On the fate and consequences of conscious and non-conscious vision

Thesis by

Lisandro Nicolas Kaunitz

Supervisor: Professor Dr. David Melcher

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"Uno es uno y sus circunstancias", Jose Ortega y Gasset.

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Chapter 1

Introduction

The study of consciousness

What we consciously see in our everyday life is not an exact copy of the information that our eyes receive from the external world. Our brain actively elaborates and transforms the light that impinges onto the two dimensional surface of our retinas to create complex three dimensional scenes full of colorful objects of different shapes and sizes, motion and depth. Our visual perception is not a passive reception of information: our brain actively decodes and separates the retinal information into relevant and significant objects and compares this information with previous memories.

One remarkable example is the ability of the visual system to decode the information that arrives from the eyes into recognizable visual objects and scenes. We are able to recognize objects even under conditions of low illumination or low contrast, when these objects are

partially occluded, presented among other objects or when they are defined by textures, for example. In addition to this process of recognition, the visual system generates the conscious sensations of those objects and scenes.

Even though we need our eyes to see the world these are not enough by themselves to generate visual perception. The light impinging on our retinas needs further elaboration in higher areas of the brain to generate perception. Several situations in which vision is separated from perception can demonstrate this. For example, we can imagine some object with our eyes closed in our "mind's eye" or we can generate images in our dreams that are completely independent of external stimulation. Experimentally, it is possible to manipulate visual perception while keeping visual stimulation to the eyes constant. Examples of this are the changes in perception that occur with multistable phenomena (i.e, as with the Necker cube) or when subjects are presented with dissimilar images to each eye, a condition called binocular rivalry.

Without a functioning visual brain we are not able to properly see. Lesions to the visual cortex produce a wide variety of visual deficits ranging from blindness to achromatopsia (the impossibility of perceiving color), akinetopsia (the impossibility of perceiving motion) and/or visual agnosias (the difficulty in recognizing objects through vision). Also, extensive neuroimaging experiments have shown that visual information causes the activation of wide areas of the brain and the role of many of these areas has been studied in the last two decades. However, currently the neuroscientific study of perception can only be addressed with limited resources. We cannot measure the activity of the 10 billion neurons that constitute our brain. Neither can scientists manipulate the human brain by disrupting, modifying or altering the activity of neuronal circuits. The current imaging methods for studying the brain can only provide incomplete information at different spatial levels of analysis and with different temporal resolutions. Thus, the conclusions that neuroscientists we can extract from these data are only partial attempts to reach to a better understanding of the functioning of the brain.

Despite these limitations, few neuroscientists would disagree today with the fact that visual perception has a basis on distributed neuronal circuits in the brain. In the same line of thought, it is agreed that there must be circuits of neurons that code for the conscious perception of those objects.

Consciousness has always been considered as one of the major mysteries of life. The study of the origins of sensations and "feelings" from the operations of our brain is for many scientists one of the final challenges for the biological sciences (Koch, 2003). The mystery of consciousness is considered to be at the same level of the mystery of the creation of the universe and the mystery of the origin of life out of inanimate matter.

The topic of this thesis is the study of visual consciousness. Considering its complexity, we do not intend to provide a final answer to the explanation of consciousness. Instead, this thesis will focus on the study of vision and it will describe some properties of conscious vision as opposed to unconscious vision. We will explore the fate of unseen vision: the information that reaches the retina but that does not generate any conscious sensation. We will analyze the processing and limits of unseen visual stimuli and we will compare them with conscious processing of the same objects. In doing this we expect to shed light into some of the properties of conscious and unconscious visual perception and on the role that visual awareness might have had in evolution.

The pre-scientific approach

The question about the source of our sensations dates from the very beginnings of civilization. It is in the very nature of what has been called as the mind-body problem for philosophers and psychologists of all ages.

Until the 19Th century the empirical study of the brain was highly limited due to technical resources and therefore the field of study of our cognitive processes was dominated by speculative and philosophical ideas about the mind. From a philosophical perspective, the

study of consciousness has corresponded from the times of Aristotle and Plato to the study of the soul/body problem (Plato et al., 1997). The question of how our "feelings" emerge from our bodies, together with the questions about the origin of the universe and the origin of life, have constituted the main questions about existence for human beings since the beginning of civilizations.

From the middle of the nineteenth century the mind-body problem has been transformed into the mind-brain problem. Growing evidence from brain-damaged patients indicated that our perception of the external world, the feelings from our own body and the workings of our mind critically depend on the proper functioning of the brain (though the idea that the brain is the center of our mind dates back to the ancient Greeks and Egypt's it fell into oblivion for the western cultures for more than 2000 years, maybe as a consequence of its incompatibility with the main catholic religious ideas).

In his 1916 essay "Introductory lectures on psycho-analysis" Sigmund Freud described what he called the three biggest narcissistic injuries of humanity: the discovery that the earth is not the center of the universe, the finding that human beings are the product of years of evolution among species and the fact that most of our mental processes are not conscious to ourselves. In Freud's terms, the last of these narcissistic injuries made reference to the psychological discovery of cognitive processes such as thoughts, desires or impulses that were not fully aware to the subject but that nevertheless had significant effects on behavior. These ideas were corroborated by Freud in the origin of the symptoms of his neurotic patients and in the dreams, lapses and involuntary errors of healthy subjects (Freud, 1901). Undoubtedly, the first psycho-analysts, by showing how psychological processes could indeed affect body health, were the pioneers and founders of modern psycho-somatic medicine. Nevertheless Freud, a neurologist and active researcher in neuroscience during his youth, could never make use of sophisticated ways of measuring brain activity at the time he lived and the information about the workings of the nervous system was still in a preliminary phase of exploration (i.e, the discovery of the neuron as the units of the organization of the nervous

system was discovered by Santiago Ramon y Cajal 1905 (Cajal, 1995).

In spite of these limitations, the advent of Psycho-analysis was a major step in the twentieth century towards the study of consciousness. It helped to promote and make available to a wide audience the awesome fact that most of our cognitive processes take place outside of awareness (a fact that is acknowledged by today's cognitive theories and models of the brain). In this way, the Psycho-analysis movement helped to give publicity to the study of awareness. However, the use of Psycho-analysis as a psychological research technique was very early criticized for lacking a rigorous scientific method. As Karl Popper, one of the most renown critics of psychoanalysis, stated out: most of the psycho-analytic models and theories regarding the workings of the unconscious could not be tested or refuted, and therefore were not falsifiable (Popper, 1992). In Popper's own words Psycho-analysis was termed a "pseudoscience".

Most of the theories of Psycho-analysis remained therefore segregated from the theoretical frameworks of cognitive psychologists. Moreover, one of the responses to psychoanalysis was a strong move of many departments of psychology of American Universities towards behaviorism, which might be considered one of the main causes of the oblivion that the study of consciousness suffered for several decades of the twentieth century. During the years of behaviorism the study of consciousness was considered as an exclusively philosophical problem not worth of scientific inquiry.

From the 1980's, and with the advent of cognitivism and an increasing interest on the processes that reside inside the "black box" of our mental operations, the study of consciousness has become again an accepted scientific field of research. An international organization, the Association for the Scientific Studies of Consciousness (ASSC, `www.assc.org`), together with specialized journals such as "Consciousness and Cognition", "Psyche" and "Journal of Consciousness Studies", have been created. In many research centers, departments and universities around the world the scientific study of consciousness is considered again a serious topic of debate and research. The implications of the study of consciousness for areas

such as the workings of anesthesia, the diagnosis of comatose and vegetative patients, the development of neuroprotheses and for the knowledge of the workings of the sensory systems could not be avoided or delayed anymore. The study of the consciousness entered again into the realm of scientific exploration.

A scientific approach

On the mystery of sensations

Perhaps one of the most striking demonstrations of the mystery of the origin of sensations and of the mind/body problem comes from the electrical recordings and stimulation of cortical and subcortical brain areas of awake human beings. On every day, brain surgical interventions in awake patients are routinely carried out around the world in subjects that suffer from diseases such as intractable epilepsy (i.e, patients whose epileptic seizures do not respond well to medication and cannot therefore lead a normal life) or brain tumors. Under these circumstances, for same patients the last and most efficient resource to alleviate their symptoms is surgical intervention.

The epileptic surgeries are primarily focused on identifying and extracting the cortical source of epileptic activity. For this reason the patient's skull is opened and electrodes are positioned on or implanted into several brain cortical areas in order to monitor the sources of epilepsy. Usually, patients are kept in ward for around week while the brain activity is monitored. Once the source areas of the epileptic seizures are identified patients can undergo brain surgery during which they are kept awake for some time so that their online reports during the intervention can guide and help surgeons to minimize the risk of damaging brain areas important for language, memory and/or other cognitive processes. These clinical situations provide a unique opportunity for neuroscientists to directly register the activity of the cortex and to study the responses of subjects to direct electrical stimulation of the brain electrically stimulate the human brain to electrical stimulation.

One of the first researchers to perform these interventions was the neurologist Wilder Penfield at the Montreal Neurological Institute in Canada. Starting in the early 1930s, Penfield and his colleagues were one of the first to describe the functional properties of the cerebral cortex using electrodes to record and stimulate the human brain in controlled settings. Employing these interventions they were able to produce the first functional maps of the cerebral cortex, which shed light into the human somatosensory and motor homunculus (Penfield, 1978).

Penfield's research is a nice demonstration of the limits of the scientific materialistic point of view. For decades he worked applying electrical stimulation *directly on the brain*, while concurrently registering the reports of his patients. As a neurosurgeon trained to detect the symptoms of the malfunctioning of the brain originating from epileptic seizures, tumors, traumatic injuries, isquemia, or hemorrhages, Penfield knew better than anyone else that without a properly functioning brain there cannot exist a properly working mind. Interestingly, after more than 30 years of studying the electrical responses of the brain Penfield addressed himself the problem of consciousness. In spite of all the before-mentioned evidence on brain dysfunction, Penfield appeared to surrender himself to the mystery of the origin of the mind, acknowledging that the dualist hypothesis of the mind-brain problem could not be *empirically refuted* (Penfield, 1978).

Hard and easy problems

What Penfield called in his book "The mystery of the mind" today has been formulated in philosophical terms as the *hard and easy problem* (Chalmers, 1995). In the realm of philosophy of the mind (the philosophical study of the relationship between mind and brain) philosophers have defined "Qualia" as the personal subjective conscious experiences. The explanation of whether qualia really exist and if so how they emerge from the physical brain, is the main topic of the philosophical debate.

According to philosopher David Chalmers, the study of consciousness can be divided into

a hard and an easy problem. The easy problem corresponds to the study of the biological models whose activity correlate with the contents of consciousness. These correlation is called the "neural correlates of consciousness" and is usually known as NCC. The hard problem regards to the difficulty of still explaining consciousness even with a precise knowledge of the physical phenomena that causes it. It refers to "the explanatory gap" or the impossibility of explaining conscious subjective experience beyond a simple correlation.

Other philosophical lines of thought do not ascribe to Chalmers point of view. The philosopher Daniel Dennet holds one of the most critical positions of Chalmers proposal (for length purposes we cannot review all of them here). Dennet overtly denies the idea that there is a hard problem. For this theorist, "qualia" is a term that cannot be unequivocally defined and for that purpose the problem of consciousness is ill-posed. In Dennet's argument, the phenomenon of having experience is nothing more than the performance of functions or the production of behavior (Dennett, 2004). Once the easy problem will be addressed, nothing more will be needed to say about consciousness. As opposed to Chalmers he does not consider consciousness as a fundamental feature of the universe but a process that will be fully explained one day by natural phenomena (Dennett, 1996).

An experiment of imagination

For a short moment, let's imagine a future in which neuroscience has evolved to the point of discovering the neural codes of vision. As proposed by some philosophers, we can assume that in this future scenario neuroscientists will know all there is to know about neuronal connections, neurotransmitters, and the flow of information in the brain. They will also be able to build neuroprotheses and external devices (presumably of silicium) that will be assembled to the cortical and subcortical neural circuits. These devices will be connected to the brain and at the same time to an external computer: they will constitute a highly accurate and sophisticated brain-computer interface which will allow communication with the brain by sending and receiving the appropriate electrical signals.

Thanks to these devices neuroscientists will be able to tell, for example, what color a subject is seeing on a screen by just looking at recordings in neural signals. Also, they will be able to program specific patterns of electrical stimulation to induce subjects to perceive a particular color (for simplicity let's think of the simplest situation, just images of plain backgrounds, each one of a different color). Neuroscientists will know which are the neural mechanisms that code, for example, for the color "red" and for the color "blue". Whenever the appropriate electrical activity associated with "red" is generated the subject being stimulated will report seeing red, and the same will be for "blue".

At this point neuroscientists would be able to manipulate subject's perception but they would still not know *why* a sensation occurs. They will know what types of neural activity correlate with subjective perception and what types of activity are not sufficient to produce conscious perceptions, but in any case the hard problem would still be present, as mysterious as usual. Will these scientists be in a different position as that of Penfield? A partial answer to this question is that we should ask at that point in time whether the information about *why* there is any conscious sensation is of interest anymore.

