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**Neural mechanisms underlying conscious and unconscious
vision**

Evidence from event-related potentials and transcranial magnetic stimulation

by Henry Railo

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ABSTRACT

Vision affords us with the ability to consciously see, and use this information in our behavior. While research has produced a detailed account of the function of the visual system, the neural processes that underlie conscious vision are still debated. One of the aims of the present thesis was to examine the time-course of the neuroelectrical processes that correlate with conscious vision. The second aim was to study the neural basis of unconscious vision, that is, situations where a stimulus that is not consciously perceived nevertheless influences behavior.

According to current prevalent models of conscious vision, the activation of visual cortical areas is not, as such, sufficient for consciousness to emerge, although it might be sufficient for unconscious vision. Conscious vision is assumed to require reciprocal communication between cortical areas, but views differ substantially on the extent of this recurrent communication. Visual consciousness has been proposed to emerge from recurrent neural interactions within the visual system, while other models claim that more widespread cortical activation is needed for consciousness.

Studies I-III compared models of conscious vision by studying event-related potentials (ERP). ERPs represent the brain's average electrical response to stimulation. The results support the model that associates conscious vision with activity localized in the ventral visual cortex. The timing of this activity corresponds to an intermediate stage in visual processing. Earlier stages of visual processing may influence what becomes conscious, although these processes do not directly enable visual consciousness. Late processing stages, when more widespread cortical areas are activated, reflect the access to and manipulation of contents of consciousness.

Studies IV and V concentrated on unconscious vision. By using transcranial magnetic stimulation (TMS) we show that when early visual cortical processing is disturbed so that subjects fail to consciously perceive visual stimuli, they may nevertheless guess (above chance-level) the location where the visual stimuli were presented. However, the results also suggest that in a similar situation, early visual cortex is necessary for both conscious and unconscious perception of chromatic information (i.e. color). Chromatic information that remains unconscious may influence behavioral responses when activity in visual cortex is not disturbed by TMS. Our results support the view that

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early stimulus-driven (feedforward) activation may be sufficient for unconscious processing.

In conclusion, the results of this thesis support the view that conscious vision is enabled by a series of processing stages. The processes that most closely correlate with conscious vision take place in the ventral visual cortex ~200 ms after stimulus presentation, although preceding time-periods and contributions from other cortical areas such as the parietal cortex are also indispensable. Unconscious vision relies on intact early visual activation, although the location of visual stimulus may be unconsciously resolved even when activity in the early visual cortex is interfered with.

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- III 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.
- IV Railo, H., & Koivisto, M. (2012). Two means of suppressing visual awareness: A direct comparison of visual masking and transcranial magnetic stimulation. *Cortex, 48*, 333–343.
- V Railo, H., Salminen-Vaparanta, N., Henriksson, L., Revonsuo, A., & Koivisto, M. (2012). Unconscious and conscious processing of color rely on activity in early visual cortex: A transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience, 24*, 819–829.

ABBREVIATIONS

EEG	electroencephalography
ERP	event-related potential
fMRI	functional magnetic resonance imaging
LGN	lateral geniculate nucleus of the thalamus
LP	late positivity
MEG	magnetoencephalography
MRI	magnetic resonance imaging
NCC	neural correlate of consciousness
SOA	stimulus onset asynchrony
TMS	transcranial magnetic stimulation
VAN	visual awareness negativity

1. Introduction

One of the most remarkable facts about brain is that it provides us with the ability to consciously perceive the environment. Conscious perception is intimately linked with our ability to function in the world, but also unconscious processing of visual information can guide behavior (Milner & Goodale, 2006). As an example, take the well-known phenomenon called blindsight: despite being blind in parts of the visual system due to damaged primary visual cortex, these patients can make accurate judgments about the visual stimuli they claim they cannot (consciously) see. The cortical damage interferes with the patient's ability to consciously see, but nevertheless the brain has somehow gained knowledge of these stimuli, and can use it to influence behavior. What are the neural processes that correlate with, and perhaps enable, conscious visual perception? How can visual information that is not consciously experienced nevertheless influence behavior?

The studies of this thesis examined the timing of the processes that underlie vision. First, using event-related potentials (ERP) we examined the timing and rough localization of the neuroelectrical processes that correlate with conscious visual perception (Studies I–III). Second, using transcranial magnetic stimulation (TMS), we studied which neural mechanisms are necessary for conscious and unconscious vision, concentrating on early levels of cortical processing (Studies IV–V). Each empirical study of the thesis employed metacontrast masking to manipulate visual consciousness.

1.1. Consciousness research

1.1.1. Psychological and philosophical basis

As you read these words, your eyes convey visual information to your brain, whose neural networks then extract the words and their meaning. But how can this information processed in neural networks be available to consciousness? This question has its roots in the classical philosophical mind–body problem, according to which subjective mental contents seem to be fundamentally different from the material world.

The central defining feature of consciousness (or awareness, which I will use as a synonym of consciousness) is the presence of subjective experiences (Nagel, 1974). Philosophers use the term *qualia* to refer to the qualitative features of conscious experience. For example, the subjective phenomenal feel of red color — how it appears to you — is a quale. Quantitative descriptions, no matter how detailed, can never fully capture, for instance, why light whose wavelength is ~ 700 nm, causes experiential contents with the qualia of redness. Why should any physical process give rise to any experience? This is what Chalmers (1996) has called *the hard problem* of consciousness research.

Conscious experience was considered a central theme in the early days of psychological science (James, 1892/2001; Titchener, 1928), but then deemed to be beyond the reach of science by the school of behaviorism (Watson, 1913). Cognitive science rekindled the interest in studying the mind, but the investigations went on largely without making references to consciousness, until the issue surfaced in the late 1980's in cognitive psychology (Baars, 1988) and neuroscience (Logothetis & Schall, 1989).

Although the hard problem of consciousness at present seems to be beyond the grasp of science, empirical facts nevertheless demonstrate that the brain is crucial for consciousness. Damage the brain and you are also likely to damage the mind, and consciousness. What neural mechanisms, then, are crucial for consciousness? Why do blindsight patients lose conscious vision but retain the ability to use the visual information from the blind part of their visual field in their behavior? What is the difference between conscious and unconscious vision in terms of neural processes involved?

The current aim of the neuroscientific study of consciousness is to find the neural correlates of consciousness (NCC) (Crick & Koch, 1990). Is the activity of specific kinds of neurons sufficient for visual experience? Is some specific interaction between neurons required to form conscious vision? Do unconscious and conscious modes of processing depend on different neural pathways? The objective is to find out the “minimal neuronal mechanisms jointly sufficient for any one specific conscious percept” (Crick & Koch, 2003, p. 119). Although finding the NCC will not solve the hard problem, together with theories of neural mechanisms of consciousness, it will increase our knowledge about what kind of neural processes are associated with, and perhaps enable consciousness.

1.1.2. Defining consciousness

The concept “consciousness” is typically assumed to refer to several distinct, but closely related phenomena (Block, 1995; Chalmers, 2000). One basic division is between state of consciousness and contents of consciousness. A subject is in a *conscious state* when she has any subjective experiences, but subjects who are in a conscious state can vary in the level of arousal or wakefulness (Laureys, 2005). Metaphorically, a conscious state can be viewed as a medium which can hold a range of different contents of consciousness (e.g. conscious visual experiences).

The present thesis is about conscious and unconscious visual processing. I will use “visual consciousness” to refer to visual *contents of consciousness*. Arguably, the most basic form of visual consciousness consists of visual qualia; fleeting, subjective visual experiences. This type of consciousness has been termed *phenomenal consciousness* (Block, 1995). When the contents of phenomenal consciousness are accessed, selected as contents of working memory so that they can be manipulated and reflected upon, *reflective consciousness* emerges (Revonsuo, 2006; this has also been termed “access” consciousness; Block, 1995; Lamme, 2003). Naming and reporting the contents of phenomenal consciousness is the function of reflective consciousness, whereas phenomenal consciousness refers to experience per se. Other researchers have denied the possibility of pure phenomenal consciousness, and argue that all consciousness is necessarily reflective: Sensory representations cannot enter consciousness unless they are selected into working memory by attention (Dehaene, et al., 2006), or unless they are selected by higher-order representations (Lau & Rosenthal, 2011). These diverging

views of what consciousness consists of are also reflected in the theories about the neural basis of conscious perception, as the phenomenal-reflective distinction implies that they also have different neural correlates.

1.1.3. Measuring consciousness

Consciousness is notoriously hard to measure due to its private character. One solution is to examine participants' "objective" performance; for example, accuracy in recognizing a visual stimulus (e.g. van Aalderen-Smeets, et al., 2006). The problem of this objective approach is that it does not directly assess consciousness. A stimulus might, for example, be consciously perceived, but distorted, and hence hard to identify. Similarly, even stimuli that remain unconscious may guide a participant's behavior, enabling them to perform above chance-level (Cowey, 2010). This is why "forced-choice" response paradigms, where the participants are required to make a choice between different response alternatives (even when they did not consciously see the target), are often employed to study unconscious perception.

Arguably, when the aim is to study whether or not a participant saw a stimulus, the most direct way is to ask the participant to report her subjective percepts. The report could be a dichotomous "Yes, I did see"/"No, I did not see" button press decision (e.g. Boyer, et al., 2005), but this type of categorization is insensitive to small but possibly significant differences in conscious perception. Hence, the use of continuous (Sergent & Dehaene, 2004) or ordinal (Likert-type) rating scales is often advisable (Ramsøy &

Overgaard, 2004). The advantage of using an ordinal scale with few alternatives is that it is intuitive and each alternative can be precisely described and characterized (Ramsøy & Overgaard, 2004; Overgaard, et al., 2006). Other methods to measure consciousness include asking participants to rate their confidence concerning a decision, or ask them to wager after they have made a task-related decision (Dienes & Seth, 2010).

