Feedback connections act on the early part of the responses in monkey visual cortex. *Journal of Neurophysiology, 85*, 134–145.

Intaitė, M., Koivisto, M., Rukšėnas, O., & Revonsuo, A. (2010). Reversal negativity and bistable stimuli: Attention, awareness, or something else? *Brain and Cognition, 74*, 24–34.

James, W. (1890). *The principles of psychology*. New York: Holt.

Kaernbach, C., Schöger, E., Jacobsen, T., & Roeber, U. (1999). Effects of consciousness on human brain waves following binocular rivalry. *NeuroReport, 10*, 713–716.

Kammer, T., Puls, K., Strasburger, H., Hill, N. J., & Wichmann, F. A. (2005). Transcranial magnetic stimulation in the visual system. I. The psychophysics of visual suppression. *Experimental Brain Research, 160*, 118–128.

Karnath, H.-O., Himmelbach, M., & Küker, W. (2003). The cortical substrate of visual extinction. *NeuroReport, 14*, 437–442.

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience, 23*, 315–341.

Koivisto, M., Railo, H., Revonsuo, A., Vanni, S., & Salminen-Vaparanta, N. (2011). Recurrent processing in V1/V2 contributes to categorization of natural scenes. *The Journal of Neuroscience, 31*, 2488–2492.

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., Mäntylä, T., & Silvanto, J. (2010). The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. *NeuroImage, 51*, 828–834.

Koivisto, M., & Revonsuo, A. (2003). An ERP study of change detection, change blindness, and visual awareness. *Psychophysiology, 40*, 423–429.

Koivisto, M., & Revonsuo, A. (2005). Prechange event-related potentials predict change blindness in various attention conditions. *Neuro Report, 16*, 869–873.

Koivisto, M., & Revonsuo, A. (2007). Electrophysiological correlates of visual consciousness and selective attention. *NeuroReport, 18*, 753–756.

Koivisto, M., & Revonsuo, A. (2008a). The role of selective attention in visual awareness of stimulus features: Electrophysiological studies. *Cognitive, Affective, & Behavioural Neuroscience, 8*, 195–210.

Koivisto, M., & Revonsuo, A. (2008b). Comparison of event-related potentials in attentional blink and repetition blindness. *Brain Research, 16*, 115–126.

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.

Kornmeier, J., & Bach, M. (2005). The Necker cube – An ambiguous figure disambiguated in early visual processing. *Vision Research, 45*, 955–960.

Kornmeier, J., & Bach, M. (2006). Bistable perception—along the processing chain from ambiguous visual input to a stable percept. *International Journal of Psychophysiology, 62*, 345–349.

Kouider, S., Dehaene, S., Jobert, A., & Le Bihan, D. (2007). Cerebral bases of subliminal and supraliminal priming during reading. *Cerebral Cortex, 17*, 2019–2029.

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

Lamme, V. A. (2004). Separate neural definitions of visual consciousness and visual attention; a case for phenomenal awareness. *Neural Networks, 17*, 861–872.

Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience, 1*, 204–240.

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences, 23*, 571–579.

Lamme, V. A., Supèr, H., Landman, R., Roelfsema, P. R., & Spekreijse, H. (2000). The role of the primary visual cortex (V1) in visual awareness. *Vision Research, 40*, 1507–1521.

Lamy, D., Salti, M., & Bar-Haim, Y. (2009). Neural correlates of subjective awareness and unconscious processing: An ERP study. *Journal of Cognitive Neuroscience, 21*, 1435–1446.

Lavie, N. (2006). The role of perceptual load in visual awareness. *Brain Research, 1080*, 91–100.

Llinás, R., Ribary, U., Contreras, D., & Pedroarena, C. (1998). The neuronal basis for consciousness. *Philosophical Transactions of the Royal Society B, 353*, 1841–1849.

Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society B, 353*, 1801–1818.

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

Mack, A., & Rock, I. (1998). *Inattentional blindness*. Cambridge, MA: MIT Press.

Macknik, S. L., & Martinez-Conde, S. (2007). The role of feedback in visual masking and visual processing. *Advances in Cognitive Psychology, 3*, 125–152.

Marzi, C. A., Girelli, M., Miniussi, C., Smania, N., & Maravita, A. (2000). Electrophysiological correlates of conscious vision: Evidence from unilateral extinction. *Journal of Cognitive Neuroscience, 12*, 869–877.