A Scientific explanation of consciousness

Without hesitation, the hard problem is today a limit that cannot be overlooked in the study of consciousness: even though the majority of the scientific community advocates for a materialistic point of view, we cannot refute the dualistic hypothesis of the mind/brain problem. There is a clear limit here and we are in no better position than that of Wilder Penfield to explain the origin of sensations. However, the scientific study of visual awareness should not be stopped by this fact. Instead, the actual view is that we can study the correlations, the neural correlates of consciousness (NCC), and leave history to decide whether the hard problem will be ever solved or whether it will become of no interest for scientists anymore.

The scientific approach to consciousness, in Christoph Koch terms, is "an empirical one": to try to gain knowledge on the psychological and brain processes that correlate with visual

awareness. The ultimate goal of the scientific study of visual awareness is to find out whether a pattern of brain activity exists in neural circuits, ideally across species, that correlates with the appearance of conscious sensations. This pattern could be content specific -one pattern for each sensation that we perceive, a problematic hypothesis considering the huge number of sensations that we are capable of perceiving- or content unspecific -one general neural mechanism for all conscious percepts-. In any case, the actual state of the scientific study of visual awareness is reduced to a correlation study.

The experiment of imagination posed before might look like science fiction for the reader. However, is it not the main goal of the research on neuroprotheses to reach one day to the development of devices that can restore sight to the blind or hearing to the deaf? Is it not the objective of brain-computer interfaces and visual neuroscience to create devices that can communicate brain activity with external devices?

The main subject of the present thesis is the *scientific* study of visual awareness. For practical reasons, we will only focus on the visual system and not on awareness as a general process. Throughout the thesis we will refer to awareness as a synonym of consciousness and both terms will be used interchangeably. We will use an operational definition of visual awareness. The search for the neural correlates of visual awareness will be defined as the search for the "necessary and sufficient neural activity that is able to produce a particular subjective experience" (Koch, 2003). This is the main agreed definition of visual awareness employed in the scientific approach. Even though this definition might seem incomplete for some scholars most scientists studying visual awareness agree on that the problem in defining awareness is not very different from the problem of defining "light" of a "gene" (Koch, 2003).

If we consider the operational definition of awareness we can start asking questions that can be empirically addressed: What are the main differences between conscious and unconscious percepts? Can we differentiate the neural activity of two invisible visual stimuli? How early in visual processing can we distinguish processing for visible visual stimuli or what are the first marks of visual awareness? and what function plays visual awareness on visual

processing?

Theoretical frameworks of visual awareness

Most of the motor, cognitive and sensory operations that our brain performs on every day take place outside of awareness. We are usually aware of the final stages of our cognitive processes but greatly unaware of the way these processes are initiated and of the necessary steps to achieve them. Examples abound in the sensory, motor and cognitive domain. While we speak we are not aware of the mechanisms that we employ to continuously select the syntactical order of the words we are uttering: we simply choose the contents of what to say and several automatic processes get in charge of choosing the correct order of articles, verbs and nouns. Similarly, when we need to recover a memory we simply "instruct" ourselves to do so and approximately a second later the memory pops-out magically into our conscious mind, without given us not even a single clue about the process of finding and selecting a memory among several past events. We are also as much unaware of the mechanisms that we employ to recover memories as we are of those we use to initiate and execute a motor command. In the sensory domain of vision, we simply open our eyes and the visual world magically appears before us. But how does the brain segregate stimuli from the background in the visual field, calculate depth, distance or the speed of the objects?

Strong evidence shows that most of our visual sensory operations are run in a non-conscious manner. What are the implications for the study and conceptualization of consciousness? One of the psychologists that provided a theoretical framework for the understanding of the automatic processes that bypass awareness was Bernard Baars (Baars, 1988). In his book "A Cognitive Theory of Consciousness" Baars proposed that the empirical approach to the study of the NCC relied on "contrastive phenomenology", a method in which minimal contrasts between conscious and unconscious stimuli are used. Contrastive phenomenology is simply the application of the scientific method to the study of conscious-

ness. The key idea here is to study experimental conditions in which the same stimuli is sometimes consciously perceived and sometimes not. In this way researchers can observe the behavioral and physiological differences between conscious and unconscious stimuli and draw conclusions on the particularities of conscious processing.

Baars proposed a theoretical framework called the Global Workspace to explain conscious access. At each moment in time, only a limited amount of information can enter the global workspace and become conscious. The rest of the processes remain unconscious. In his theoretical model Baars understood consciousness as "access consciousness", which refers to the specific processing of a piece of information that subjects can verbally report. By consciousness, he referred to the content of consciousness and not to states of consciousness (such as wakefulness, dreamless sleep or coma).

The main hypothesis of the global workspace framework states that awareness plays the role of synthesizing and broadcasting information to many areas in the brain. One of the most compelling examples provided by Baars to support this hypothesis is perhaps neurofeedback. If a subject is implanted with an electrode in his hand that registers the activity of terminal fibers of one motor neuron, and the spiking activity is amplified with a speaker and presented online to the subject, he/she can learn to voluntarily control the firing of the neuron within some practice period (usually after half an hour). This learning process occurs *only if conscious feedback* is given to the subject. The same results can also be seen using EEG recordings or electromiographic recordings (for example in the case of patients that need to learn how to relax the muscles of the back in order to alleviate strong muscular contractures, which can be done in the case that subjects receive conscious feedback of the times at which muscles relax and the times at which muscles contract). Baars claimed that most of the automatic processes that our brain generates can be altered by conscious control with feedback. From this idea he proposed that the role of awareness was to broadcast information to the many automatic modules that process cognitive and motor operations so that they can modify and adjust their behavior. With practice, each new behavior can

become routine and proceed unconsciously.

Stanislas Dehaene and colleagues at the University of Descartes in Paris developed the computational model of the global workspace framework and, in a series of experiments, tested it empirically. To begin with, they introduced a taxonomy in which stimuli could be classified as subliminal, preconscious and conscious (Dehaene et al., 2006). Usually a conscious stimuli is fully attended and aware. Under certain conditions though, as in the case of inattentional blindness, a stimuli that is usually conscious can be unnoticed by an observer due to the lack of attention. Dehaene et al. (2006) called this stimuli preconscious, indicating that they were potentially conscious as its duration and strength are such that it could be seen under normal conditions of attention. On the other hand, the authors defined a separate category of stimuli that they defined subliminal: stimuli whose energy is so weak that cannot be detected consciously. These stimuli conform the last two types of the taxonomy as they can be either attended or unattended (see section on attention and awareness for a better explanation of the influence of attention on nonconscious stimuli).

The main goal of Dehaene and colleagues was to study the link between the global workspace framework and brain activity. Combining subliminal priming and the attentional blink with neuroimaging data such as fMRI, EEG or EcoG recordings they were able to study the differences in brain activity produced by the minimal contrast between conscious and nonconscious stimuli. The main neural correlates of access of sensory stimuli to verbal report were the activation of higher fronto-parietal associative cortices and anterior cingulate areas.

In fMRI experiments, after performing the minimal contrast comparisons between conscious and nonconscious stimuli those were the regions that systematically signaled the presence of sensory consciousness. This result was found in experiments of visual masking (Dehaene et al., 2001), change blindness (Beck et al., 2001; Pessoa & Ungerleider, 2004), attentional blink (Sergent et al., 2005; Marois et al., 2004; Kranczioch et al., 2005) and in a study of visual extinction in a neglect patient (Vuilleumier et al., 2002).

Another important characteristic of the model is that the fronto-parietal activation is accompanied by an amplification in stimulus-specific early sensory areas (Dehaene et al., 2001; Gross et al., 2004). In this way, fronto-parietal activation followed by top-down early sensory areas amplification are considered the most frequent signatures of conscious access.

One of the main conclusions drawn from these experiments was that for the global neural workspace framework early visual activation is necessary but not sufficient for conscious report. Instead, long distance connectivity in fronto-parietal areas and reverberation of neural activity were claimed to be highly correlated with conscious report: "We and others have suggested that, in addition to vigilance and bottom-up activation, a third factor underlying conscious access is the extension of brain activation to higher association cortices interconnected by long-distance connections and forming a reverberating neuronal assembly with distant perceptual areas" (Dehaene et al., 2006).

Their claim is that once long-distant fronto-parietal are activated two main changes happen: this activation can reverberate for a long duration in an unrelated way to sensory fluctuations; and the information can be broadcasted to many brain systems. These two properties are key aspects of conscious processing: "We argue that both properties are characteristic of conscious information processing which in our view is associated with a distinct internal space, buffered from fast fluctuations in sensory inputs, where information can be shared across a broad variety of processes including evaluation, verbal report, planning and long-term memory" (Dehaene et al., 2006). However, one open issue with the interpretation of these results is the distinction of whether the widespread activation of the brain associated with conscious stimuli is the NCC or the consequences of information gaining access to consciousness. Many processes are automatically activated after conscious access but they might not be the NCC by themselves. For example, subjects generate long-term memories, plan actions/strategies and produce verbal reports after a stimuli has become conscious. The behavioral responses to nonconscious stimuli are much more limited (see chapter **??**).

Besides the Global Neuronal Workspace many other theories of conscious processing have

been proposed in the past years. Recently, a core set of principles that are common to these theories started to emerge (Seth, 2007; Dehaene & Changeux, 2011). The dynamic core hypothesis (Edelman, 1993; Tononi & Edelman, 1998) proposes that every conscious percept is generated by the activity of groups of neurons that are both differentiated (i.e, each content of consciousness is unique and different from the others) and integrated (i.e, each unified representation of the contents of awareness carries more information than its constituent elements). Tononi (2008) derived from this hypothesis a quantitative mathematical measure of information integration which he called ϕ. This measure was included in his information integration theory of consciousness. High values of ϕ are achieved through thalamocortical reentrant and recurrent activity and would indicate conscious experience. Even though the proposal has raised great interest among researchers studying visual awareness, it has still not been as much tested as the global workspace framework.

Similarly to the dynamic core hypothesis, for Llinás et al. (1998) conscious contents depend on a thalamocortical closed-loop. In this line of research Crick & Koch (1995, 2003) first argued that the principal mechanism of the thalamocortical closed-loop was reverberating activity in the gamma band around 40 Hz, but this idea was later discarded. However, their claim that the reverberating activity should be later in time (similar to the global workspace sustained activity principle) was in agreement with the proposals of Lamme and colleagues who suggested that bottom-up processing is not sufficient for conscious access. In their model, recurrent feedback signals from non sensory cortical areas are fundamental to conscious perception.

As mentioned above, a chain of sensory, cognitive and motor processors can unfold without our awareness. However, conscious perception seems needed for the flexible control of their execution (i.e, for inhibition, repetition, or serial chaining of a task). For this reason Posner & Rothbart (1998) proposed that only information represented in an "executive attention" system becomes conscious. This supervision system is associated with prefrontal cortex activity and is thought to regulate early sensory-motor routines.

The presentation of a conscious stimulus renders temporarily unable to consciously perceive a second stimuli presented in a time window shortly after. This phenomena was termed the "attentional blink" (Shapiro et al., 1997). Many psychological models take the data from the attentional blink paradigm along with the evidence from the psychological refractory period to propose that conscious processing is serial and has a later central bottleneck (Pashler, 1994) or second processing stage (Chun & Potter, 1995). A serial processing system: for these theories access consciousness depends on a serial processing of one object at a time while non-conscious stimuli can occur in parallel.

On attention and awareness

Attention and awareness have always been close concepts: our common sense tells us that whenever we direct our attention to an object in the visual world we become aware of that object. In more formal terms, attention has been theorized as the "gateway to consciousness" based on the way that orienting attention improves the speed and accuracy of our ability to report the presence of a target stimulus (Posner, 1994; Maunsell & Cook, 2002; Moran & Desimone, 1985). Attention and awareness have long been theorized as almost undifferentiated processes for many scholars (Posner, 1994; Mack & Rock, 1998). Attention, though, is not a unitary process: it can be dissociated into vigilance (the state of alertness of a subject), involuntary orienting of attention (the exogenous attraction of attention by external objects) and selective attention (the endogenous, or top-down, direction of attention irrespective of external stimuli). In our work we use as a convention the term attention as a synonym of selective attention. It is necessary to mention that selective attention can be divided into at least three different subtypes: spatial attention (when endogenous attention is directed towards a portion of the visual field), featured-based attention (when focused on a visual feature, i.e color) or object-based attention (when focusing on a combination of visual features that form a visual "object" segregated from the background).

Undoubtedly, selective attention modulates our conscious percepts. Spatial attention enhances detection and discrimination, and it can also shorten reaction times for stimuli located in an attended region of the visual field (Posner, 1994; Maunsell & Cook, 2002). Similarly, feature-based attention can also influence subjects' responses (Schmidt & Schmidt, 2010; Kanai et al., 2006). Interestingly, both spatial and feature-based attention can be directed to stimuli that are invisible to subjects (Naccache et al., 2002; Kanai et al., 2006) and that the attention directed to seen features can spread to unseen stimuli (Melcher et al., 2005).