Trying to demonstrate that a stimulus remained unconscious is similarly challenging. How to know that a participant did not see a stimulus at all, not even for a very brief glimpse? For the reasons cited above, a Likert-scale with a few alternatives is often the most useful (Ramsøy & Overgaard, 2004; Overgaard, 2011). It should be noted, however, that subjective ratings always require the participants to employ some decision criterion. For example, in order to judge whether a stimulus was “not seen at all”, or “barely seen”, the participants use some criterion to determine which alternative to select. Therefore participants who employ a loose criterion might falsely report “not seeing a stimulus at all” when in fact they might have had some conscious percept of the stimuli. To some extent, this problem can be handled by giving the participants sufficiently many alternatives (i.e. to use a high-resolution scale).

1.1.4. Manipulating consciousness and studying its neural correlates

In order to study consciousness experimentally, it must somehow be manipulated. There are multiple different methods for manipulating visual consciousness (Kim & Blacke, 2005), but the present thesis focuses on two methods: metacontrast masking

and TMS. As discussed later in detail, in metacontrast masking a visual “mask stimulus” prevents the conscious perception of another, preceding visual stimulus. In TMS the same is accomplished by directly interfering with neural activity in cortex by electric fields induced by magnetic pulses. One crucial question is what causes the suppression of conscious visual perception as this tells us what processes are necessary for conscious perception. A further question is does the suppression of conscious vision also suppresses unconscious perception? This kind of analysis might shed light on what neural mechanisms underlie unconscious perception, and what are the crucial differences between unconscious and conscious processes.

Comparison of brain activity of situations that differ with respect to contents of consciousness, but are almost or completely identical with respect to physical stimulation, allow the investigation of the NCC. That is, if in one situation a visual stimulus is consciously seen, but in another condition the same stimulus remains outside consciousness (although the same stimulus is presented), then the neural processes that are associated with conscious perception should only be present in the former condition. Comparison of brain activity in the two conditions should thus reveal the NCC of that type of visual experience. Nevertheless, all processes that correlate with conscious perception might not be those that directly enable visual experience. For example, selective attention might influence what sensory representations become conscious (Lamme, 2004), and cognitive manipulation of the contents of consciousness (i.e. reflective consciousness; Block, 1995) might show up as a NCC, but these processes might not be sufficient for conscious experience to emerge. In summary, the comparison of neural processing during conditions where a stimulus is or is not consciously

perceived will reveal a causal chain of processes of which only a subset might directly correspond to the neural events that enable visual experience (Aru et al., 2012).

1.2. Theories and findings about the neural correlates of consciousness

1.2.1. Cortical areas involved in conscious vision

Conscious vision is largely dependent on the cortical areas that analyze visual information. Damage to V1 produces blindness in the visual field locations that correspond to the damaged neural tissue (e.g. damage to left V1 leads to blindness in the right visual field; Holmes, 1918). Lesions to specific higher-order visual areas produce more limited deficits in visual perception. Damage to ventral cortical area labeled V4, for instance, results in an inability to consciously see colors (achromatopsia) (Heywood & Cowey, 1999).

Lesions outside classical sensory visual areas may also produce deficits in conscious vision. Hemispatial neglect syndrome, which often results from damage to right inferior parietal cortex, produces an inability to consciously perceive contralesional sensory stimuli (Mesulam, 1999). Because hemispatial neglect cannot be explained by assuming damaged low-level sensory processors, it is often described as an “attentional” deficit (Mesulam, 1999). This shows that cortical areas that do not directly and solely analyze visual information may nevertheless be crucial for conscious vision.

When cortical activity elicited by consciously seen versus unseen is compared, increased activation is typically observed in visual cortical areas, especially in the ventral visual cortex (Logothetis, 1998; Tong, et al., 1998). Many studies have also reported increased activity in parietal and frontal cortices (Beck, et al., 2001; Kouider, et al., 2007; Panagiotaropoulos et al., 2012). Although this is in concert with the fact that lesions to extrasensory areas may produce deficits in conscious perception (e.g. Mesulam, 1999), the exact role of these areas is not understood. These areas might directly contribute to conscious perception, but they might also reflect factors such as attention, or decision making, that is, reflective consciousness. This question is significant because some theories assume that frontoparietal activity is necessary for conscious perception (Dehaene, et al., 2006) whereas others do not (Lamme, 2010).

1.2.2. Theories about neural mechanisms of visual consciousness

Neural processing of stimulus information can be categorized as feedforward or feedback, depending on whether it consists of bottom-up flow of sensory information, or whether it reflects modulation from other, higher cortical areas (in the processing hierarchy), respectively (Bullier, 2001; Rockland, 2003). Feedback connections are sometimes divided to “local” and “global” (e.g. Lamme, 2004). Although this distinction is somewhat vague and descriptive, in the present thesis, “local feedback” activation means feedback signals from higher visual cortical areas to lower visual cortical areas (e.g. from V4 to V1). “Global feedback” refers to modulatory activity between different cortical lobes (e.g. from frontal lobe to occipital lobe). In addition to feeding back

sensory signals, feedback connections can also convey top-down “attentional” modulation to lower cortical areas (Klimesch, 2011).

The response of a single neuron can also be classified as feedforward or feedback. The feedforward response of a neuron can further be subdivided into specific components. For example, the first feedforward response of a neuron is typically a transient burst of action potentials, which is followed by a phase of more sustained firing (Macknik & Martinez-Conde, 1998).

Perhaps the simplest hypothesis is that a sufficiently strong feedforward activation of certain visual areas is sufficient for conscious perception (Zeki & Bartels, 1999; Macknik & Martinez-Conde, 1998). A somewhat modified view assumes that feedforward activation that reaches the highest visual cortical areas also enables rough conscious vision (Hochstein & Ahissar, 2002). Some researchers have pinpointed the specific parts of a neural feedforward response that correlates with conscious visual perception (Macknik & Martinez-Conde, 1998; Breitmeyer & Ögmen, 2006).

In contrast to the feedforward accounts, other models propose that interaction between cortical areas via feedback connections is a crucial component of conscious vision (Pollen, 1999; Dehaene, et al., 2006; Lamme, 2010). Lamme and colleagues have proposed that feedforward activation remains outside consciousness, although it might be sufficient for unconscious vision (Lamme, 2010). According to the theory, visual *phenomenal consciousness* is enabled by local recurrent activity within the ventral visual areas. *Reflective consciousness* emerges as the recurrent activations connect frontal and parietal areas with sensory cortices (Lamme, 2010).

Some researchers maintain that consciousness requires the recruitment and communication of cortical areas outside sensory areas (Dehaene, et al., 2006; Baars, 2002; Lau & Rosenthal, 2011). The global workspace theory denies the existence of pure phenomenal consciousness, and presupposes that conscious perception is always coupled with cognitive access of the contents of visual perception (Dehaene, et al., 2006; Baars, 2002). The argument for this view is that consciousness serves an important function: it enables flexible voluntary behavior (in contrast to the rigid and automatic unconscious perception). The global workspace theory thus assumes that recurrent activation within the visual system remains outside of consciousness (“preconscious”, to use their term). In order to become conscious, the preconscious visual information must be selected into the global cortical activity network, consisting of frontal and parietal cortices (the “global workspace”), by selective attention.

Other theories have proposed that attention and consciousness are more independent, although intertwined. Hochstein and Ahissar (2002) proposed that conscious perception of the gist of a scene can be accomplished by the feedforward activation of the highest levels of the hierarchical visual areas, that is, without focused attention. However, conscious perception of details requires feedback activation of the early visual areas (this corresponds to focused attention) which have the smallest receptive fields, and are thus capable of processing small details.

In general, different forms of attention are often assumed to rely on modulatory, feedback activity from certain brain areas to other areas (e.g. Olson, et al., 2001). Lamme (2003) argues that although feedback connections are involved in both

attention and conscious vision, the nature of these interactions is inherently different. According to Lamme (2003), attention can be described as the modulatory state that influences conscious processing. Attention may pre-activate neural networks or bias neural activation, thereby influencing what contents enter consciousness, but local *recurrent* activation in the ventral visual stream underlies phenomenal conscious perception.

1.3. Methods for suppressing visual consciousness

1.3.1. Metacontrast masking

Metacontrast masking is a form of backward masking where a spatially adjacent non-overlapping mask stimulus may reduce the visibility of a preceding stimulus. A similar version of masking where the mask precedes the target stimulus is called paracontrast. Metacontrast masking has been extensively studied in vision science in healthy and selected subject populations, and it is a commonly used method to manipulate visual consciousness (Breitmeyer & Ögmen, 2006). When target and mask stimuli have equal energies (duration, size and contrast), metacontrast typically leads to a characteristic u-shaped masking function (also called type B masking functions), shown in Figure 1A: the mask maximally suppresses the visibility of the target stimulus when the mask is presented a few tens of milliseconds after the onset of the target stimulus. The masking function of paracontrast is also often u-shaped, although paracontrast typically induces weaker visual suppression (see Fig. 1A) (Breitmeyer & Ögmen, 2006).

While a number of theories have been proposed to explain the metacontrast effect, recent explanations can be roughly divided into two categories, depending on whether metacontrast is assumed to inhibit feedforward (Macknik & Martinez-Conde, 1998) or feedback processes (Breitmeyer & Ögmen, 2006).