Mathewson, K., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus $\alpha$ phase predicts visual awareness. *Journal of Cognitive Neuroscience, 29*, 2725–2732.

Melloni, L., Molina, C., Pena, M., Torres, D., Singer, W., & Rodriguez, E. (2007). Synchronization of neural activity across cortical areas correlates with conscious perception. *Journal of Neuroscience, 27*, 2858–2865.

Merikle, P. M., & Joordens, S. (1997). Parallels between perception without attention and perception without awareness. *Consciousness and Cognition, 6*, 219–236.

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action*. Oxford, New York: Oxford University Press.

Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature, 429*, 410–423.

Moutoussis, K., & Zeki, S. (2002). The relationship between cortical activation and perception investigated with invisible stimuli. *Proceedings of the National Academy of Sciences of the USA, 99*, 9527–9532.

Moutoussis, K., & Zeki, S. (2006). Seeing invisible motion: A human fMRI study. *Current Biology, 16*, 574–579.

Niedeggen, M., Wichmann, P., & Storeig, P. (2001). Change blindness and time to consciousness. *European Journal of Neuroscience, 14*, 1719–1726.

Ojanen, V., Revonsuo, A., & Sams, M. (2003). Visual awareness of low-contrast stimuli is reflected in event-related brain potentials. *Psychophysiology, 40*, 192–197.

Olson, I. R., Chun, M. M., & Allison, T. (2001). Contextual guidance of attention – Human intracranial event-related potential evidence for feedback modulation in anatomically early, temporally late stages of visual processing. *Brain, 124*, 1417–1425.

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.

Parvizi, J., & Damasio, A. (2001). Consciousness and the brainstem. *Cognition, 79*, 135–159.

Peelen, M. V., & Mruczek, R. E. B. (2008). Sources of spatial and non-spatial attention in the human brain. *Journal of Neuroscience, 17*, 9328–9329.

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

Pitts, M. A., Neger, J. L., & Davis, T. J. R. (2007). Electrophysiological correlates of perceptual reversals for three different types of multistable images. *Journal of Vision, 7*, 1–14.

Pourtois, G., De Pretto, M., Hauert, C.-A., & Vuilleumier, P. (2006). Time course of brain activity during change blindness and change awareness: Performance is predicted by neural events before change onset. *Journal of Cognitive Neuroscience, 18*, 2108–2129.

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. (2011). Two means of suppressing visual awareness: A direct comparison of visual masking and transcranial magnetic stimulation. *Cortex*, doi:10.1016/j.cortex.2010.12.001.

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

Revonsuo, A. (2006). *Inner presence: Consciousness as a biological phenomenon*. Cambridge, Massachusetts: The MIT Press.

Ringach, D. L., Hawken, M. J., & Shapley, R. (1997). Dynamics of orientation tuning in macaque primary visual cortex. *Nature, 387*, 281–284.

Roeber, U., & Schröger, E. (2004). Binocular rivalry is partly resolved at early processing stages with steady and with flickering presentation: A human event-related brain potential study. *Neuroscience Letters, 371*, 51–55.

Roeber, U., Trujillo-Barreto, N. J., Hermann, C. S., O'Shea, R. P., & Schröger, E. (2008). Early correlates of visual awareness in human brain: Time and place from event-related brain potentials. *Journal of Vision, 8*, 1–12.

Sack, A. T., van der Mark, S., Schumann, T., Schwarzbach, J., & Goebel, R. (2009). Symbolic action priming relies on intact neural transmission along the retino–geniculo-striate pathway. *NeuroImage, 44*, 284–293.

Schankin, A., & Wascher, E. (2007). Electrophysiological correlates of stimulus processing in change blindness. *Experimental Brain Research, 183*, 95–105.

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology, 79*, 3272–3278.

Schroeder, C. E., Mehta, A. D., & Givre, S. J. (1998). A spatiotemporal profile of visual system activation revealed by current source density analysis in the awake macaque. *Cerebral Cortex, 8*, 575–592.

Scwartz, S., Vuilleumier, P., Hutton, C., Maravita, A., Dolan, R. J., & Driver, J. (2005). Attentional load and sensory competition in human vision: Modulation of fMRI responses by load at fixation during task-irrelevant stimulation. *Cerebral Cortex, 15*, 770–786.

Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience, 8*, 1391–1400.

Sergent, C., & Dehaene, S. (2004). Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychological Science, 15*, 720–729.

Shapiro, K. L., Arnell, K. M., & Raymond, J. E. (1997). The attentional blink. *Trends in Cognitive Sciences, 1*, 291–296.

Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences of the USA, 94*, 3408–3413.

Silvanto, J., Cowey, A., Lavie, N., & Walsh, V. (2005). Striate cortex (V1) activity gates awareness of motion. *Nature Neuroscience, 8*, 143–144.

Silvanto, J., Lavie, N., & Walsh, V. (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cerebral Cortex, 15*, 1736–1741.

Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences, 1*, 261–267.

Supèr, H., Spekreijse, V., & Lamme, V. A. F. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience, 4*, 304–310.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature, 381*, 520–522.

Tong, F. (2003). Primary visual cortex and visual awareness. *Nature Reviews Neuroscience, 4*, 219–229.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron, 21*, 753–759.

Treisman, A. (1996). The binding problem. *Current Opinion in Neurobiology, 6*, 171–178.

Treisman, A., & Gelade, G. (1980). A feature integration theory of attention. *Cognitive Psychology, 12*, 97–136.

Tse, P. U., Martinez-Conde, S., Schlegel, A. A., & Macknik, S. L. (2005). Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the occipital cortex beyond human V1/V2. *Proceedings of the National Academy of Sciences of the USA, 102*, 17178–17183.

Turatto, M., Angrilli, A., Mazza, V., Umilta, C., & Driver, J. (2002). Looking without seeing the background change: Electrophysiological correlates of change detection versus change blindness. *Cognition, 84*, 1–10.

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

Vanni, S., Revonsuo, A., Saarinen, J., & Hari, R. (1996). Visual awareness of objects correlates with activity of right occipital cortex. *NeuroReport, 8*, 183–186.

Vanni, S., Tanskanen, T., Seppä, M., Uutela, K., & Hari, R. (2001). Coinciding early activation of the human primary visual cortex and anteromedial cuneus. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 2776–2780.

Veser, S., O'Shea, R. P., Schröger, E., Trujillo-Barreto, N. J., & Roeber, U. (2008). Early correlates of visual awareness following orientation and binocular rivalry. *Vision Research, 48*, 2359–2369.

Vogel, E. K., & Luck, S. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology, 37*, 190–203.

Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 1656–1674.

Vuilleumier, P., Sagiv, N., Hazeltine, E., Poldrack, R. A., Swick, D., & Rafal, R. D. (2001). Neural fate of seen and unseen faces in visuospatial neglect: A combined event-related functional MRI and event-related potential study. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 3495–3500.

Vuilleumier, P., Schwartz, S., Verdon, V., Maravita, A., Hutton, C., Husain, M., et al (2008). Abnormal attentional modulation of retinotopic cortex in parietal patients with spatial neglect. *Current Biology, 18*, 1525–1529.

Wilenius, M. E., & Revonsuo, A. (2007). Timing of the earliest ERP correlate of visual awareness. *Psychophysiology, 44*, 703–710.

Wilenius-Emet, M., Revonsuo, A., & Ojanen, V. (2004). An electrophysiological correlate of human visual awareness. *Neuroscience Letters, 354*, 38–41.

Wilson, C. L., Babb, T. L., Halgren, E., & Crandall, P. H. (1983). Visual receptive fields and response properties of neurons in human temporal lobe and visual pathways. *Brain, 106*, 473–502.

Wolfe, J. (1999). Inattentional amnesia. In V. Coltheart (Ed.), *Fleeting memories* (pp. 71–94). Cambridge, MA: MIT Press.

Wyart, V., & Tallon-Baudry, C. (2009). How ongoing fluctuations in human visual cortex predict perceptual awareness: Baseline shift versus decision bias. *Journal of Cognitive Neuroscience, 29*, 8715–8725.

Zeki, S. (2003). The disunity of consciousness. *Trends in Cognitive Sciences, 7*, 214–218.

Zhang, W., & Luck, S. (2009). Feature based attention modulates feedforward visual processing. *Nature Neuroscience, 12*, 24–25.