Recently, based on experiments that manipulate independently the influences of attention and awareness on visual processing it has been proposed that attention and awareness can be dissociable processes (Lamme, 2003; Koch & Tsuchiya, 2007; van Boxtel et al., 2010b). In particular, it was proposed the idea that attention acts an analyzer mechanism whereas visual awareness acts as a synthesizer and/or broadcasting mechanism (van Boxtel et al., 2010b). The question posed is whether attention can occur without awareness and whether awareness can emerge without attention. In the following sections we consider recent research which assesses the assumption that attention is dissociable from awareness.

Attention without awareness

Nowadays, psychologists and neuroscientists can count on several psychophysics techniques to render stimuli invisible. Some examples of those techniques are as visual masking, visual crowding, inattentional blindness, change blindness, color dichoptic masking, binocular rivalry, flash suppression and continuous flash suppression. Different studies have shown that stimuli that are rendered unconscious to subjects produce measurable behavioral responses and are processed in the cerebral cortex (Dehaene et al., 2001; Sergent et al., 2005; Bahrami et al., 2008; Logothetis & Schall, 1989). In addition, a number of psychophysics experiments have demonstrated that attention can modulate invisible stimuli. On the one hand, salient invisible stimuli tend to attract more attention, on the other hand the responses to unseen

stimuli are modulated when attention is diverted from the spatial position where unseen stimuli are being presented. We briefly describe some of these experiments as we consider them important for theorizing the differences between awareness and attention.

The responses to unseen stimuli can be affected by directing or diverting spatial attention from the portion of the visual field where unconscious stimuli are presented. This effect has been demonstrated with priming (Naccache et al., 2002; Finkbeiner & Palermo, 2009) and adaptation (Kanai et al., 2006; Shin et al., 2009) studies. In addition to spatial attention, feature-based attention can also modulate unconscious priming (Melcher et al., 2005).

With regards to sensory adaptation, several studies have shown that the behavioral responses of subjects to unseen stimuli vary with the type of paradigm and the type of stimuli employed. Adaptation to unseen gratings generates afterimages (Tsuchiya & Koch, 2005; van Boxtel et al., 2010a), and the tilt aftereffect (He et al., 1996; Bahrami et al., 2008). Also, unseen translational motion has been shown to generate motion aftereffects (Lehmkuhle & Fox, 1975; Oshea & Crassini, 1981; Wiesenfelder & Blake, 1990).

Endogenous spatial of feature-based attention modulates unseen stimuli. This is the main message of the before-mentioned experiments. Similarly, unseen stimuli can attract attention in a non-conscious automatic way: invisible stimuli that are emotionally salient such as invisible images of naked women (Jiang et al., 2006) or invisible faces gazing directly towards experimental subjects (Stein et al., 2011) tend to attract subjects attention to the portion of the visual field where they are presented.

All this evidence clearly shows that attention can indeed occur without visual awareness. The implications of these studies are that attention and awareness should be considered, at least, as separable processes. However, for a full 2x2 factorial dissociation between awareness and attention we must address first the question whether awareness can occur without attention.

Awareness without attention

The visual system can extract impressive amounts of information from visual images presented as briefly as 30ms, a fact that was demonstrated more than 50 years ago. George Sperling was one of the pioneers in studying the short buffer of visual information of our visual system, the iconic memory (Sperling, 1960). Sperling briefly presented subjects with arrays of letters and asked them to report as many of them as they could. In his experiments, subjects usually reported only a fraction of the briefly presented array of letters but claimed to perceive more than they could remember.

Cleverly, Sperling employed subject's attention to manipulate the incoming information in the arrays. When an attentional cue was presented immediately *after* the presentation of the array of letters subjects were able to report the items that appeared on the spatial location where the cue was pointing to (either employing visual or auditory cues). The key point of these experiments is that subjects were able to perceive more than they can remember and report. The letters that could not be reported without the cue were nevertheless perceived at a first stance.

Nowadays, a new term has been coined for the fast extraction of the general meaning of a visual scene: the "gist" (Biederman, 1972; Fei-Fei et al., 2002). To study the role of awareness without attention Christoph Koch and colleagues at Caltech, California, employed the dual-task paradigm in conjunction with different types of stimuli. In the dual-task paradigm attention is focused on a central task while subjects' responses are measured for a simultaneous peripheral task. Usually a decrement in the peripheral task is expected if subjects are engaged in a central task. However, Koch and colleagues have shown that discriminating Ls from an array of Ts, or discriminating the orientation of red-green discs can be harder than discriminating the gist of a scene. Thus, discriminating the gist of a scene and the category of an object (the gender of a face or a natural scene) is possible under the dual-task conditions (Reddy et al., 2006). The authors claim that this is evidence that the gist of a scene can occur in the "near absence of awareness" (Koch & Tsuchiya, 2007). This

claim has led the author to state that awareness can occur in the absence of attention.

Another piece of evidence to claim a dissociation of awareness from attention comes from the study of afterimages. While a decrease in attention enhances afterimage durations (Suzuki & Grabowecky, 2003) the lack of visual awareness diminishes afterimages (Tsuchiya & Koch, 2005; Gilroy & Blake, 2005). These experiments were conducted, however, with different paradigms and stimuli. For this reason, van Boxtel et al. (2010a) used a 2x2 factorial design with a single paradigm to study the effect of attention and awareness on afterimages. These experiments were in accordance with the findings that awareness increased the duration of afterimages attention decreased it and were interpreted as evidence that attention and awareness can have opposing effects on visual perception.

Different influences of attention and awareness on visual processing

If, as proposed by some scholars (Koch & Tsuchiya, 2007; Lamme, 2003), attention and awareness are different processes then they should carry distinct physiological and behavioral consequences for visual processing. As a general rule both unseen and unattended stimuli generate weaker behavioral responses (Blake et al., 2006) and weaker signals in the visual cortex as compared to attended (Maunsell & Cook, 2002) and conscious stimuli (Dehaene et al., 2001). However, the magnitude of the decrease in behavioral and physiological responses depends on the type of paradigm and stimuli employed. For example, the behavioral effects of presenting unseen stimuli seem to be more deeply suppressed with interocular suppression than with visual masking or the attentional blink.

The lack of awareness or attention does not disrupt orientation adaptation as shown by studied that employed the tilt aftereffect (He et al., 1996; Bahrami et al., 2008). Similarly, unseen translational motion produces an motion aftereffect (Lehmkuhle & Fox, 1975; Wiesenfelder & Blake, 1990) and invisible cues influence motion priming (Melcher et al., 2005). However, while the effects of orientation processing are similar with seen or unseen stimuli, the effect of motion adaptation seem to decay with both unseen and unattended

adaptors (Blake et al., 2006). As for face adaptation, consciousness (Alais & Melcher, 2007; Stein & Sterzer, 2011; Amihai et al., 2011) and attention (Moradi et al., 2005) seem both to be necessary to generate face aftereffects. Afterimages can occur in the absence of awareness (Tsuchiya & Koch, 2005; Gilroy & Blake, 2005) and attention (van Boxtel et al., 2010a). However, van Boxtel et al. (2010a) found that attention and awareness have opposing effects on afterimage formation: an increase in attention decreases the duration of afterimages while a decrease in awareness increases the duration of afterimages.

In general, with unseen images the more complex the stimuli the more difficult to trace any physiological or behavioral effects. The effects found with semantic priming, face processing, manipulable objects, gender discrimination or gaze orientation become harder to track or even disappear as compared to the effects or orientation processing, for example (for a review see Lin & He (2009)). In the hierarchy of visual processing different stimuli are not equally suppressed and suppression occurs at different levels of visual processing (Blake & Logothetis, 2002).

Physiologically, spatial attention influences sensory neurons by making them respond stronger to their preferred stimuli when these fall inside the portion of the visual field that is being attended (Maunsell & Cook, 2002; Moran & Desimone, 1985; Desimone & Duncan, 1995). Spatial attention generates a change in the gain of neurons but not in the tuning of neurons which means that spatial attention does not alter the preferences of sensory neurons for certain stimuli but only increases their sensitivity to their preferred stimuli. On the other side, feature-based attention enhances the responses of sensory neurons (Treue & Trujillo, 1999) but also modulates the tuning responses of neurons (Ling et al., 2009).

Attention has been shown to influence sensory neurons in all areas of visual cortex (Maunsell & Cook, 2002). However, this influence varies across areas, usually with higher areas of visual processing showing stronger modulation effects. This is consistent with the fact that stimuli that are processed in higher visual areas such as faces, houses, animals and manipulable objects show small or null modulation of unattended or unseen stimuli.

Attention and awareness appear to influence visual processing in different ways. Based on these evidence van Boxtel et al. (2010b) have proposed that attention functions as an analyzer mechanism while visual awareness operates as a broadcasting mechanism. It is still not clear from a theoretical perspective why attention and awareness have opposing effects on afterimages and also if this phenomena is strictly limited to afterimages or to other phenomena as well. Similarly, it should be further studied why attention and awareness have a different influence on visual adaptation than on visual perception.

Can attention and Awareness be dissociated?

Salient visual objects and large changes occurring in the visual field can go completely unnoticed when attention is diverted from them. Inattentional blindness (Mack & Rock, 1998; Simons & Chabris, 1999), change blindness (Grimes, 1996) and the attentional blink (Sergent et al., 2005) are a clear demonstration of this. These results seem to suggest that attention is needed for visual awareness. Nonetheless, as manifested by the fact that attention influences unconscious visual processing, attention and awareness can be considered as separate processes.

Recently, it has been proposed that visual awareness can occur in "the near absence of top-down attentional processing" (Koch & Tsuchiya, 2007). This proposal raised the question whether attention is a prerequisite to visual awareness or not. In order to fulfill the requirements for a complete dissociation between attention and awareness one question must be addressed: can visual awareness occur without any kind of attention?

The efforts to prove that awareness and attention are indeed dissociable face some problems. The most serious is the difficulty to demonstrate that awareness can occur in the absolute absence of attention. The problem has its roots in the way attention is measured in psychophysics experiments. As a variable, attention cannot be measured in a quantitative scale (i.e, in a range from 0 to 1) and therefore experimenters can only report the effects that directing or diverting attention has on subjects responses, but not its absolute value.

In this way it is almost impossible to assess a "zero" level of attention: the complete absence of attention cannot be measured experimentally. This drawback has been addressed even by the supporters of the view that attention and awareness can be dissociated (Koch & Tsuchiya, 2007; van Boxtel et al., 2010b). To claim that awareness can occur without attention is then similar to say that a variable A can occur in the absence of a variable B, while being incapable of measuring the absence of B.

Assuming a "near absence" of attention level, the dual task paradigms face another problem. The interpretation of an absence of attention in these paradigms relies on a strong assumption: that selective attention is a unitary resource and that different stimuli in the visual field compete for it. However, as shown by Cavanagh & Alvarez (2005), the existence of multitracking of attention in different hemifields challenges this assumption. There is no way to prove that attention cannot switch fast from one place to the other while subjects are engaged in the dual task paradigm, and so there is no way to prove that a certain amount of attention has not been paid to those stimuli.

In conclusion, attention and awareness can be considered different processes but a complete dissociation still needs to be proved: attention is not sufficient to cause visual awareness in itself but it cannot be ruled out its role as a necessary preliminary step. In spite of these difficulties, attention and awareness seem to differ in their function. Attention can be thought of as an analyzer mechanism that selects information from the visual environment to avoid overloading of the system (van Boxtel et al., 2010b). This mechanism is graded in nature and can be observed even prior to the emergence of visual awareness. On the other side, visual awareness can be considered as an "all or none process" with the function of synthesizing and broadcasting information through different regions of the brain (Baars, 1988). This line of thought is in agreement with the theoretical ideas proposed by Dehaene et al. (2006) and Srinivasan (2008).

Chapter 2

Non-conscious visual motion

Brief history of the study of non-conscious motion

At any moment in time, we are only aware of a fraction of the information impinging on our senses. In order to understand the role of unconscious information in guiding action, it is critical to examine to what extent sensory stimuli are processed outside of awareness. A second, related question is how, and why, some stimuli gain access to awareness and how this access influences the way information about those stimuli is processed.

In the case of vision, it is generally agreed that a stimulus which falls on the retina may activate neural processing even when the participant is unaware of that stimulus (for review, see Kim & Blake (2005); Koch (2003)). It has been proposed that visual information suppressed from awareness reaches subcortical areas (Schmid et al., 2010, 2009; Wilke et al., 2009; Haynes et al., 2005), striate cortex (Crick & Koch, 1995; Blake & Logothetis, 2002; Tong, 2003; Keliris et al., 2010) and early extra-striate cortex (Rees, 2007; Vuilleumier et al., 2002; Sincich et al., 2004). These claims are supported by neurophysiological, neuroimaging and behavioral evidence. In the case of backward masking, there is evidence that information outside of awareness can travel beyond visual areas in order to influence language and decision-making processes in the parietal and frontal lobes (Dehaene et al., 2001; De Pisapia

et al., 2011).