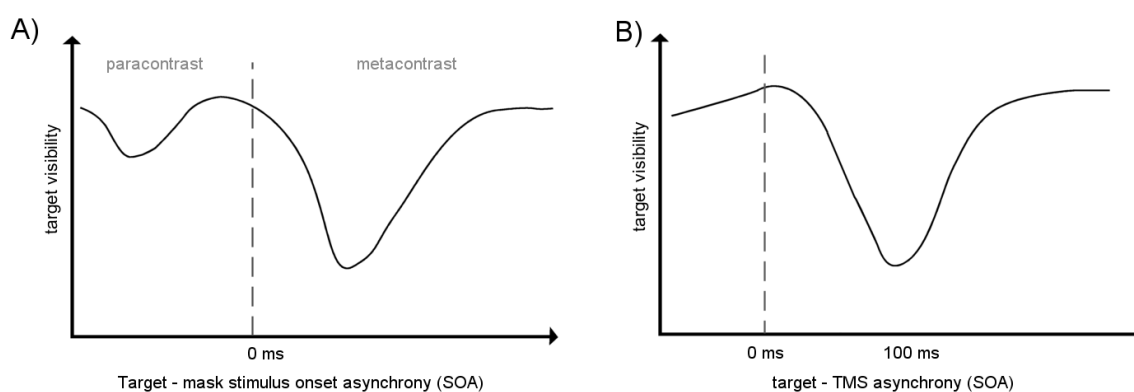


Figure 1. A) Typical para- and metacontrast masking functions. When SOA is 0 ms (dashed line), the target and mask stimuli are presented simultaneously. Positive SOAs correspond to metacontrast masking, i.e., the mask is presented after the target. B) A “classical” suppressive effect of TMS to occipital pole is observed when pulses are applied ~100 ms after the visual stimulus onset.

1.3.2. Transcranial magnetic stimulation (TMS)

The weakness of classical brain imaging methods is that they can only reveal what neural processes correlate with a given cognitive process, but they do not allow researchers to make conclusive causal inferences. For example, the study of NCC cannot be assumed to reveal only those neural processes that directly underlie, or “cause” consciousness. However, the main advantage of transcranial magnetic stimulation (TMS)

is that it allows researchers to probe the causal relevance of specific cortical areas to given cognitive tasks.

In TMS, magnetic pulses are used to induce an electric (E) field in cortical tissue (Walsh & Pascual-Leone, 2003). Using a focal coil the maximal magnetic field can be focused with high spatial precision. This means that in optimal circumstances, TMS pulses may be used to target single visual areas (Salminen-Vaparanta, et al., 2012). In practice, however, the induced electric field cannot be limited to any specific areas, but it decays gradually with distance from the center of stimulation (Walsh & Pascual-Leone, 2003).

TMS can be assumed to typically affect different types of neurons (e.g. excitatory and inhibitory) within a stimulated area (Walsh & Pascual-Leone, 2003). Behaviorally, TMS may have inhibitory or facilitatory effects. In the present studies, we were especially interested in how TMS can be used to interfere with visual perception (see Fig. 1B). We used a single-pulse TMS approach where single TMS pulses are applied to a selected cortical area while a participant is performing a perceptual task. The causal contribution of a specific cortical area at specific time-points can be studied by varying the timing when a TMS pulse is applied relative to the task a participant is performing.

1.3.3. Event-related potentials (ERPs)

ERP is a method of averaging sequences of electroencephalogram (EEG; measurement of the brain's electrical activity) that are time-locked to some event, usually the presentation of a stimulus. The ERP thus represents the brain's average response to some event. Random "neural noise" is assumed to be eliminated after the averaging,

leaving only the neural signal that is time-locked to the specific event (Luck, 2005). However, phase-locked neural oscillations may also contribute to the ERPs (Makeig, et al., 2002).

Although ERP's have a relatively low spatial resolution (e.g. compared to TMS or fMRI), they have very high temporal resolution. Hence, by comparing ERPs produced by stimuli that are consciously perceived with those that are not, one can estimate when, and roughly in which parts of the brain, the processes that correlate with visual awareness take place.

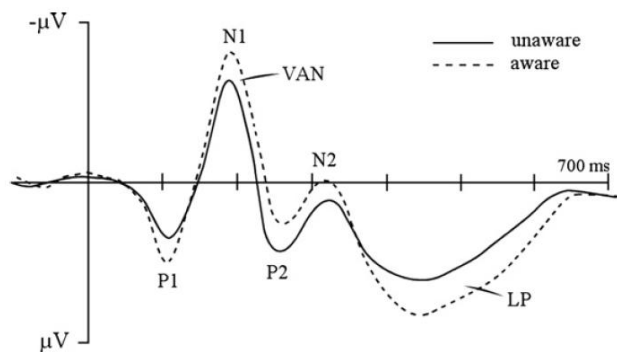


Figure 2. A typical visual ERP waveform. Notice that negativity is plotted upwards, and that positive or negative ERP peaks are labeled according to their order. The figure also depicts the three proposed correlates of consciousness: an enhanced P1 wave, VAN (negative difference between amplitudes), and the LP (positive difference). Dashed line represents stimuli that were consciously perceived, while the solid line those stimuli the participants did not consciously see. (from Study III)

An ERP waveform consists of a sequence of positive and negative voltage deflections (see Fig 2). The deflections are labeled with respect to their polarity and order (P1, N1, P2 etc.). Importantly, the deflections of an ERP waveform are the sum of many “latent components” (Luck, 2005). Thus, different latent components, each reflecting a specific

neural generator, contribute to the shape and timing of visible ERP waves, meaning that single deflections typically cannot be associated with any sole neural or cognitive process. Nevertheless, the early parts of a visual ERP (e.g. P1) reflect more low-level visual processes, whereas later components (e.g. P3) are more related to higher cognitive processes.

2. Aims of the studies

The general aim of the present thesis was twofold. First, to investigate the ERP correlates of conscious vision. How is visual consciousness reflected in ERPs during metacontrast masking? More generally, what is the empirical support for different proposed ERP correlates of visual consciousness? The second aim was to study suppression of visual consciousness by TMS and metacontrast masking. Does TMS or metacontrast suppression result from inhibition of feedforward (Thielscher, et al., 2010; Sack, et al., 2009), or feedback (Beckers & Zeki, 1995; Corthout, et al., 1999) activity, or a combination of these (Koivisto, et al., 2011)? Do these methods disturb only conscious, or also unconscious perception?

Below I will discuss the specific aims of each study in more detail.

2.1. Studies I-III: ERP correlates of visual consciousness

In Study I we examined the ERP correlates of metacontrast masking. Classical ERP studies of metacontrast masking, which showed that metacontrast influences

“intermediate” ERP components (roughly 200 ms after target onset), were completed over twenty years ago (e.g. Andreassi, et al., 1976; Bridgeman, 1988). The conclusions of these studies have been challenged by van Aalderen-Smeets et al. (2006) who argued that metacontrast modulates, not intermediate, but later, “post-perceptual” processes (specifically, the P3 component). In their MEG study, Van Aalderen-Smeets et al. (2006) compared metacontrast masking to a similar “pseudomasking” condition, that didn’t induce masking. This allowed the examination of the metacontrast effect while minimizing confounds that are due to summation of the ERPs produced by the target and mask stimuli. Although this is an important methodological improvement compared to prior metacontrast ERP studies, the study by van Aalderen-Smeets et al. (2006) lacked empirical and statistical examination of the control (pseudomask) condition. We used a similar pseudomasking condition as van Aalderen-Smeets et al. (2006), but also statistically examined the pseudomask condition.

Study II is a reply to a commentary by Bachmann (2009) on the above presented Study I.

Study III is a review of ERP studies of visual consciousness. Different ERP deflections have been suggested as the correlates of consciousness. Major differences in the timing and scalp topography of these components reflect major differences in the models of consciousness they support. Our aim in reviewing the evidence for the proposed correlates was to examine which of the proposed correlates gains strongest empirical support for reflecting neural activity underlying visual consciousness.

2.2. Study IV: Mechanisms of visual suppression in TMS and metacontrast masking

Metacontrast masking is assumed to leave the earliest feedforward signals intact, although views differ as to exactly what later visual processes metacontrast masking is assumed to suppress (later feedforward signals, Macknik & Martinez-Conde, 1998; or feedback signals, Breitmeyer & Ögmen, 2006). The sparing of the earliest feedforward signals could explain the availability of unconscious visual information despite metacontrast masking (Vorberg, et al., 2003; Breitmeyer & Ögmen, 2006).

Unlike metacontrast, paracontrast masking, which is the forward masking version of metacontrast, has been suggested to inhibit the target-related feedforward neural response (Breitmeyer & Ögmen, 2006; Ögmen, et al., 2003). Hence, it should suppress not only conscious visual perception but also unconscious processing (Breitmeyer & Ögmen, 2006). Nevertheless, paracontrast masking is relatively little studied, compared to metacontrast masking.

Adjusting the delay at which occipital TMS is delivered after visual stimulation influences which part of the visual-response the TMS pulses affect. The typical finding after occipital stimulation is the classical suppressive effect (the “dip”) centered around 100 ms (Fig. 1B). The dip begins after 60 ms (Amassian, et al., 1989; Beckers & Zeki, 1995), and depending on the study, has been observed to continue up to 200 ms after visual stimulus onset (Corthout, et al., 1999). Some studies have also reported additional time-periods, before and after the classical dip, where occipital TMS can disturb visual perception (Corthout, et al., 1999; Camprodon, et al., 2010).

In study IV we directly compared visual suppression by metacontrast, paracontrast and TMS. The aims were to examine, first, if the suppressive time windows observed in TMS studies are comparable to those observed in paracontrast and metacontrast, as suggested by Breitmeyer, Ro and Öğmen (2004). Second, our study included a forced-choice location detection task, in addition to reports about the conscious visibility of a stimulus. This allowed us to examine whether the participants could guess the location of a stimulus rendered invisible by TMS, metacontrast or paracontrast, and thus directly test the predictions of different models of visual suppression and unconscious visual processing.

2.3. Study V: Unconscious and conscious processing of chromatic information in the early visual cortex

Unconscious information can be studied by using subliminal priming, where stimuli that remain unconscious (i.e. subliminal) influence responses to subsequent target stimuli (Jacobs & Sack, 2012; Vorberg, et al., 2003). Metacontrast masked stimuli can produce unconscious priming when participants respond to the color of the mask (Schmidt, 2000), and psychophysical evidence suggests that V1 is crucial for this unconscious priming by color (Breitmeyer, Ro, & Singhal, 2004). However, in concert with studies on blindsight patients (Stoerig & Cowey, 1992), a TMS study by Boyer et al. (2005) showed that the early visual cortex might not be essential for unconscious processing of color. The authors suggested that geniculate projections that bypass V1 can mediate unconscious processing of chromatic information.

In study V we examined if the early visual cortex contributes to unconscious processing of chromatic information by measuring unconscious forced-choice color recognition and unconscious, metacontrast masked priming by color. We also studied how occipital TMS affects conscious color recognition. If the processing of chromatic information relies on the geniculostriate projection, both conscious and unconscious perception of color should be disturbed (assuming the TMS pulses suppress feedforward visual activation of early visual cortex).

3. Methods and results

3.1. Study I: An ERP-study of metacontrast masking

ERP's elicited by metacontrast masked targets were compared to pseudomasked at three different SOAs (0, 50, and 130 ms) (Fig. 3A). The participants' (N = 14) task was to recognize the shape of the target and rate how visible the target was.

As expected from previous studies (van Aalderen-Smeets, et al., 2006), only metacontrast masking (and not pseudomasking) produced a significant reduction in target visibility (and recognition performance) during the middle SOA (50 ms) (Fig. 3B).

Metacontrast masking (when compared to pseudomasking) was reflected in ERPs at two time-windows (Fig. 3C). First, consciously perceived, pseudomasked, stimuli produced more negative amplitudes 300 ms after stimulus onset in occipito-temporal sites than metacontrast masked stimuli. A similar negative amplitude difference revealed by the comparison of ERPs to consciously perceived and unperceived stimuli

in several previous studies, has been called visual awareness negativity (VAN) (Ojanen, et al., 2003; Wilenius-Emet, et al., 2004; Koivisto & Revonsuo, 2010). Second, like many previous ERP studies of visual consciousness (Sergent, et al., 2004; Koivisto & Revonsuo, 2010), VAN was followed by a more centrally localized positive difference in the ERPs, beginning around 450 ms (late positivity, LP): consciously perceived stimuli produced more positive amplitudes than stimuli that were not consciously perceived. The timing and scalp topography of LP corresponds to the P3 wave (Del Cul, et al., 2007). Our results show that although metacontrast masking is reflected in the late positive ERP component as van Aalderen-Smeets et al. (2006) suggested, an earlier correlate is VAN. Another important issue is that by examining the ERPs of trials where only the masks were presented, we were able to show the differences between metacontrast masking and pseudomasking were probably not due to different ERP responses to the masks per se (i.e. to physically different stimuli).

Our results are in good agreement with the “classical” ERP studies of metacontrast (e.g. Andreassi, et al., 1976; Bridgeman, 1988). These classical studies compared masking conditions that differed with respect to stimulus presentation timing (thus confounding visibility with SOA), but we compared target-mask sequences that had identical timing.

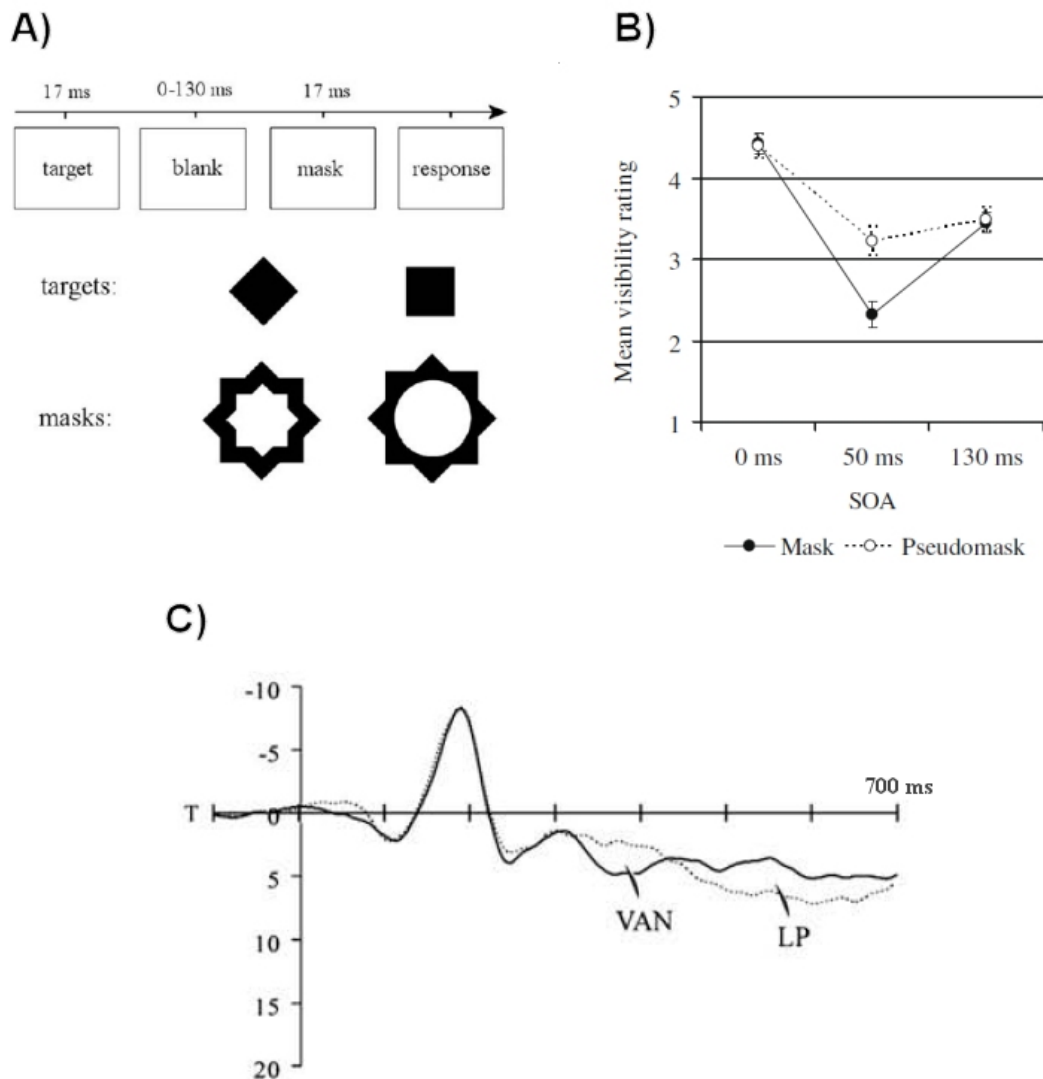


Figure 3. A) A schematic presentation of the visual sequence presented on each trial. The mask on left is the metacontrast mask while the mask on right is the less effective “pseudomask”. B) Behavioral results show that metacontrast masking (solid line) reduces target visibility more than the pseudomask during the 50 ms SOA. At the two other SOAs the two mask types have similar masking strengths. Error bars represent the standard error of mean. C) ERPs from the temporal electrodes show VAN and LP (dashed line = pseudomask; solid line = metacontrast masking) (From Study I).

3.2. Study II: Response to Bachmann's (2009) comments on Study I

Study II is a reply to Bachmann's (2009) commentary on our metacontrast ERP study. Bachmann's main concern is that our ERP result might have been, not due to differences in the subjective perception of the target stimulus, but due to small differences in physical stimulation between the conditions. Respectively, Bachmann further argues that studies of the NCC should always compare two physically identical conditions. While the issues Bachmann raises are important, a number of issues speak against his interpretations. First, although the metacontrast and pseudomask conditions did differ physically in our study, we also included a control condition (masks presented alone, without the target stimuli) to statistically examine this confound. Second, our approach was clearly hypothesis-driven: based on extensive research (Koivisto & Revonsuo, 2010), we were expecting the VAN-late positivity combination. Third, the biggest difference caused by the physical difference between the metacontrast and the pseudomask is arguably their different masking strengths, which was the object of our study, and verified by behavioral results. The differences between the mask types may also have other, smaller effects on the ERPs, but these differences can be assumed to be minor compared to the differences in masking strength. Fourth, we do not completely agree with Bachmann in that invariant experimental conditions are always superior when studying the NCC, as invariant conditions are also subject to confounds (e.g. differences in attention levels may explain differences in conscious perception).

3.3. Study III: Review of ERP correlates of consciousness

VAN and the late positive deflection (LP) are the two ERP correlates of consciousness that have been most frequently observed in studies. In addition, some studies have reported an earlier correlate of consciousness, an enhanced P1 component (see Fig. 1) (Pins & ffytche, 2003). We reviewed the literature supporting these three proposed correlates of consciousness, each of which offers a quite different view to the mechanisms behind conscious vision. A central theme in our review was the interaction between attention and the processes that underlie consciousness.