Visual motion provides a particularly interesting domain in which to study unconscious visual processing (Lehmkuhle & Fox, 1975; Oshea & Crassini, 1981; Wiesenfelder & Blake, 1990; Blake et al., 1999; Rajimehr, 2004; Andrews & Blakemore, 1999; Melcher et al., 2005). One advantage of using moving stimuli is that even when motion stimuli are invisible they may still evoke a measurable motion aftereffect (MAE) or "waterfall illusion" (Mather et al., 1998). In the classic version of the waterfall illusion, staring at a pattern of downward movement for a period of seconds then causes a static pattern to appear to move upwards. However, there are more complicated versions of the MAE for complex motion patterns such as expansion, contraction or spiral motions. Since complex motion processing is thought to involve areas beyond primary visual cortex (V1), it is assumed that the presence of a MAE to complex motion reflects processing beyond early monocular cells in V1.

The current study fits into the tradition of studying aftereffects evoked by a non-conscious visual stimulus (for reviews, see Lin & He (2009); Kim & Blake (2005)). Historically, many of the seminal studies on this issue used the method of binocular rivalry (BR) in which different and incompatible images are presented to the two eyes creating a conscious percept that alternates between the two images. Previous studies employing BR have shown that the duration of the MAE for simple linear motion was independent of the duration in which the adaptors were visible (Lehmkuhle & Fox, 1975; Oshea & Crassini, 1981) while for the spiral MAE the magnitude was reduced as a function of the time of visibility of the adaptors (Wiesenfelder & Blake, 1990; Van Der Zwan et al., 1993). Based on these results it has been proposed that the spiral MAE, but not the linear MAE, depends on visual awareness (Wiesenfelder & Blake, 1990). Models of binocular rivalry assume that rivalry suppression occurs prior to processing of such complex stimuli (Wiesenfelder & Blake, 1990; Van Der Zwan et al., 1993).

However, a reduction in size of the spiral MAE does not provide definite evidence of a complete abolishment of the MAE when generated with non-conscious adaptors: the be-

havioral effects of non-conscious stimuli can be reduced in magnitude (Blake et al., 2006) but still measurable. Moreover, binocular rivalry has some important methodological limitations (Kim & Blake, 2005) which should be taken into account when interpreting the prior results. In BR, switches in perceptual dominance occur randomly and the duration of the dominance phases is relatively short. Thus, adaptors cannot be rendered completely invisible for long periods of time. This means that it is possible to measure whether an adaptation aftereffect is independent of the time that a stimulus is visible, but it is not possible to conclusively state that an aftereffect cannot occur without awareness. For this reason, it is useful to test the MAE using continuous flash suppression (CFS), which is a variant of binocular rivalry in which a series of mondrian images are presented in rapid succession to one eye causing the stimulus projected to the other eye to remain invisible for periods of seconds (Tsuchiya & Koch, 2005). With CFS it is possible to directly test aftereffects evoked by a stimulus that never reaches awareness but is nonetheless shown long enough that it would evoke a strong aftereffect if visible.

The second aim of the present study is to investigate the role of inattention on the MAE. Given the complex nature of the relationship between attention and awareness (for reviews, see Dehaene et al. (2006); Lamme (2003); Koch (2003)), it is useful first of all to compare the influences of adding or taking away these two factors on the same behavioral measure (in this case the MAE). Using different MAE types, both simple and complex motion, allows us to test whether these two factors act at the same level of visual processing and whether their influence on the MAE is similar. Moreover, manipulating awareness and attention independently allows us to test the relative independence of these two variables (Kanai et al., 2006; van Boxtel et al., 2010a).

It is well known that attention can influence the strength of adaptation aftereffects (Lankheet & Verstraten, 1995; Alais & Blake, 1999; Bahrami et al., 2008). Attention can, within certain limits, influence the phases of perceptual dominance during binocular rivalry, meaning that subjects are able to exert some attentional control over what they perceive during ri-

valry (Ooi & He, 1999; Mitchell et al., 2004; Meng & Tong, 2004), in particular if they are given a visual task that requires focused attention to the stimuli in one eye (van Ee et al., 2005). Of particular relevance to the current study is the finding that inattention can reduce both the size of the MAE (Chaudhuri, 1990) and the responses of neurons coding motion stimuli (Rees et al., 1997). In addition, attention can influence the processing of both simple translational and spiral motion (Aghdaee, 2005; Aghdaee & Zandvakili, 2005).

The current study compared the effects of attention and of awareness on simple and complex motion. In the first three of our experiments, we measured the magnitude of MAEs for conscious and non-conscious spiral and linear adaptors. In the fourth and fifth experiments, we investigated the effects of inattention on the generation of MAEs with conscious and non-conscious adaptors. In this way, for the first time, we could directly compare the roles of attention and awareness on motion processing in a single study.

Rendering motion invisible with continuous flash suppression

Subjects

Twenty four subjects (11 male, 13 female, mean age 27.5, SD 4.8) participated in 5 experiments: six subjects per experiment with one subject (LK, one of the authors) participating in all experiments and AF (another author) participating in two. All had normal or corrected-to-normal vision and, except for LK and AF, were naïve with respect to the purpose of the task. All participants gave informed consent according to the guidelines of the University of Trento ethical committee.

Stimuli

Stimuli were generated using the Matlab Psychtoolbox (Brainard, 1997) and displayed on a 21" Samsung SyncMaster 753DF monitor (resolution = 1024 x 768; 85Hz refresh rate; gamma corrected) at a viewing distance of 60cm. Stimuli were presented against a light

brown background (CIE coordinates: $X = 0.44, Y = 0.44, Z = 0.12$, luminance 11 cd/m^2, see figure 3.2). For experiments 1, 2 and 4 the adapting stimuli were gabor patches of 2.5 by 2.5 degrees in size, with a spatial frequency of 4 cycles/deg, presented at a speed of 0.6 deg/sec, yielding a temporal frequency of 2.4 Hz. The test probes were equal in every aspect to the adapting gabors except that their speed was 0.02 deg/sec and their temporal frequency 0.08 Hz. For experiments 3 and 5 sine wave rotating spirals were used as stimuli. The spirals were defined by $sin(r + \theta)$ where 'r' is the distance from the origin to a point in the x-y plane and θ is the angular displacement in radians from the positive x-axis. The adaptation spirals were rotated at 67 revolutions per minute (rpm) and the test spirals at 6.7 rpm.

A total of 20 pairs of masks were created for each experiment and one pair was randomly selected for each trial. They had a size of 4x4 degrees of visual angle and were constructed by assigning each dot of the image (2 pixels each, 4.8 arc min size) either a light or a dark luminance value (Figure 3.2). Each trial in the non-conscious condition began with the presentation of a mask that had been randomly assigned with dots in the luminance range of 0 - 0.3 (where 0 means black pixels and 1 means white). This mask was replaced 106ms later by a second mask, which had the exactly same dot distribution with the only difference that the values of 75% of its dots were changed to a luminance range between 0.8 - 1. The masks alternated on the screen every 106ms (9.4 Hz) and the 75% of dots that changed luminance were always the same throughout the trial. In this way only luminance changes were perceived and no first order motion was present from adjacent pixels in the masks.

Experimental procedures

All subjects viewed the stimuli through a pair of red-green anaglyph glasses. Before starting the experiments eye dominance was assessed for each subject (`http://www.archeryweb.com/archery/eyedom.htm/`). The adapting stimuli were always presented in the green channel to the non dominant eye (NDE) and the masks on the red channel to the dominant eye
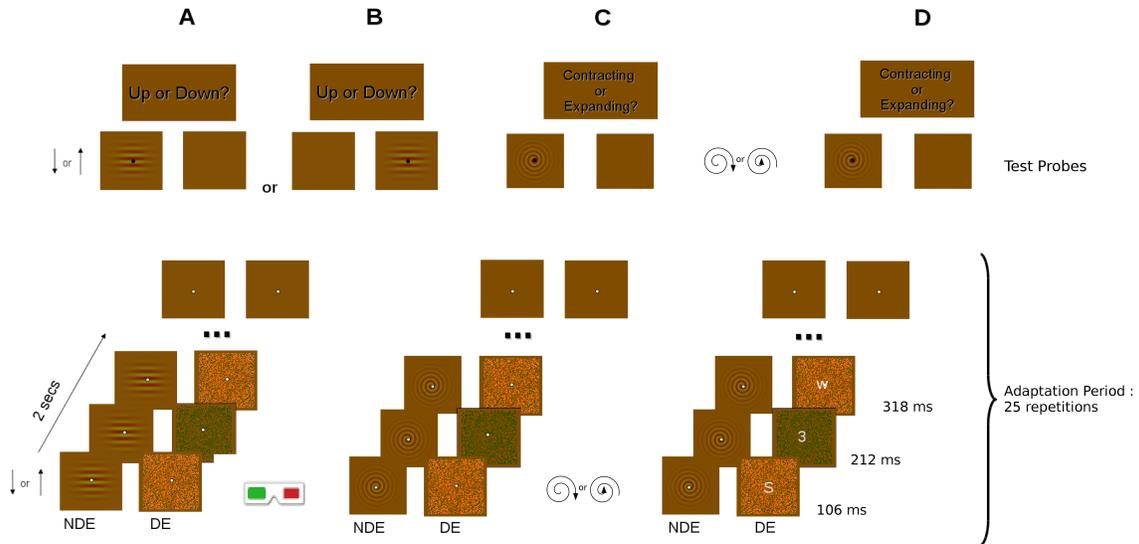
Figure 2.1. Top up procedure. On each trial, the adaptation pattern was presented for 2 s and, after an interval of 753 ms, the test probe was displayed for 494ms. The first trial of the block was preceded by an adaptation period of 68 s. The procedure was the same for all experiments. After the test probe disappeared, observers pressed one of two buttons to indicate the perceived direction (upward, downward, contracting or expanding). The beginning of the test probes was signaled by a color change in the fixation dot. Only the invisible conditions are shown in the figure, for the conditions with visible adaptors a blank screen was presented to the dominant eye instead of the mondrians. Subjects performed the task wearing a pair of red-green anaglyph glasses. The colors and contrast of the stimuli in the figure resemble those colors presented on the screen. DE: dominant eye; NDE: non dominant eye. **A-** Monocular translational motion. **B-** Interocular trials of translational motion. **C-** Adaptation to spiral motion. **D-** Spiral motion adaptors with the attentional task at fixation. The presentation rate of the letters varied for the high and low attentional tasks.

(DE). Adaptors were never presented to both eyes. On the first experiment we used contrast modulated gabor patches to measure MAEs under monocular conditions. The same stimuli were adopted also for experiment 2, testing the MAE interocular transfer, presenting test probes to the non-adapted eye. The third experiment evaluated the spiral MAE again under monocular conditions. Finally, on experiments 4 and 5 we tested translational and spiral MAEs while manipulating subjects attention.

Top-up adaptation procedure. Each run of the adaptation experiments began with a 1 minute period of adaptation in which the adapting stimuli were presented for 2 seconds interspaced with 750ms of a blank screen (Figure 3.2). After the initial adaptation period, subjects were presented repeatedly with two seconds of adaptation followed by the presentation of a test probe (Figure 3.2). Participants' task was to respond whether the test probes were moving upwards or downwards (experiments 1, 2 and 4) or whether they were expanding or contracting (experiments 3 and 5). Test probes moved half of the time in the direction of the adaptor and half of the trials in the opposite direction of the adaptor. Subjects responded by pressing two keyboard keys, with their index and middle finger. To avoid finger biases we counterbalanced the order of the responses. As an example, for each block of trials in experiments 1 and 2 on half of the trials the index finger presses corresponded to "up" and middle finger to "down" and on the other half of the trials the index corresponded to "down" and the middle finger to "up". No feedback was given to subjects after the response.

Experiments 1 (figure 3.2A), 2 (figure 3.2B) and 4 comprised 4 conditions: conscious adaptor moving up, conscious adaptor moving down, non-conscious adaptor moving up and non-conscious adaptor moving down. For experiments 3 (Figure 3.2C) and 5 the conditions were the same except that the adaptors were spirals moving clockwise (expanding) or counterclockwise (contracting). Experiments 4 and 5 were equal to experiments 1 and 3 (respectively) except for the addition of an attentional task at fixation (Figure 3.2D). A stream of letters (all of the letters of the alphabet) and numbers (from 1 to 4 and from 6 to 9) of 1.5 degrees in size were continuously presented to the dominant eye during the adaptation period

and prior to the test probe presentation on the fixation point (Figure 3.2D). The presentation rate of digits (letters and numbers) was 2.85 HZ: they appeared for 250ms on the screen interleaved with 106ms with no numbers/digits. Subjects were told to consider numbers as targets and letters as distractors, and to respond as fast as possible whether the targets were numbers bigger or smaller than '5', while adaptors were presented to the other eye. Letters and numbers were randomly chosen but with the restriction that two consecutive numbers were never presented. To vary the attentional load of the task we used two rates of number presentation (numbers presented over letters presented). In experiments 4 and 5 the rate of appearance of numbers among letters was of 1/8 (low attentional load) or of 1/3 (high load attentional task). The rate of appearance of numbers for the high and low attentional load was obtained in previous pilot studies (see methods). For all five experiments, we ran each condition separately in blocks of 6 consecutive top-up runs, each one containing 20 trials, totaling 120 trials per condition per subject. Test probes were pseudo randomly distributed inside each run, with the same amount of test probes moving in both directions. Half of the subjects performed first the conscious conditions and on a separate day the unconscious conditions, and half of the subjects performed it the other way around.