Although numerous studies have reported that the P1 correlates with consciousness, the studies fail to provide convincing evidence that P1 is a genuine correlate of consciousness. The problem, which is typically acknowledged in the studies, is that the proposed P1 correlate of consciousness could instead be a correlate of attention. That is, the P1, which is known to be influenced by different types of attention mechanisms (Hillyard & Anllo-Vento, 1998; Zhang & Luck, 2009), could be generated by early neural processes that co-vary with visual consciousness, but do not necessarily themselves directly “produce” visual consciousness.

VAN, the second earliest proposed ERP correlate of consciousness, observed using a wide range of techniques (Koivisto & Revonsuo, 2010), also occurs in a time-window that is known to be modulated by attention. However, research has shown that VAN is at least partially independent of attention, and might thus reveal a direct correlate of conscious processing. The early part of VAN seems to emerge independently of top-down feature-based attention (Koivisto, et al., 2006). The fact that top-down attention

seems to interact with conscious perception and VAN only at later stages suggests that VAN reflects a set of different neural and cognitive processes that underlie the emergence of conscious vision. We also suggested that differences in the processing demands of visual stimuli might explain why the timing of VAN varies across studies. Strong stimuli that are easily resolved might reach consciousness faster than perceptually demanding stimuli that require extensive attentional processing.

According to another interpretation, LP is the direct correlate of conscious processing (Sergent, et al., 2004; Del Cul, et al., 2007). The proponents of the LP thus claim that the processing reflected in VAN serves to make visual representations *preconscious*, that is, make them potential future contents of consciousness (Dehaene, et al., 2006). The motivation behind this argument comes (at least partly) from the theoretical view that conscious processing is associated with widespread distribution of information in the brain which enables conscious access of those contents. An alternative interpretation of the LP is that it is a marker of reflective consciousness, leaving VAN as the correlate of phenomenal visual consciousness (Koivisto & Revonsuo, 2010).

In our review, we conclude that the interpretation of LP as a correlate of any type of consciousness may be false. Most problematic for the view that LP marks conscious processing are reports that have dissociated LP from consciousness: studies where LP is not observed in comparisons of unconscious and conscious conditions (although earlier correlates are observed; Koivisto, et al., 2006), or where similar late positive deflection (P3) is observed, even in the absence of conscious perception (Cavianto, et al., 2012).

3.4. Study IV: Comparison of metacontrast masking and TMS

Eleven participants took part in Study IV. The experimental procedure is depicted in Figure 4A. The participants were presented with small ($.2^\circ$) target stimuli (a grey dot) for one screen refresh (at 60 Hz, i.e. ~ 17 ms). The target was presented either in left or right visual field, and the participant's first task (forced-choice) was to report on which side the target was presented. Secondly, the participant was asked to rate the visibility of the stimulus. On some experimental blocks the visibility of the target was manipulated by paracontrast or metacontrast masks, presented on both visual field locations (SOAs: -117–217 ms). In another experimental condition the visibility of the target was manipulated by occipital single-pulse TMS (no masks were presented). The TMS SOAs corresponded to the visual masking SOAs, assuming a 60 ms retinocortical transmission time (TMS SOAs: -42–275 ms). TMS was applied to the early visual cortex in left or right hemisphere.

Occipital TMS led to the expected results: Visibility of the target stimulus was suppressed in particular during SOAs near 100 ms (i.e. the “classical dip”). Also the analysis of metacontrast masking returned expected results: target visibility was reduced at intermediate SOAs, leading to the characteristic u-shaped masking profile. Comparison of the SOAs at which TMS and metacontrast masking maximally suppressed target visibility (by taking account 60 ms of retinocortical transmission time) revealed that maximal metacontrast masking occurred after maximal TMS suppression (Fig. 4B). This suggests, in concert with previous studies (Breitmeyer & Ögmen, 2006; Macknik & Martinez-Conde, 1998), that metacontrast more strongly inhibited later target-related

neural responses. Our conclusion rests on the assumed 60 ms retinocortical transmission time. This estimate of retinocortical transmission latency is based on intracranial recordings in humans (e.g. Wilson et al., 1983). Given that our targets were small, low-contrast dots, the 60 ms estimate of retinocortical transmission time is conservative: decreases in stimulus intensity are known to greatly increase the feedforward response latencies of neurons (Gawne et al., 1996). Assuming a longer retinocortical delay, in concert with the low-intensity of the stimuli, would yield stronger support for the view that metacontrast suppresses feedback activity.

Although TMS clearly suppressed conscious visibility of the targets, target detection rates did not reveal a strong suppression. Analysis of the trials where subjects reported “not seeing the target at all”, showed that the detection of target location was nevertheless above 70% correct (Fig. 4C), which is statistically significantly above chance (i.e. 50%). The above chance unconscious performance could be explained by projection through the lateral geniculate nucleus (LGN) or through superior colliculus that bypass V1.

Similarly, if metacontrast masking leaves the initial feedforward responses uninhibited, it should also enable unconscious location detection (similar to TMS results). Conversely, does paracontrast masking, which has been suggested to inhibit the target’s transient onset-response, also block unconscious location detection? Our results on the trials where subjects reported “not seeing the target at all” confirmed this prediction: Statistically significant (above chance) unconscious location detection was possible during efficient metacontrast but not during paracontrast masking (Fig. 4C).

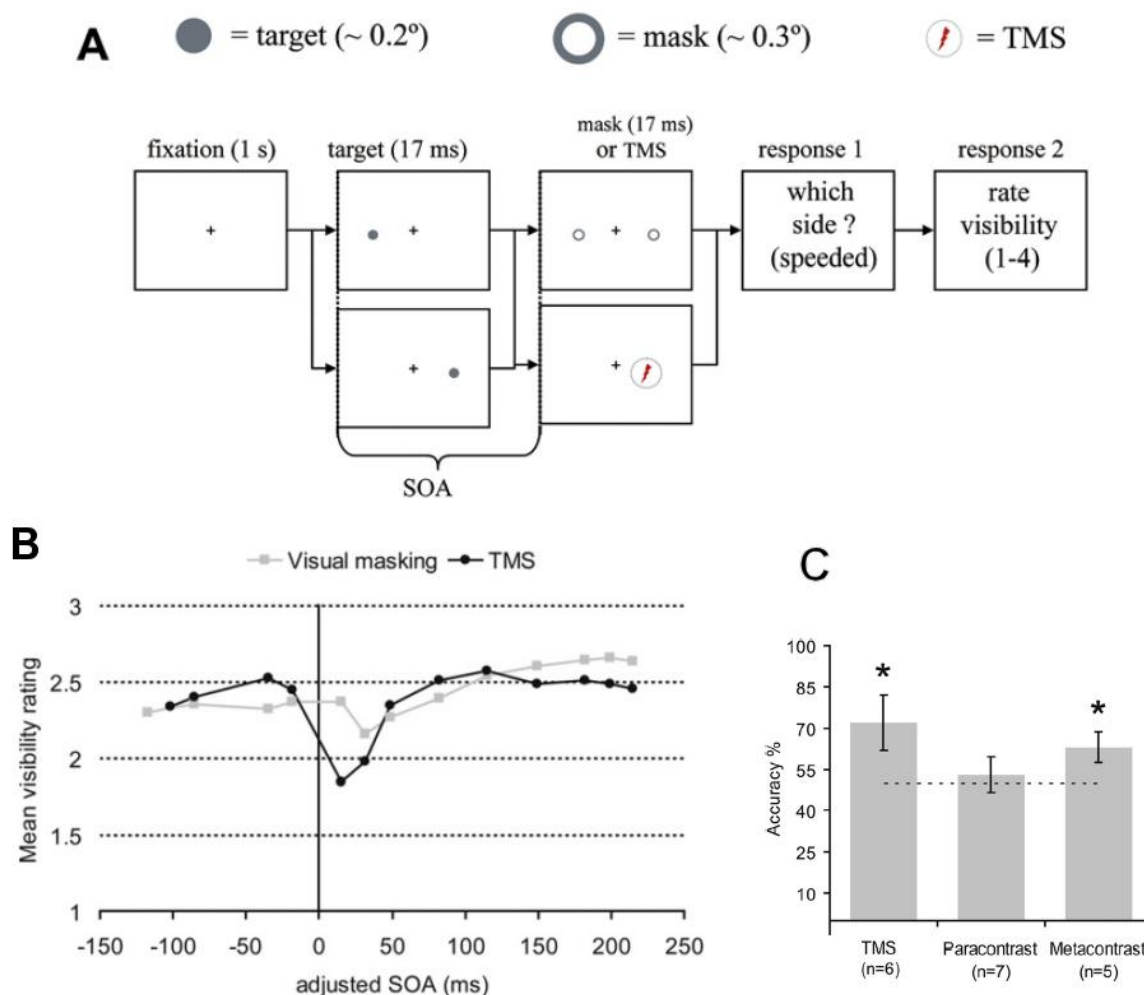


Figure 4. A) The experimental procedure. B) Comparison of TMS and visual masking. Grey line represents para- and metacontrast. Black line shows TMS results (stimulated hemifield), when the retinocortical delay is taken into account (see Study IV for details). Note that maximal visual masking takes place after maximal TMS masking. C) Forced-choice location detection accuracy in different experimental conditions during those trials where the participant reported not seeing the stimulus at all. Error bars represent the standard error of mean. (Study IV)

3.5. Study V: Unconscious processing of chromatic information

To investigate conscious and unconscious processing of chromatic information, we employed early visual cortex stimulation at three TMS SOAs (40, 70, and 100 ms after

stimulus onset), in three different experimental conditions: 1) Conscious recognition of color, 2) unconscious, metacontrast masked color priming, and 3) forced-choice recognition of consciously invisible color (see Fig. 4 for details of the experimental procedure). Thirteen participants were tested.

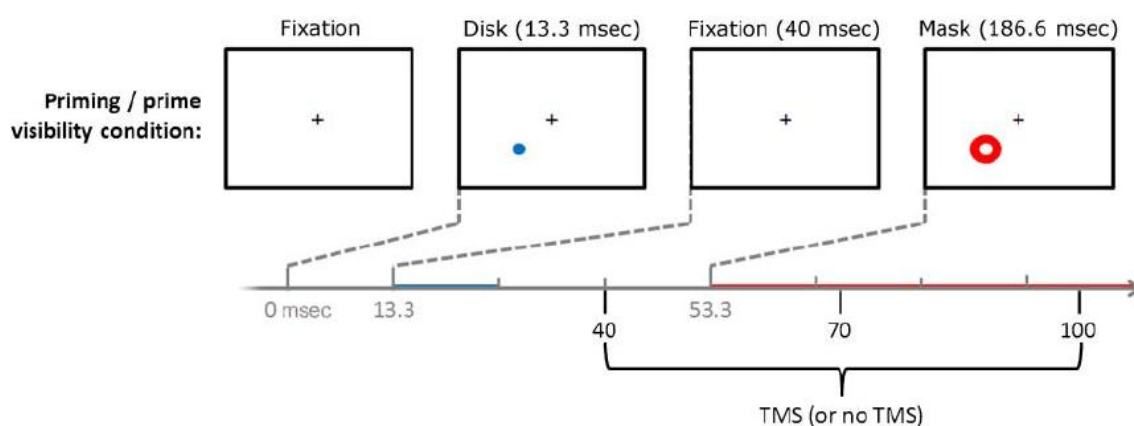


Figure 4. In the metacontrast masked priming the participants were asked to report the color of the mask annulus (red or blue). They were not informed that a heavily masked prime stimulus was presented before the mask (red or blue). A control condition verified that the participants were indeed unconscious of the prime. The experiment also included a conscious color recognition condition where the participants were asked to recognize the color of the prime disk without the mask. Stimulus durations and TMS SOAs are presented on the horizontal bar. TMS was applied to right early visual cortex, so the processing of primes/targets presented in the lower left visual field (i.e. right hemisphere) were directly interfered with TMS (ipsilateral targets are a control condition)(Study V)

The results of the conscious color recognition condition revealed that early visual cortex stimulation 70 or 100 ms after stimulus onset interfered with conscious color visibility and color recognition performance. Also unconscious metacontrast masked chromatic priming was interfered at a similar SOA (relative to prime), suggesting that early visual cortex activation 70–100 ms after stimulus onset underlies both conscious and unconscious processing of chromatic information (Fig. 5). Moreover, the forced-choice

color recognition performance was also dependent on early visual cortex stimulation (all SOAs pooled together to maximize the number of trials). When the participants reported perceiving the stimulus faintly, without consciously seeing the color, color recognition performance was above chance-level. However, when only those trials were included in which the subjects reported being *completely* unconscious of the stimulus, recognition of color was at chance-level. This suggests that early visual cortex activation underlies not only conscious color recognition, but also unconscious color recognition in healthy participants.

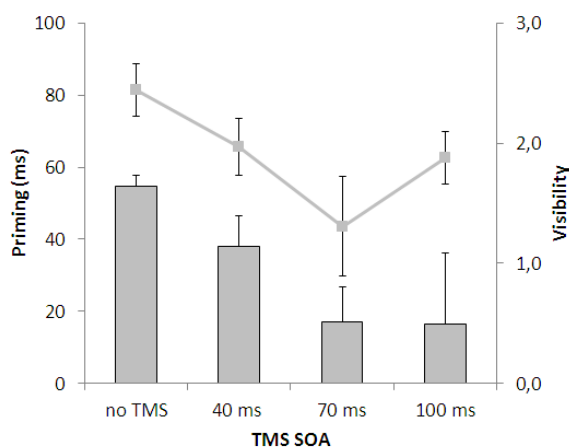


Figure 5. Line graph (right vertical axis) shows the TMS results of the conscious color recognition condition (left hemifield targets). Bars represent the magnitude of priming in the unconscious masked priming condition during different TMS SOAs. Note that TMS pulses decrease unconscious priming during the same time-windows as they suppress conscious vision. Error bars represent the standard error of mean. (Study V)

4. Discussion

The main findings of the present thesis are the following:

- 1) Although visual consciousness is reflected in the ERPs as early as ~100 ms after stimulus onset, later (~200 ms; VAN) differences in the occipito-temporal visual cortex most closely correlate with conscious visual perception. We suggest that

any ERP correlates of visual consciousness that emerge after VAN, such as LP, are signs of post-perceptual cognitive processing.

- 2) The classical suppressive time-window (~100 ms after stimulus onset) of early visual cortex TMS reflects inhibition of preconscious processing. The early parts of this suppressive time-window (~60 ms) may correspond to feedforward activity, but later periods (i.e. ~100 ms) probably already include local feedback communication in the visual cortex.
- 3) Unconscious detection of target *location* is possible when stimulus visibility is completely suppressed by TMS of early visual cortex. However, in a similar situation, TMS suppression of conscious vision also disturbs unconscious perception of chromatic information.
- 4) Evidence from ERPs (Study I) and comparison of metacontrast masking to TMS-induced suppression (Study IV) suggest that metacontrast masking suppresses the conscious visibility of a target by inhibiting target-related feedback activity.
- 5) Stimuli that are unconscious due to metacontrast masking may influence behavior. The results of Study V support the view that unconscious processing of chromatic information in metacontrast masking relies on early visual cortex (arguably feedforward activation).

4.1. Tracking the time-course of conscious perception

ERP investigations of the temporal evolution of conscious perception suggest that conscious vision is enabled following number of different cognitive and neural processing stages. Based on ERP evidence (Foxye, et al., 2008), and intracranial recordings (Wilson, et al., 1983), the initial activation of V1 after thalamic inputs takes place about 60 ms after stimulus onset, which coincides with the beginning of the “classical” dip in TMS studies. Hence, TMS pulses around this time-window can be assumed to co-occur with the initial feedforward activation of early visual cortex. Although TMS can suppress consciousness at this time-window, it cannot be said that TMS inhibited the NCC in particular, assuming that feedforward activation is insufficient for conscious perception. None of the ERP studies of visual consciousness have suggested that feedforward activation (reflected in the visual C1 component; Foxye, et al., 2008) would be the NCC. Early visual cortex TMS can have a smaller disturbing effect on visual perception also during considerably later time-windows (~200 ms; Corthout, et al., 1999; Camprodon, et al., 2010).

The second earliest visual ERP deflection is the P1, which has been suggested to be generated in extrastriate cortical areas (Di Russo, et al., 2003). If local cortical feedback connections activate rapidly (Hupe, et al., 2001), the P1 might already include sensory feedback signals from extrastriate areas to V1. For example, the TMS results of Pascual-Leone and Walsh (2001) suggest that the (feedback) projections from the cortical “motion area” V5 to early visual cortex operate in approximately 20 ms, and that these projections are necessary for conscious perception of motion.

Although the P1 has been proposed to be the ERP correlate of consciousness, our review suggests that P1 modulation in these studies is better explained by differences in attentional processing between the consciously perceived and unperceived conditions. The attentional mechanisms that take place in the P1 time-window may influence what information reaches consciousness, but the P1 cannot be assigned the label NCC. According to a theory proposed by Klimesch (2011), the P1 is generated by alpha oscillations that reflect top-down attentional *inhibition* from parietal areas. This way alpha oscillation could influence what stimuli enter consciousness, without being the direct correlate of conscious perception. On the other hand, other evidence suggests that the attentional modulation in the P1 time-window does not influence what becomes conscious (Wyart, et al., 2012). Both lines of evidence, however, agree that the attentional influences during P1 do not constitute a true NCC.

We have argued that strongest evidence for the ERP correlate of phenomenal visual consciousness is for VAN, a negative amplitude difference typically onsetting before 200 ms after stimulus onset and lasting up to 400 ms. The VAN localizes predominantly to the occipito-temporal cortex, which is in concert with other studies indicating involvement of the ventral visual stream in conscious perception (Milner & Goodale, 2006; Logothetis, 1998; Tong, et al., 1998). VAN has also been demonstrated using MEG (Liu et al., 2012), and intracranial recordings (Fisch, et al., 2009; Gaillard, et al., 2009).

VAN seems to emerge independently of top-down feature-based attention, but attention later interacts with VAN, so that attended stimuli produce stronger VAN, compared to unattended stimuli (e.g. Koivisto, et al., 2006). Hence, if VAN is taken as the correlate of

consciousness, it consists of different phases, the early part of it being independent, and later phase dependent of top-down attention. Evidence concerning spatial attention, however, suggests that under situations where subjects are attending solely to one location while completely ignoring the other location (where distracter stimuli are nevertheless presented), VAN is only observed in the attended locations (Koivisto, et al., 2009).

However, VAN has also been argued to be an ERP correlate of preconscious processes that bring perceptual contents to the verge of consciousness (Sergent, et al., 2004; Salti, et al., in press). According to this interpretation the LP is the ERP correlate of consciousness. However, this view does not explain why the early part of VAN has been shown to be independent of attention. That is, if VAN cannot be explained as an attention-related effect, what preconscious processes does VAN reflect? Furthermore, there is evidence that LP can be dissociated from consciousness (Koivisto, et al., 2006; Koivisto & Revonsuo, 2008). Nevertheless, the question whether LP reflects consciousness or related cognitive processing, remains a central issue for future research. Furthermore, although VAN localizes to the ventral cortical areas, top-down modulation other cortical areas such as the parietal cortex, may be indispensable for consciousness (Mesulam, 1999).