Stimuli invisibility assessment: Prior to the start of each experiment we ran a staircase procedure (a one down one up procedure leading to 50% correct performance (Levitt, 1971) to determine each subject's invisibility contrast threshold. Throughout the experiments contrast was measured employing the Michelson contrast, defined as $[LMAX - LMIN]/[LMAX + LMIN]$. Once this threshold was estimated we tested subjects with a detection task using contrast values below the estimated invisibility contrast threshold (80 trials, with 40 moving and 40 static stimuli). Subjects responded whether the masked target grating was either moving or static (2AFC). We calculated the d' for each of these contrast values and for each subject we selected a final contrast value that yielded a d' between -0.5 and 0.5 (Figure 2.2). This contrast value was finally used in the adaptation experiments. In all cases subjects reported to be unable to perceive whether a grating had been presented to

them or not under the masked conditions.

We ran a control experiment to rule out the possibility of leakage between the eyes. We checked to be sure that the visual stimulus presumed to be suppressed were not visible to the other eye (figure 2.2, control condition). We tested 6 subjects with a simple detection task consisting of 60 trials: 30 with a moving gabor presented on the screen for 2 seconds at fixation and 30 with a blank screen of background color. Subjects had to detect whether a moving gabor was present of absent on the screen. Gabors had a Michelson contrast value of 5% (the highest contrast value employed throughout the experiments across subjects) and a speed of 0.6 deg/sec. Subjects wore anaglyph glasses during the task and they were requested to close the eye that corresponded to the green filters of the anaglyph glasses. Therefore, only the eye wearing the red filter of the anaglyph glasses was used for this experiment. No mondrians were displayed during this task. The results of this control experiment showed that subjects could not detect the presence or absence of the gabors with the non dominant eye. We found no evidence of leakage between the eyes for the adapting stimuli with these contrast values.
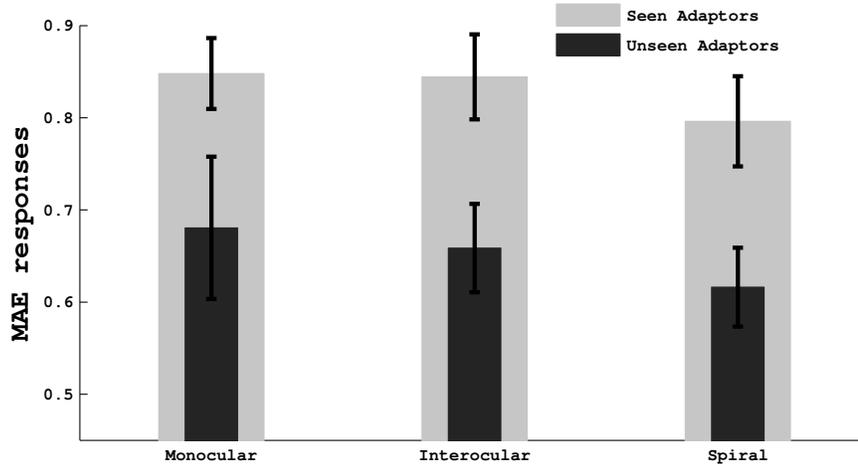
Conscious and non-conscious motion aftereffects

In each experiment we measured the MAE by assessing the proportion of responses opposite to the direction of the adaptor (up-down or expanding-contracting). For each subject this proportion was averaged across the two different adaptor directions (e.g., the average of the responses âĂIJupâĂİ for a downward motion adaptor and responses âĂIJdownâĂİ with an upward moving adaptor). For each condition we assessed whether the proportion of responses opposite to the adaptor direction across subjects was above chance level (one-tailed t-test against a mean of 0.5). We estimated the MAE size for each condition by subtracting 0.5 (chance level) to the proportion of responses contrary to the MAE. To compare across conditions we calculated the rate between MAE sizes.
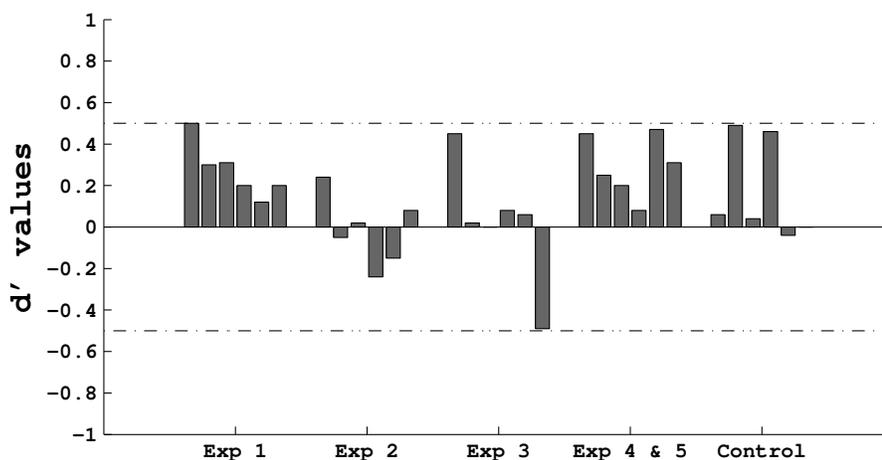
Figure 2.2. Objective measure of visibility. d' values of participants for each of the experiments (N=6 for each experiment, mean d' value = 0.14, SD = 0.23). For *each participant* we ran a visibility detection task prior to the adaptation task and selected a contrast for the adaptors that yielded a d' between -0.5 and 0.5. In addition to these objective measures subjects reported being completely unaware of the presence or absence of the stimuli when the mondrians were displayed on the screen. The same 6 subjects participated in experiment 4 and 5 (low and high attentional load) and for this reason we only report one d' (the same contrast value was used for adaptors in both experiments. The final condition shows the results of a control experiment to test for leakage between the eyes. Subjects were unable to detect with their dominant eye the stimuli presented in the green channel even when the mondrians were not displayed on the screen (see methods section for details).

Initially, we examined whether linearly moving gabors that had been completely rendered invisible would still produce an MAE on visible test probes (Figure 2.3 monocular). We observed, as expected, a strong MAE for the conscious adaptors (one-tailed t-test, $t = 9.0461$, $df = 5$, $p < 0.001$). Also, in line with previous studies that made use of binocular rivalry (Wiesenfelder & Blake, 1992) and CFS (Maruya et al., 2008), we found an MAE for the non-conscious adaptors with translational motion. The effect of the non-conscious adaptors, though reduced to half the size of the conscious MAE, was consistent and statistically different from chance level (one-tailed t-test, $t = 2.3403$, $df = 5$, $p < 0.05$). In our second experiment we measured the interocular transfer of the MAE. Test probes were presented to the eye that was not stimulated by the adapting gabors (Figure 3.2B). We found interocular transfer of the MAE using both conscious (one-tailed t-test, $t = 7.4649$, $df = 5$, $p < 0.001$) and non-conscious adaptors (one-tailed t-test, $t = 3.3113$, $df = 5$, $p < 0.05$, Figure 2.3 in-

Figure 2.3. MAE with conscious and non-conscious adaptors. The proportion of responses contrary to the adaptor direction are plotted for the first three experiments. We compared the generation of MAEs when adaptors were visible with the conditions in which adaptors were invisible to participants. Though reduced in size, monocular, interocular and spiral MAEs were found using non-conscious adaptors. Error bars represent one s.e.m.

terocular). The third experiment evaluated the spiral motion aftereffect (Figure 2.3 spiral). As in experiments 1 and 2 we could observe an MAE both with conscious (one-tailed t-test, $t = 6.0507$, $df = 5$, $p < 0.001$) and non-conscious adaptors (one-tailed t-test, $t = 2.7143$, $df = 5$, $p < 0.05$). The MAEs obtained under suppressed visual awareness were reduced on average to 45% for our first 3 experiments as compared to MAEs obtained under the visible conditions (reduced by 52% for the translational motion, 44% for the interocular transfer and 40% for the spiral motion). A 2x3 ANOVA with visibility (conscious and non-conscious) and experimental condition (Monocular, Interocular and Spiral) as factors revealed a main effect for visibility ($F(1, 30) = 17.65$, $p < 0.001$) but no effect for experimental condition ($F(2, 30) = 0.69$, $p = 0.5$) nor for an interaction between the factors ($F(2, 30) = 0.01$, $p = 0.98$).

Our fourth and fifth experiments studied the influence of attention on the generation of translational and spiral MAEs (Figure 2.4). Accuracy in the secondary task (discriminating the numbers as bigger or smaller than 5) was on average 93% across participants (SD 2%) for the low attentional load task and 76% (SD 3%) for the high attentional load task. Subjects
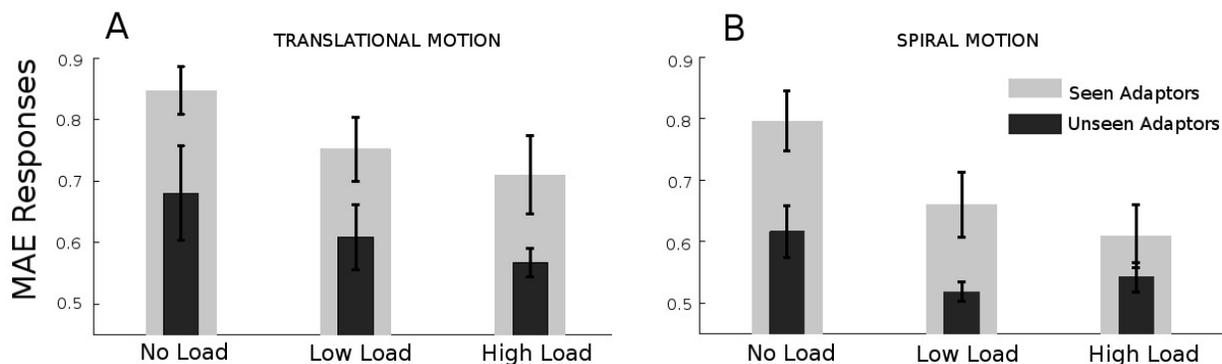
Figure 2.4. The motion aftereffect, awareness and attention. The proportion of responses contrary to the adaptor direction are plotted as a function of 3 tasks with varying levels of attentional load and 2 types of adaptors. Either the lack of attention (high load / light gray bars) or visual awareness (no load / black bars) did not impede the formation of translational and spiral MAEs. However, non-conscious and unattended adaptors generated a reduction of 50% of the MAE size as compared to the fully conscious and attended adaptors (no load / light gray bars). Both visibility and attention consistently modulated the magnitude of the linear (A) and spiral (B)MAEs. However, under conditions of inattention and CFS (low load and high load / black bars) only the responses to the linear adaptors (A) were above chance level and generated an MAE (see results section). Error bars represent one s.e.m.

were more accurate on the low attentional task compared to the high attentional task (two-tailed t-test, $t = -21.44$, $df = 9$, $p < 0.001$). In the case of translational motion (Figure 2.4 A), between subjects ANOVA with visibility as a categorical variable (conscious and non-conscious) and attentional level as linear predictor (no task, low load, high load) showed main effects of visibility ($F(1, 32) = 12.33$, $p < 0.01$) and attentional level ($F(1, 32) = 5.64$, $p < 0.05$), but no interaction ($F(1, 32) = 0.05$, $p = 0.81$). Non-conscious adaptors were able to generate an MAE with a low attentional load task (one-tailed t-test, $t = 2.0462, df = 5$, $p < 0.05$) and with a high attentional load task (one-tailed t-test, $t = 2.8465, df = 5$, $p < 0.05$). In the conscious conditions, allocating attention away from the adaptor reduced the linear MAEs by 27% in the low attentional task and by 40% in the high attentional task compared to the no load task.