4.2. Unconscious and conscious perception

Our results from metacontrast masking support the view that feedforward signals can trigger unconscious perception (e.g. Lamme, 2010). Study IV suggests that metacontrast,

unlike paracontrast, does not eliminate unconscious detection of stimulus location. However, Study V provided direct evidence that the early, possibly feedforward, activity of early visual cortex is important for metacontrast masked color priming. Importantly, similar color priming can be reduced by paracontrast masking (Breitmeyer, Öğmen, & Chen, 2004), again supporting the view that paracontrast suppresses feedforward activity that is crucial for unconscious and conscious perception. However, it should be noted that paracontrast is still a relatively little studied form of masking. This, and the fact that paracontrast masking can affect visibility during a wide-range of SOAs (suggesting of different suppression mechanisms), means that the conclusions about paracontrast should be taken cautiously. A potential confounding factor for interpreting visual masking results is also that the location of a target, for instance, might be inferred from the appearance of the mask (e.g. in our Study IV). That is, although the target remains invisible, it might influence the appearance of the mask (e.g. making the centre of the mask “blink”).

Occipital TMS studies have demonstrated that visual stimuli that are not consciously perceived can nevertheless guide hand movements (Christiansen, et al., 2008; Ro, 2008). As only stimulus location needed to be processed in these studies to accomplish corrective movements, the results are similar to our reports of unconscious processing of target location (Study IV; see also Koivisto, et al., 2011). The ability to unconsciously resolve stimulus locations could be mediated by a visual pathway that bypasses the LGN (Christiansen, et al., 2008; Ro, 2008). An alternative possibility is the pathway through LGN to early visual cortex, as the TMS studies may have not been able to completely suppress the feedforward signals in early visual cortex (see Study V). In neurological

patients, however, evidence supports the conclusion that pathway bypassing the LGN mediate at least some blindsight abilities (Leh, et al., 2006; Tamietto, et al., 2008).

Unconscious processes other than the processing stimulus location might rely on the early visual cortex. Study V suggests that unconscious processing of chromatic information relies on the early visual cortex in healthy participants. Early visual cortex may also be necessary for the processing of detailed spatial information. Koivisto et al. (2012) showed that unconscious, metacontrast masked symbolic priming depended on early visual cortex, suggesting that early visual cortex is necessary for unconscious processing of shape (see also, Koivisto, et al., 2011).

Koivisto, Mäntylä and Silvanto (2010) have provided evidence that feedback is involved also in unconscious processing. The authors used motion stimuli and observed two time-periods during which TMS suppressed the conscious perception of motion. Following earlier studies (Silvanto, et al., 2005), these two periods were interpreted as markers of feedforward and feedback signals, because V5 stimulation suppressed conscious perception of motion at an intermediate SOA (with respect to early visual cortex stimulation). Next, Koivisto et al. (2010) examined forced-choice motion direction judgments during the trials when the participants reported not perceiving motion. Critically, accuracy was above chance-level when no TMS was applied, and during the early TMS time-window, but not during the second TMS time-window, which was assumed to correspond to the feedback activity. Hence, the results suggest that feedback activity (to V1) contributes not only to conscious, but also to unconscious perception (Koivisto, et al., 2010). Consistent with this, unconscious modulation of ERPs

is observed at intermediate (Pitts, et al., 2011), and late (Gaillard, et al., 2009) latencies, demonstrating that more than just feedforward activation is involved in unconscious processing.

The argument that feedforward activation of visual areas is sufficient for unconscious perception is based on the premise that neurons' receptive field properties and response selection can be engaged by simple activation of cortical areas. Although salient visual features (such as location) can be assumed to require mere feedforward activation, resolving more perceptually demanding stimuli might require feedback processing (e.g. Pitts et al., 2011). We have also suggested that this (unconscious) disambiguation and amplification of visual representations might explain why the emergence of NCC is sometimes delayed (Studies I and III).

4.3. Conclusions and future directions

During the last few years, the discussion concerning the NCC has concentrated on feedback activity, and there is strong evidence that feedback connections are involved in visual consciousness (Pascual-Leone & Walsh, 2001). Since feedback connections are a ubiquitous feature of the brain (Pollen, 1999; Gilbert & Sigman, 2007), a critical question is what separates consciousness-related feedback activity from unconscious feedback activity. According to Lamme's theory, the crucial element of conscious processing is not mere feedback, but *recurrent processing*. This can be interpreted as coherent and sustained reciprocal communication between different cortical areas

(Lamme, 2010). However, a similar mechanism has been proposed to underlie neuronal communication in general (Fries, 2005), underlining the need for a more comprehensive view of the neural mechanisms underlying consciousness. A potential answer could be, for instance, the information integration theory of consciousness, which proposes an explanation why the information processed in certain recurrently communicating neural ensembles enters consciousness while others do not (Tononi, 2004). Tononi (2004) proposes that a system's capacity to integrate information determines the system's level of consciousness, whereas the contents of consciousness are provided by the specific relationships between the elements of the system.

A crucial next step in the study of ERP correlates of consciousness is to link the ERP correlates to their neural mechanisms. What exactly happens in visual cortex electrophysiology during VAN? How is VAN related to other features of neural activation (e.g. oscillations)? Although VAN localizes to the ventral visual sites, how do parietal or frontal cortices influence VAN and other electrophysiological correlates of visual consciousness? Finally, as discussed in Study III, it is critical that the relationship of the NCC and cognitive functions such as types of attention and decision making are further studied.

TMS offers an excellent opportunity to investigate the contributions of not only lower but also higher levels of cortical areas to unconscious perception. A shortcoming for most TMS-induced blindsight studies (e.g. Studies IV and V) is that they concentrate merely on single TMS SOAs or pool a number of SOAs together (for practical reasons and to maximize statistical power). Hence, on the whole the studies have not been able

to directly test the hypothesis that feedback stages of visual processing are crucial for unconscious vision (but see, Koivisto, et al., 2010). Another problem for TMS studies is that due to small sample sizes they might lack statistical power to observe the small effect-sizes associated with unconscious processing (e.g. Study V).

In conclusion, the results of this thesis support the view that conscious vision is enabled by a series of processing stages. The processes that most closely correlate with conscious vision take place in the ventral visual cortex (~200 ms after stimulus presentation, VAN), although preceding time-periods and contributions from other cortical areas such as the parietal cortex are also indispensable. Unconscious vision relies on intact early visual activation, although the location of visual stimulus may be unconsciously resolved even when activity in the early visual cortex is interfered with.

6. References

Alkire, M. T., Hudetz, A. G. & Tononi, G. (2008). Consciousness and anesthesia. *Science*, 322, 879-880.

Amassian, V. E. et al. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalography and Clinical Neurophysiology*, 74, 458-462.

Andreassi, J. J., De Simone, J. J. & Mellers, B. W. (1976). Amplitude changes in the visual evoked potential with backward masking. *Electroencephalography*, 41, 387-398.

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

Baars, B., (1988). *A Cognitive Theory of Consciousness*. New York: Cambridge University Press.

6. References

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

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

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

Beckers, G. & Zeki, S. (1995). The consequences of inactivating areas V1 and V5 on visual motion perception. *Brain*, 118, 49-60.

Block, N. (1995). On the confusion about a function of consciousness. *Behavioral and Brain Sciences*, 18, 227-247.

Boyer, J. L., Harrison, S. & Ro, T. (2005). Unconscious processing of orientation and color without primary visual cortex. *Proceedings of the National Academy of Sciences*, 102, 16875-16879.

Breitmeyer, B. G., Ro, T. & Singhal, N. S. (2004). Unconscious color priming occurs at stimulus- not percept-dependent levels of processing. *Psychological Science*, 15, 198-202.

Breitmeyer, B. G., Ro, T. & Ögmen, H. (2004). A comparison of masking by visual and transcranial magnetic stimulation: implications for the study of conscious and unconscious visual processing. *Consciousness and Cognition*, 13, 829-843.

Breitmeyer, B. G., Ögmen, H. & Chen, J. (2004). Unconscious priming by color and form: Different processes and levels. *Consciousness and Cognition*, 13, 138-157.

Breitmeyer, B. & Ögmen, H. (2006). *Visual Masking*. 2 ed. Oxford University Press.

Bridgeman, B. (1988). Visual evoked potentials: Concomitants of metacontrast in late components. *Perception and Psychophysics*, 43, 401-403.

Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, 36, 96-107.

Camprodon, J. A., Zohary, E., Brodbeck, V. & Pascual-Leone, A. (2010). Two phases of V1 activity for visual recognition of natural images. *Journal of Cognitive Neuroscience*, 22, 1262-1269.

Cavianto, M. et al., (2012). Preservation of auditory P300-like potentials in cortical deafness. *PLOS One*, 7, e29909.