Employing spiral motion adaptors (Figure 2.4 B), between subjects ANOVA with visibility (conscious and non-conscious) and attentional level as a linear predictor (no task,
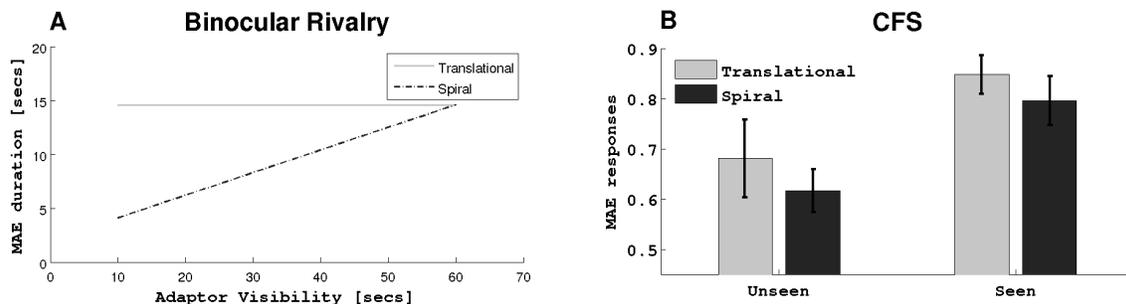
Figure 2.5. Differences between binocular rivalry and CFS. Binocular rivalry experiments make use of the MAE duration to infer the possible sites of adaptation. **A-** Schematic representation of binocular rivalry results with motion adaptors. Binocular rivalry cannot maintain motion adaptors completely invisible for the whole adaptation period. Based on the linear relation between spiral MAE duration and adaptor visibility it was inferred that non-conscious spiral motion could not generate spiral MAEs (Wiesenfelder & Blake, 1990). **B-** CFS is able to render motion stimuli invisible for the whole adaptation time. The results in panel B are equivalent to the results that should be observed in panel A with a visibility of adaptors equal to 0. Under these conditions linear and spiral MAEs can be observed. Though reduced in size they were nevertheless statistically different from chance level.

low load, high load) revealed main effects of visibility ($F(1, 32) = 14.36$, $p < 0.001$) and attentional level ($F(1, 32) = 9.75$, $p < 0.01$), but no interaction ($F(1, 32) = 0.19$, $p = 0.4$). We observed an MAE with conscious adaptors for the low attentional load task (one-tailed t-test, $t = 3.02, df = 5$, $p < 0.05$) and for the high attentional load task (one-tailed t-test, $t = 2.1071, df = 5$, $p < 0.05$). However, no MAE was found with non-conscious adaptors, both for low and high attention tasks (two one-tailed t-tests, $t = 1.12, df = 5$, $p > 0.05$, and $t = 1.6992, df = 5$, $p > 0.05$, respectively). In the conscious conditions, allocating attention away from the adaptor reduced the spiral MAEs by 47% in the low attentional task and by 67% in the high attentional task compared to the no load task.

Summary and conclusions

The two main findings of these experiments were that a spiral MAE was found even with stimuli suppressed from awareness and that attention and awareness had similar, but independent, effects on reducing the magnitude of both linear and spiral MAEs. The first finding, that invisible spiral motion was able to generate a visible MAE during interocular

suppression, differs from prior reports (Wiesenfelder & Blake, 1990). As described above in the Introduction, this may reflect methodological differences in the two designs, as we used continuous flash suppression of the adapter rather than inferring the influence of suppression based on binocular rivalry durations. Neurophysiology studies in monkeys have shown that approximately half the neurons in MT respond to non-conscious motion during BR (Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). In principle, adaptation in higher-level motion processing areas could result either from the normal cortical pathway, via area V1, or through a separate pathway. Studies of patients suffering from blindsight (Weiskrantz, 1997) and lesion studies in monkeys (Schmid et al., 2010, 2009) have shown the residual capacities of the visual system to process motion in the absence of V1. Such studies suggest that visual motion information does not operate as a strictly serial process in the visual cortex, since motion information can bypass V1 and arrive quickly and directly to MT (Sincich et al., 2004; Schmid et al., 2009, 2010). Therefore, extensive evidence favors the idea that some type of degraded motion information can be processed via subcortical connections in V5/MT as well as in V2/V3 (Schmid et al., 2009) in the absence of the striate cortex.

Alternatively, local gains at the level of V1 might be responsible for global MAEs. We can only speculate that non-conscious spiral motion is able to activate neurons in a degraded manner up to area MT, perhaps by modulating a sub-population of neurons in MT that respond to the physical retinal stimulation (Logothetis & Schall, 1989). Further physiological experiments should be conducted to test this possibility. To the best of our knowledge no neurophysiological experiment has been conducted in non human primates combining binocular rivalry or CFS with spiral motion.

Here we were able to directly compare the influences of attention (via a distractor task) and awareness (via CFS) on the formation of motion aftereffects. This direct comparison within a single experiment is relevant to the current debate over the relationship between these two factors (Dehaene et al., 2006; Lamme, 2003; Koch, 2003). Moreover, by including both a simple and complex motion stimulus we were able to see if there was any dissoci-

ation/interaction between the two factors. Our results are consistent with additive effects with no interaction between attention and awareness. Both inattention and suppression from awareness led to a similar reduction in the MAE. In the case of non-conscious adaptors, reducing attention to the adaptor region of the display reduced the magnitude of the MAEs. This result is consistent with previous reports that attention can modulate non-conscious visual motion under condition of crowding and motion priming (Aghdaee, 2005; Melcher et al., 2005). Interestingly, the effect of diverting attention was qualitatively similar to the effect of interocular suppression. Both attention and awareness were necessary to have the maximum MAE, indicating that both factors contributed separately to the degree to which motion stimuli were processed.

Attention reduced similarly the magnitude of the linear and spiral MAEs (Figure 2.4). However, under conditions of inattention and CFS only the responses to the linear adaptors were still above chance level and generated an MAE .We can speculate that these small but statistically significant differences in the changes due to inattention may be due to these two types of motion being processed at different levels of the visual system. Presumably linear motion is processed at earlier stages and therefore is more resistant to inattention and interocular suppression. Rotational, radial, spiral and plaid motion patterns are thought to be processed mainly in the complex MT/MST (Tanaka et al., 1989; Rodman & Albright, 1989; Morrone et al., 1995; Moutoussis et al., 2005). Visual information in the ventral stream is known to suffer from increased inhibition in higher areas of the visual processing (Sheinberg & Logothetis, 1997). Similarly, it has been suggested that the interocular suppression mechanisms of motion perception operate at multiple areas of the visual cortex (Blake & Logothetis, 2002), perhaps with deeper suppression at higher levels of processing (Alais & Melcher, 2007). Our results cannot confirm or refute this depth-of-suppression hypothesis since both linear and spiral MAEs were reduced by CFS in this study.

We also investigated the involvement of binocular and monocular neurons during interocular suppression by employing the IOT. We found an IOT of the MAE with both conscious

and non-conscious linear motion. The magnitude of the IOT with conscious adaptors was the same as previously reported by Raymond (1993) and in agreement with Nishida & Ashida (2000), who showed that the IOT can be perfect or nearly perfect for stimuli that are presented in the central visual field with full attention. Other studies have reported a reduction in the IOT (Steiner et al., 1994; Smith & Hammond, 1985). Importantly, the differences between studies might arise from the types of test probes employed to measure the MAE. Our results have shown the existence of an IOT generated with non-conscious adaptors and have extended the finding that the IOT *size* depends critically on eccentricity, attention and the type of tests probes employed to measure it (Nishida & Ashida, 2000): we also show that the IOT depends on awareness of the adaptor. Our data suggests, in agreement with previous studies (Meng et al., 2004; Macknik & Martinez-Conde, 2004; van Boxtel et al., 2008), that both monocular and binocular channels are involved during interocular suppression.

Overall, the strength of the MAEs obtained with invisible or unattended stimuli were reduced, on average, to *around half the size* of the MAEs with full visible adaptors, a decrease in magnitude that is in accordance with recent studies (Blake et al., 2006; Maruya et al., 2008) but challenges the results of early binocular rivalry reports (Lehmkuhle & Fox, 1975; Oshea & Crassini, 1981). There is an important difference between these early binocular rivalry reports and our paradigm. With binocular rivalry, as stated by Lehmkuhle & Fox (1975) "...it is not possible to suppress an inducing stimulus for the complete duration of the observation period". Previous studies that employed binocular rivalry with linear and spiral motion have assessed the duration of the MAE as a function of adaptor visibility. Based on this relationship between duration of visibility and the MAE, inferences were made about the types of neuronal mechanisms involved in non-conscious motion perception. For example, the decrease of the MAE duration for spiral motion found by Wiesenfelder & Blake (1990) was interpreted as showing that the spiral motion perception depended on awareness (Figure 2.5 A). However, a reduction of the size of the MAE does not mean its complete abolishment. In our CFS paradigm, adaptors were invisible for the whole adapting period and our results

show that, while awareness certainly influences the magnitude of the MAE, spiral visual adaptation can take place with invisible adaptors (Figure 2.5 B).

The fact that smaller MAEs emerge with non-conscious adaptors raises the question about the role of visual awareness and attention on visual motion processing. While orientation aftereffects are relatively unaffected by the lack of awareness (Tsuchiya & Koch, 2005) or attention (He et al., 1996), face adaptation aftereffects are effectively eliminated by suppression (Alais & Melcher, 2007; Amihai et al., 2011). This transition from relatively bottom-up processing of orientation, independent of attention or awareness, to perception of complex objects which is attention- and awareness-dependent, remains a key issue in the attempts to understand the nature of conscious awareness. Our current results add to this literature by showing that the magnitude of adaptation to visual motion depends both on attention and awareness and that the neural mechanisms that operate outside of visual awareness are not sufficient to account for normal visual motion adaptation.

Chapter 3

Rapid categorization of conscious and non-conscious stimuli

As fast as you can see it

The human brain continuously performs visual categorization of stimuli in everyday life. Studies of rapid visual categorization suggest that the first 100-200ms are crucial to this process, consistent with categorization during the first pass of visual processing (Potter & Faulconer, 1975; VanRullen & Thorpe, 2001b; Liu et al., 2009). For go/no go tasks, for example, early event-related potentials at approximately 150ms reflect the decision that there was a target present in a natural scene (Thorpe et al., 1996; VanRullen & Thorpe, 2001b). This first rapid categorization appears to be similar for diverse categories such as means of transportation or living objects (VanRullen & Thorpe, 2001a; Thorpe & Fabre-Thorpe, 2001).

An open issue regards the capacity of invisible stimuli to influence visual categorization

and to activate different areas of the visual cortex. Experiments employing change blindness and inattentional blindness have clearly documented that important visual events that impinge on our retina can go widely unseen when attention is diverted from them (Mack & Rock, 1998; Simons & Chabris, 1999). On the other side, it has been also demonstrated that visual category detection can be rapidly achieved even in the near absence of visual attention (Fei-Fei et al., 2002). Psychophysical studies using interocular suppression as well as neuroimaging studies have given conflicting reports on the degree to which suppressed information activates areas of the brain (Alais & Melcher, 2007; Blake & Logothetis, 2002). Visual information arriving to the ventral stream appears to be deeply suppressed under interocular suppression, as shown by psychophysics (Alais & Melcher, 2007; Zimba & Blake, 1983), neurophysiological data in monkeys (Logothetis, 1998) and in single cell recordings in humans (Kreiman et al., 2005). However, it has recently been proposed that there is a difference between the ventral and dorsal stream for the processing of invisible pictures of animals and tools (Fang & He, 2005; Almeida et al., 2008, 2010). It was suggested that while dorsal stream neurons responded to invisible tools that carried the characteristic of being "graspable" the categorization of invisible animals was widely suppressed in the ventral stream (Fang & He, 2005).

Even though the human and non human primate brain can achieve visual categorization very fast, theories of visual awareness propose that a rapid feed-forward mechanism might not be sufficient for visual awareness, which might also require horizontal connections between different brain areas (Lamme, 2000) and/or late feedback projections from prefrontal areas (Sergent et al., 2005). The study of the neural correlates of invisible stimuli is valuable to disentangle the minimal set of processes that are necessary and sufficient for visual awareness to occur (Koch, 2003). Further investigation is needed to understand the relationship between the first, rapid feed-forward pass of information and the emergence of visual awareness.

We studied the timing of categorization of conscious and non-conscious images of animals,

tools and scrambled control images employing continuous flash suppression (CFS) (Tsuchiya & Koch, 2005), EEG recordings and single trial analysis. Based on the EEG signal, our classifiers were able to predict the visual category on single trials of conscious but not non-conscious stimuli. Fast categorization of conscious images could be detected around 100 ms on the occipital electrodes, suggesting a fast, feed-forward mechanism responsible for the fast recognition of visual categories. For the unconscious images of animals and tools, however, no trace of a distinction between semantic categories was found in the EEG signal. The claim that processing of non-conscious tools but not of non-conscious animals can occur in the dorsal stream (Fang & He, 2005) was not be replicated with EEG recordings. Overall, these results provide further evidence that categorization occurs early in visual processing (VanRullen & Thorpe, 2001b; Hung et al., 2005) and that this early, initial and (perhaps) approximate categorization plays a role in later semantic processing and in conscious awareness.

EEG recordings

Participants: We recruited 12 students - 2 female and 10 male, mean age 26.7 ranging from 21 to 31 years old- from the university of Buenos Aires for the experiment. All subjects had normal or corrected to normal visual acuity and were tested for ocular dominance before running the experiment. All participants gave informed consent according to the guidelines of the University of Trento ethical committee.

Stimuli: For the current experiments we used 50 images of animals, 50 tools (all downloaded from the Internet), 100 phase-scrambled control images (figure 3.1) and a set of 40 Mondrians images (Tsuchiya & Koch, 2005) (figure 3.2A). All images of animals and tools were converted into gray-scale images with a maximum brightness intensity value of 0.8 for every pixel in the image, while background pixels were turned into a value of 0.5 pixel brightness in a scale from 0 = black to 1 = white. No images with strong emotional saliency were

Figure 3.1. The set of 200 stimuli used in the experiments: 50 animals, 50 tools and 100 phase-scrambled controls.

used for this study (such as spiders, snakes or guns). We created 100 control phase-scrambled images (one scrambled image for each animal and tool image) with the same spatial frequencies and mean luminance values as the animal and tool images. In order to generate these images we applied the Fourier transform to each picture of an animal, tool or Mondrian and obtained the respective magnitude and phase matrices. We then reconstructed each image by using the magnitudes of the animals and tools and the phases of the Mondrian images. Finally, we multiplied each single pixel of the scrambled images by an appropriate constant to correct for any differences in mean luminance values between the original images and their scrambled counterparts. A t-test comparing the mean luminance value of the group of original images and the group of scrambled images showed no significant difference between both groups ($p = 0.6$).

Procedures: Stimuli were presented using a PC computer with a CRT display monitor (resolution = 1024x768, 75 Hz refresh rate) using Matlab Psychophysics toolbox (Brainard, 1997). Subjects were instructed to fixate on a central point while they viewed a series of pictures through a pair of red-green anaglyph glasses. These pictures were viewed from a distance of 70 cm at the center of the screen and subtended 8 by 8 degrees of visual angle. To

allow competition between stimuli on each trial we randomly selected 10 Mondrians from the set of 40 Mondrians and presented them to the red RGB channel of the image every 8 frames (10Hz, each Mondrian presentation lasting 106ms). Target animals, tools and scrambled images were presented to the green RGB channel of the image. In this way, subjects using the anaglyph glasses saw the Mondrians with their dominant eye and the animals, tools and scrambled images with their non dominant eye.

Throughout a trial Mondrians were dynamically changed every 106ms. Trials initiated with a period of 424 to 636ms (4, 5 or 6 flashes) of Mondrian presentation followed by the targets plus the Mondrians for 636ms. Once the targets disappeared, 4 more Mondrians were flashed on the screen to avoid afterimages (figure 3.2A). For the conscious conditions targets were presented at low luminance and Mondrians at high luminance whereas for the non-conscious condition targets were presented at a low luminance and Mondrians at high luminance. These luminance levels were chosen for each subject based on a visibility threshold detection task (see below). On each trial, subjects were asked to fixate at the center of the screen to avoid eye movements. Their task was to respond with their right hand index or middle fingers whether the picture of an animal or tool had appeared on the screen (2AFC). An inter-trial interval of either 1, 1.5 or 2 seconds was used in between trials to avoid attentional expectations. The EEG experiment comprised 8 conditions: 4 stimuli types (animals, tools, scrambled animals and scrambled tools) by 2 visibility levels (conscious and non-conscious). The EEG experiment consisted of 800 trials (100 trials per condition by 8 condition) and lasted approximately 70 minutes.

Invisibility assessment. On a previous session to running the EEG recordings subjects performed a visibility threshold detection task. We presented the targets at 6 different luminance levels while Mondrians were kept constant. The trial presentation was exactly the same as the sequence described above (see figure 3.2A) with the only exception that instead of scrambled images a blank green screen of the same luminance as target images was presented on half the trials to the dominant eye. Subjects had to respond whether they had seen a

target (animal or tool) or a blank screen. Using signal detection theory we calculated the d' values for each luminance condition to obtain a measure of each subject's visibility threshold (see figure 3.2C). Finally, we chose a luminance value that yielded a d' between -0.5 and 0.5. This luminance value was then assigned to the targets in the non-conscious conditions and to the Mondrians in the conscious conditions for the EEG experiment. For all subjects, the final targets were presented against a green background (commission international de l'Eclairage (CIE) coordinates X=0.414, Y=0.391) with a maximum luminance of 4.8 $cd/m2$). When presented at low luminance the mean pixel intensities for the grayscale targets was 0.26 (in a scale from 0 to 1) with an STD of 0.02. For the grayscale high luminance targets and mondrians the mean pixel intensities was 0.71 with an STD of 0.06. CFS allowed us to present constant stimuli to our subjects while they underwent two conditions: a visible condition in which pictures were consciously perceived and an invisible condition in which participants were not able to report the presence nor the identity of the suppressed stimuli.

Preprocessing of EEG data: EEG activity was recorded on a dedicated PC at 1024Hz, at 128 electrode positions on a standard 10-20 montage, using a BrainVision electrode system (`http://www.brainvision.co.uk/`). An additional electrode at the right ear lobe was used as reference. Datasets were bandpass filtered (1-120Hz), down sampled at 300 Hz, and independent component analysis (ICA) was run on the continuous datasets to detect components associated with eye blinks, eye movements, electrical noise and muscular noise. The resulting components from the ICA decomposition were visually inspected and the ones associated with eye blinks and eye movements were manually eliminated from the data. Channels containing artifact noise for long periods of time were interpolated (a maximum of 4 channels were interpolated for each dataset). The datasets were notch filtered at 50 Hz to clear out electrical noise, and the reference on the right ear was digitally transformed into an averaged reference. Once this process was finished the datasets were epoched in synchrony with the beginning of the target presentation and each epoch was corrected for baseline over a 400ms window during fixation at the beginning of the trial. An automatic method was applied to
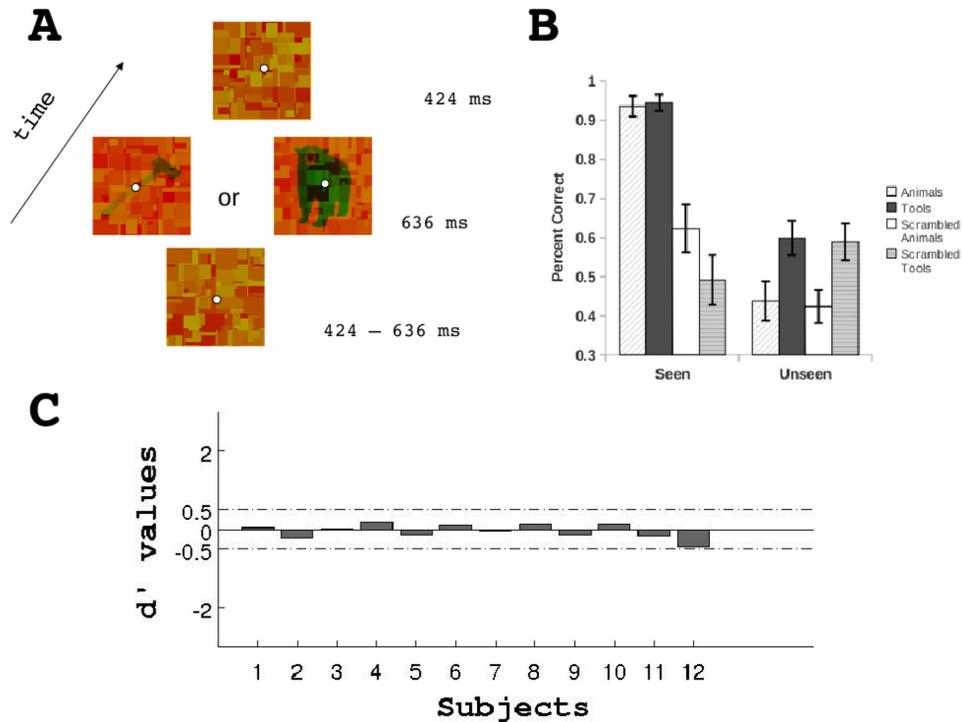
Figure 3.2. A- Schematic trial representation. Mondrians were changed on the screen every 106 ms (see methods). B- Performance at discriminating the categories of stimuli for the conscious and non-conscious conditions. C- Objective assessment of invisibility. Prior to the main experiment we conducted a detection task with targets at different low luminances to be sure that subjects were completely unaware of the target stimuli under the non-conscious conditions (see methods). This task was identical to that depicted in A but with half the trials presenting a blank screen instead of a target. Subjects had to report whether they had seen a target or nothing. Signal detection theory was used to estimate for each subject the target luminance values that yielded a d' between -0.5 and 0.5. In addition to this objective measure of invisibility subjects reported to be completely unaware of any targets presented at low luminance during CFS.

discard those trials with voltage exceeding ±200mv, transients exceeding ±80mv or oculo-gram activity larger than ±80mv. The remaining trials were then separated accordingly to the experimental conditions and averaged to create the event related potentials (ERPs). On average, 15% of trials were discarded after artifact removal. All the preprocessing steps were performed using EEGLAB (Delorme & Makeig, 2004) and custom made scripts in Matlab.

Statistical analysis of ERPs. In order to assess the earliest time point in visual cate-gorization we initially ran statistical comparisons between conscious animals versus conscious scrambled animals and conscious tools versus conscious scrambled tools (figure 3.3). In all cases we submitted each (channel, time) sample of the ERP calculated for each subject to a non parametric rank-sum test to compare the two conditions across all subjects. This implied over 5000 comparisons for each pair of conditions. We filtered these multiple comparisons across time samples and recording sites with the following criteria. 1- We kept only samples with $p < 0.01$. 2- For each channel, a given time point was considered significant if it was part of a cluster of 6 or more consecutive significant consecutive time points for a 19.5ms time window (Dehaene et al., 2001; Thorpe et al., 1996). 3- Each sample was considered significant if for the same time point at least 2 neighboring channels were also significant.

Single trial classification: We employed multivariate pattern analysis (Hanke et al., 2009) to decode visual information from the EEG recordings in single trials. All the analysis were performed in Python language adopting the software library PyMVPA [1]. For each channel we assessed the time and frequency intervals within the EEG signals that carried the biggest amount of stimuli-related information and maximized the separability between the stimuli categories. The amount of information was estimated as the accuracy of a classifier trained on single trials at predicting the stimuli of future trials. A dimensionality reduction step was performed before each classification process via a variable selection step, and for this study the selected variables were time intervals. Variable selection was conducted in order to discard irrelevant information for classification and improve the signal-to-noise ratio.

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[1] http://www.pymvpa.org.

For each subject, the dataset consisted in 3D matrices of 300 sample points by 128 channels by 800 trials containing voltage values. For all the analysis we used a 6 fold cross-validation procedure in order to estimate the accuracy of classification. We refer to "classification performance" of a subject as the average of the 6 classification accuracies obtained on the test set of each fold. At each one of the iterations of the cross-validation scheme the following variable selection procedure was applied to the training dataset. First, we computed the mean and standard deviation for each time-step and class over all training trials. Then, for each timestep and each channel we ran a one-way ANOVA between the two classes to compare the differences in signal amplitude. Next, we obtained a vector with 300 p-values (one for each sample point). The 300 time points correspond to the time range 0 to 1000 ms after stimuli presentation. The first 100 timesteps with the lowest p-value were selected for each channel and used as feature values to set up a final dataset where each trial is a vector of 100 features. Finally, the resulting dataset was used to train a classifier with a Support Vector Machine (SVM) algorithm (Schlkopf & Smola, 2002) and linear kernel.

The corresponding test dataset for the given iteration of the cross-validation scheme was reduced to the 100 features selected on the training dataset. In order to avoid circularity analysis during variable selection we performed the feature selection process jointly with the cross-validation process for each step of the multivariate analysis (Olivetti et al., 2010). For each fold of the cross validation process the SVM algorithm produced a classifier for each channel and the related accuracy on the test set was used to evaluate the informativeness of the channel. The result of these classification processes yielded a measure of the information contained in each channel to discriminate stimuli categories, a "single-channel based decoding". To obtain a global measure of classification or "all-channel based decoding" (see results section), we performed the same procedure as before with the exception that during training the 128 channels were concatenated and 12800 features were selected, i.e., the best 100 features for each of the 128 channels. The classification performance of an SVM classifier was estimated by means of cross-validation.

Results

Behavioral responses. We ran 8 bonferroni corrected one-sample t-tests (one for each condition, figure 3.2B) against the null hypothesis that subjects were performing at chance level. Subjects were above 90% accuracy at discriminating animals and tools on the conscious condition (corrected $p < 0.05$). For the remaining 6 conditions none of the tests rejected the null hypothesis that participants were responding differently from chance level.

ERP Analysis. First of all, we found three main components that distinguished targets (animals or tools) from scrambled images (figure 3.3; see methods for details on statistical criteria for ERPs comparisons). The earliest differences between ERPs of conscious animals and conscious scrambled animals, and conscious tools and conscious scrambled tools were observed for a P1 component at occipital electrodes. These components had a statistically significant onset starting at 93ms for animals and 127ms for tools. These results are in agreement with previous studies showing early categorization around 100ms (Thorpe et al., 1996; VanRullen & Thorpe, 2001b; Rousselet et al., 2007; Fabre-Thorpe et al., 2001). We also observed a second N2 component with a peak starting at ~230ms and a third late component with a peak starting at ~490ms. The pictures of seen animals or seen tools produced a widespread activation throughout the cortex as compared to the seen scrambled controls.

Second, we assessed the EEG signal associated with the presentation of non-conscious pictures of animals or tools (figure 3.4). We observed no EEG correlates of non-conscious stimuli as compared with their non-conscious scrambled controls. Even the earliest P1 components were eliminated under CFS, suggesting that under interocular suppression non-conscious stimuli were completely suppressed before 100ms or that they were too weak to be detected with ERPs.