6. References

- Chalmers, D. (1996). *The Conscious Mind*. Oxford: Oxford University Press.
- Christiansen, M. S., Kristiansen, L., Rowe, J. B. & Nielsen, J. B. (2008). Action-blindsight in healthy subjects after transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences of USA*, 105, 1353-1357 .
- Corthout, E. et al. (1999). Two periods of processing in the (circum)striate cortex as revealed by transcranial magnetic stimulation. *Neuropsychologia*, 37, 137-145.
- Crick, F. & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6, 119-126 .
- Crick, F. & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, 2, 263-275.
- Dehaene, S. et al. (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. *PLOS Biology*, 5, e260.
- Di Russo, F., Martínez, A. & Hillyard, S. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex*, 13, 486-499.
- Dienes, Z. & Seth, A. (2010). Gambling on the unconscious: A comparison of wagering and confidence ratings as measures of awareness in an artificial grammar task. *Consciousness and Cognition*, 19, 674-681.
- Fisch, L. et al. (2009). Neuronal "ignition": Enhanced activation linked to perceptual awareness in human ventral stream visual cortex. *Neuron*, 64, 562-574.
- Foxe, J. J. 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.
- Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9, 474-480.
- Gawne, T. J., Kjaer, T. W., & Richmond, B. J. (1996). Latency: another potential code for feature binding in the striate cortex. *Journal of Neurophysiology*, 76, 1356-1360.
- Gaillard, R. et al. (2009). Converging intracranial markers of conscious access. *PLOS Biology*, 7, e1000061.

6. References

- Gilbert, C. D. & Sigman, M. (2007). Brain states: Top-down influences in sensory processing. *Neuron*, 54, 677-696.
- Heywood, C. A. & Cowey, A. (1999). Cerebral Achromatopsia. In: G. W. Humphreys, ed. *Case Studies in the Neuropsychology of Vision*. Hove: Psychology Press, 17-39.
- 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.
- Hochstein, S. & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36, 791-804.
- Holmes, G. (1918). Disturbances of vision by cerebral lesions. *British Journal of Ophthalmology*, 2, 353-384.
- Hupe, J. M. et al. (2001). Feedback connections act on the early part of the responses in monkey visual cortex. *Journal of Neurophysiology*, 85, 134-145.
- Jacobs, C. & Alexander, T. S. (2012). Behavior in oblivion: The neurobiology of subliminal priming. *Brain Sciences*, 2, 225-241.
- James, W. (1892/2001). *Psychology: The Briefer Course*. New York: Dover Publications Inc.
- Kim, C. Y. & Blackie, R. (2005). Psychophysical magic: Rendering the visible 'invisible'. *Trends in Cognitive Sciences*, 9, 381-388.
- Klimesch, W. (2011). Evoked alpha and early access to the knowledge system: The P1 inhibition timing hypothesis. *Brain Research*, 1408, 52-71.
- Koch, C. & Tononi, G. (2008). Can machines be conscious? *IEEE Computer*, June, 54-59.
- Koivisto, M., Kainulainen, P. & Revonsuo, A. (2009). The relationship between awareness and attention: Evidence from ERP responses. *Neuropsychologia*, 47, 2891-2899.
- 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., Railo, H. & Salminen-Vaparanta, N. (2011). Transcranial magnetic stimulation of early visual cortex interferes with subjective visual awareness and objective forced-choice performance. *Consciousness and Cognition*, 20, 288-298.

6. References

- Koivisto, M. & Revonsuo, A. (2008). The role of selective attention in visual awareness of stimulus features: Electrophysiological studies. *Cognitive, Affective, & Behavioural Neuroscience*, 8, 195-210.
- Koivisto, M. & Revonsuo, A. (2010). Event-related brain potential correlates of visual awareness. *Neuroscience and Biobehavioral Reviews*, 34, 922-934.
- Koivisto, M., Revonsuo, A., Henriksson, L. & Railo, H. (2012). Unconscious response priming by shape depends on geniculostriate visual projection. *European Journal of Neuroscience*, 35, 623-633.
- Koivisto, M., Revonsuo, A. & Lehtonen, M. (2006). Independence of visual awareness from the scope of attention: An electrophysiological study. *Cerebral Cortex*, 16, 415-424.
- 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. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7, 12-18.
- Lamme, V. A. F., (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, 1, 204-240.
- Lau, H. & Rosenthal, D. (2011). Empirical support for higher-order theories of conscious awareness. *Trends in Cognitive Sciences*, 15, 365-373.
- Laureys, S. (2005). The neural correlate of (un)awareness: lessons from the vegetative state. *Trends in Cognitive Sciences*, 9, 556-559.
- Leh, S. E., Mullen, K. T. & Ptito, A. (2006). Absence of S-cone input in human blindsight following hemispherectomy. *European Journal of Neuroscience*, 24, 2954-2960.
- Liu, Y., Paradis, A.-L., Yahia-Cherif, L., Tallon-Baudry, C. (2012). Activity in the lateral occipital cortex between 200 and 300 ms distinguishes between physically identical seen and unseen stimuli. *Frontiers in Human Neuroscience*, 6.
- Logothetis, N. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society B*, 353, 1801-1818.
- Logothetis, N. K. & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, 18, 761-763.
- Luck, S. (2005). *An Introduction to the Event-Related Potential Technique*. Cambridge, MA: MIT-Press.

6. References

- Macknik, S. L. & Martinez-Conde, S. (1998). The spatial and temporal effects of lateral inhibitory networks and their relevance to the visibility of spatiotemporal edges. *Neurocomputing*, *58*, 775-782.
- Makeig, S. et al., (2002). Dynamic brain sources if visual evoked responses. *Science*, *295*, 690-694.
- Mesulam, M.-M. (1999). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society B*, *354*, 1325-1346.
- Milner, D. A. & Goodale, M. A. (2006). *The Visual Brain in Action*. New York: Oxford University Press.
- Nagel, T. (1974). What is it like to be a bat. *Philosophical Review*, *4*, 435-350.
- Ojanen, V., Revonsuo, A. & Sams, M. (2003). Visual awareness of low-contrast stimuli is reflected in event-related 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. *Brain*, *124*, 1417-1425.
- Overgaard, M. (2011). Visual experience and blindsight: a methodological review. *Experimental Brain Research*, *209*, 473-479.
- 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.
- Pascual-Leone, A. & Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, *292*, 510-512.
- Panagiotaropoulos, T., Deco, G., Kapoor, V., & Logothetis, N. (2012). Neuronal discharges and gamma oscillations explicitly reflect visual consciousness in the lateral prefrontal cortex. *Neuron*, *74*, 924-935.
- Pins, D. & ffytche, D. (2003). The neural correlates of conscious vision. *Cerebral cortex*, *13*, 461-474.
- Pitts, M. A., Martínez, A. & Hillyard, S. (2011). Visual processing of contour patterns under conditions of inattentive blindness. *Journal of Cognitive Neuroscience*, *24*, 287-303.
- Pollen, D. A. (1999). On the neural correlates of visual perception. *Cerebral Cortex*, *9*, 4-19.

6. References

- Ramsøy, T. Z. & Overgaard, M. (2004). Introspection and subliminal perception. *Phenomenology and the Cognitive Sciences*, 3, 1-23.
- Revonsuo, A. (2006). *Inner Presence. Consciousness as a biological phenomenon*. Cambridge, Massachusetts: The MIT-press.
- Rockland, K. S. (2003). Feedback Connections: Splitting the arrow. In: J. H. Kaas & C. E. Collins, eds. *The Primate Visual System*. CRC Press, Boca Raton, Florida, pp. 387-405.
- Ro, T. (2008). Unconscious vision in action. *Neuropsychologia*, 46, 379-383.
- Sack, A. T. et al. (2009). Symbolic action priming relies on intact neural transmission along the retino-geniculo-striate pathway. *NeuroImage*, 44, 284-293.
- Salminen-Vaparanta, N. et al. (2012). Is selective primary visual cortex stimulation achievable with TMS? *Human Brain Mapping*, 33, 652-665.
- Salti, M., Bar-Haim, Y. & Lamy, D., (in press). The P3 component of the ERP reflects conscious perception, not confidence. *Consciousness and Cognition*.
- Schmidt, T. (2000). Visual perception without awareness: Priming responses by color. In: T. Metzinger, ed. *The Neural Correlates of Consciousness*. Cambridge(MA): MIT Press, pp. 157-169.
- Sergent, C., Baillet, S. & Dehaene, S. (2004). 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, 720-728.
- Silvanto, J., Lavie, N. & Walsh, V. (2005). Double dissociation of V1 and V5/MT activity in visual awareness. *Cerebral Cortex*, 15, 1736-1741.
- Stoerig, P. & Cowey, A., (1992). Wavelength discrimination in blindsight. *Brain*, 115, 425-444.
- Tamietto, M. et al. (2008). Collicular vision guides nonconscious behaviour. *Journal of Cognitive Neuroscience*, 22, 888-902.
- Thielscher, A., Reichenbach, A., Uğurbil, K. & Uludağ, K. (2010). The cortical site of visual suppression by transcranial magnetic stimulation. *Cerebral Cortex*, 20, 328-338.
- Titchener, E. B. (1928). *A Text-Book of Psychology*. New York: MacMillan.

6. References

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

Tononi, G. (2004). An information integration theory of consciousness. *BMC Neuroscience*, 5.

Walsh, V. & Pascual-Leone, A. (2003). *Transcranial Magnetic Stimulation - A Neurochronometrics of Mind*. Cambridge, Massachusetts: The MIT Press.

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

Watson, J. B. (1913). Psychology as the behaviourist sees it. *Psychological Review*, 20, 158-177.

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.

Vorberg, D. et al. (2003). Different time courses for visual perception and action priming. *Proceedings of the National Academy of Sciences*, 100, 6275-6280.

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

Zeki, S. & Bartels, A. (1999). Towards a theory of visual consciousness. *Consciousness and Cognition*, 8, 225-259.

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

Ögmen, H., Breitmeyer, B. B. & Melvin, R. (2003). The what and where of visual masking. *Vision Research*, 43, 1337-1350.