Third, we found no differences in the ERPs for the subtler semantic categorization of animals versus tools (figure 3.5). For the conscious targets the EEG activity related to the two categories was almost identical, with only an N2 component that (even though not
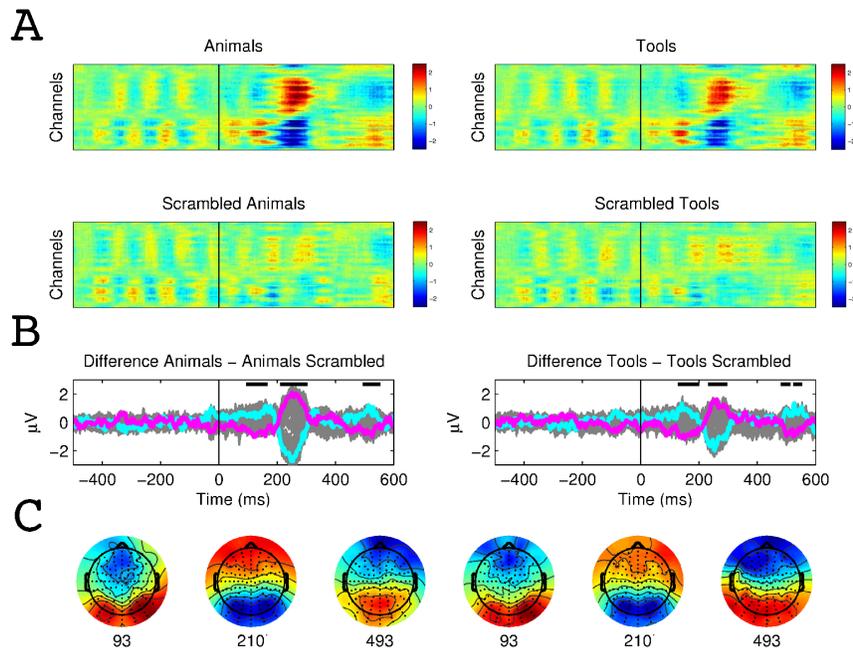
Figure 3.3. The earliest correlates of visual categorization. A- Raster plots of seen animals, tools and their scrambled control conditions. The presentation of meaningful stimuli (animal or tool) produced 3 distinctive components with respect to the scrambled pictures with onsets at 100, 200 and 500ms. The signals prior to the stimuli onset correspond to the Mondrians presentation. These plots show the average of 12 subjects. B- The difference between seen animals versus seen scrambled animals and seen tools versus seen scrambled tools are plotted for all channels (gray) and as particular examples for channel "OZ = cyan" and "FZ = magenta". The activity of Mondrians is cancelled by the subtraction between conditions. Upper dark bars indicate the time points where the signals showed statistical differences for both conditions (see results). C- Topographical maps show brain activity at the beginning of each period of significance.

statistically significant) could be still observed around 200ms after the subtraction of the two categories. For the non-conscious targets even the earliest components were nor present.

The failure in categorizing non-conscious stimuli could have been simply a matter of insufficient signal to noise ratio: the target images could have been too weak to produce a reliable EEG signal. In order to rule out this possibility we ran a control experiment (n = 6) with two conditions. We presented the same target and scrambled images as in the non-conscious condition: 1- without presenting any mondrian and 2- with low luminance mondrians presented to the dominant eye. We found that the targets -animals and tools- produced a significant cortical response at P1 and N2 components (figure 3.6). This result implies that the lack of signal under the non-conscious conditions (figure 3.4) cannot be attributed to weak visual stimulation. On the other hand, it remains possible that some form of interaction between the CFS Mondrian sequence and our already weak target stimuli could have wiped out the corresponding signals at an early cortical stage. While this possibility is, to some extent, compatible with our conclusions, it would be useful in future studies to observe the ERP signals (or lack thereof) generated by non-conscious stimuli that are physically matched to the consciously seen ones (e.g in a condition where the same target stimulus sometimes becomes conscious and generates an ERP and sometimes remains unconscious with no associated ERP)

EEG Single Trial analysis. We employed single trial multivariate analysis for all the conditions in our data (figure 3.7). We designed our classification approach with an emphasis on avoiding biases in the process of feature extraction and parameter estimation implementing a nested cross-validation scheme (Olivetti et al., 2010). For the conscious conditions the classifiers were able to discriminate well above chance animals from scrambled animals with an accuracy of 72% and tools from scrambled tools with an accuracy of 66% ($p < 0.0001$). A 55% of accuracy was obtained for the comparison of seen animals versus seen tools, which was statistically suggestive ($p = 0.0518$) but not significant at the confidence level of 0.01 that we adopted in this work. This suggestive classification performance could not be at-
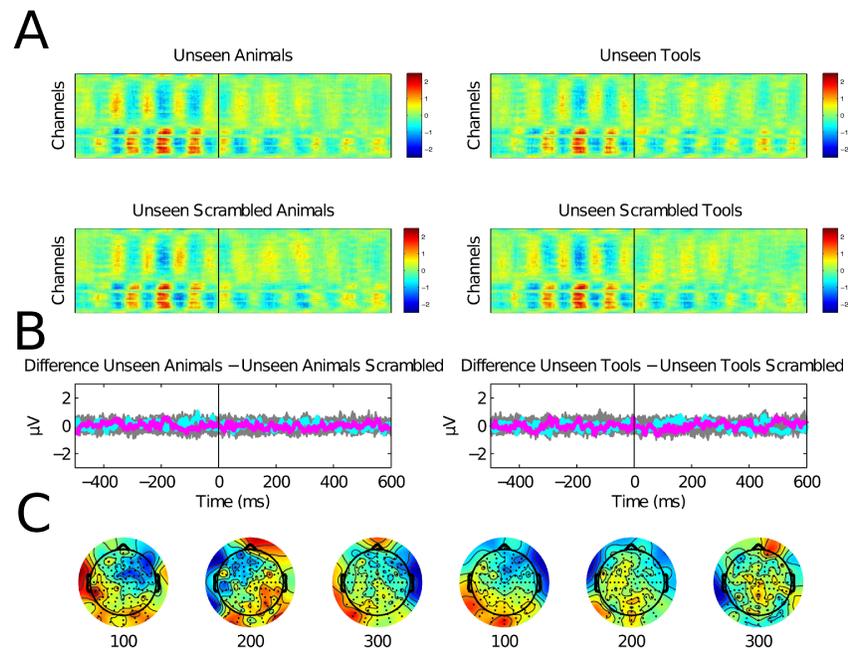
Figure 3.4. Rapid categorization is suppressed for non-conscious stimuli. A- Raster plots for stimuli presented under invisibility conditions. These plots show the average of 12 subjects. B- No ERP components were present in the data except for the activity associated to the Mondrians presentation. The difference between non-conscious animals versus non-conscious scrambled animals and non-conscious tools versus non-conscious scrambled tools are plotted for all channels (gray) and as particular examples for channel "OZ = cyan" and "FZ = magenta". The activity of Mondrians is cancelled by the subtraction between conditions. C- Topographical maps show no particular information regarding non-conscious stimuli. CFS eliminated even the earliest EEG correlates of image categorization.
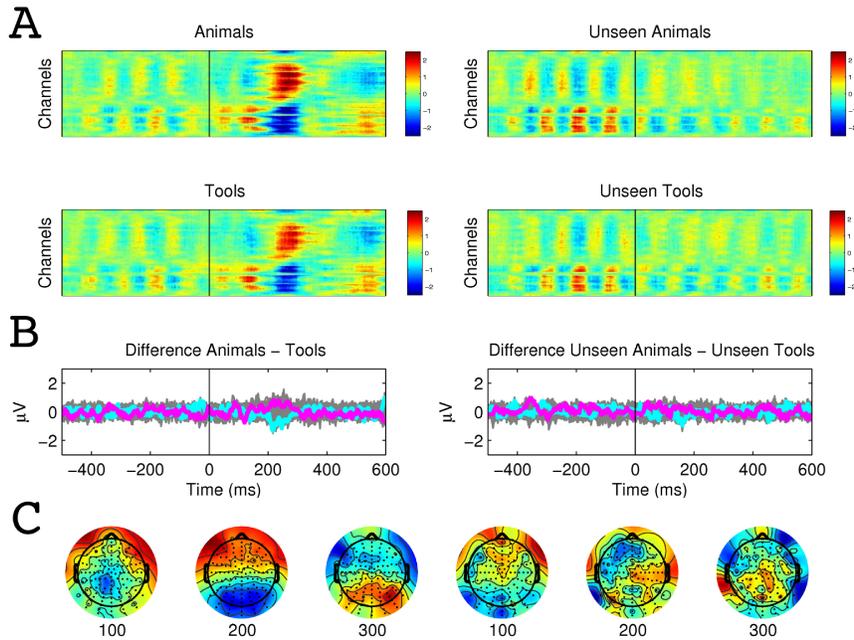
Figure 3.5. Semantic categorization between animals and tools. A- Raster plots showing activations for seen animals and seen tools. These plots show the average of 12 subjects. B- The subtler semantic categorization of animals versus tools could not be observed from the EEG recordings. The difference between seen animals versus seen tools and non-conscious animals versus non-conscious tools are plotted for all channels (gray) and as particular examples for channel "OZ = cyan" and "FZ = magenta". The activity of Mondrians is cancelled by the subtraction between conditions. C- However, even if it was not statistically significant, some type of small potential was still present after the subtraction around 200ms. We investigated this activity employing a multi pattern analysis approach (figure 3.7).
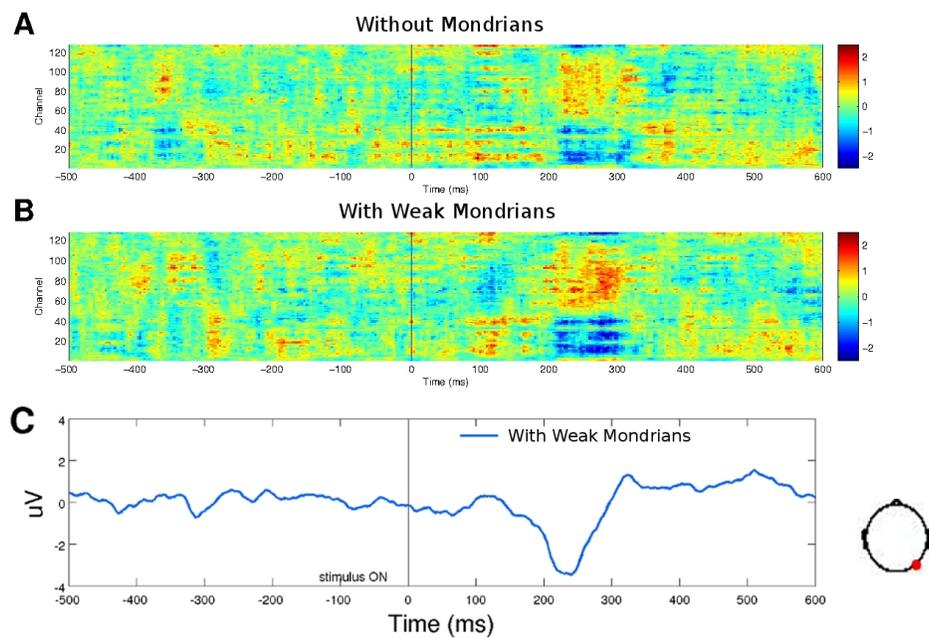
Figure 3.6. EEG signal to noise ratio of targets. A- Low luminance targets (animals and tools together) generated a reliable EEG response when presented to one eye without mondrians to the other eye, and **B**- with low luminance mondrians in the dominant eye. Six subjects participated in this control experiment. **C**- One occipital channel from panel B is shown as an example of the components generated by low luminance targets. For both conditions A and B, subjects were above 95% accuracy at discriminating the category of the stimuli and reported seeing the stimuli without difficulty. The absence of an EEG response to non-conscious targets (figure 3.4) cannot be explained by low signal to noise ratio of low luminance targets.

tributed to low level image statistics, as the comparison seen scrambled animals versus seen scrambled tools was at chance level. The most important channels contributing to the classification performance can be observed in figure 3.8. For the discrimination between seen animals, tools and their scrambled controls the occipital electrodes conveyed the highest discriminative information. For the seen animal versus tool classification performance our results were lower than in previous EEG and MEG studies (Murphy et al., 2009; Chan et al., 2011; Simanova et al., 2010). We speculate that our results might differ from these studies due to two reasons. First, the relative small number of trials used in our study (100 per category) compared to previous works (i.e, Murphy et al. (2009, 2010)) could have made the classifier and the estimation of its accuracy less precise. Second, the additive noise effect of the low luminance Mondrians in the conscious conditions might have reduced the signal to noise ratio thus decreasing the accuracy of the classifier.

Summary and discussion

The primate visual system can accomplish complex visual stimuli processing in a fraction of a second. Fast visual categorization can occur in human and non human primates as fast as 100ms after stimuli presentation (Liu et al., 2009; Oram & Perrett, 1992; Perrett et al., 1982). The nature of connections among neurons from the retina to the inferotemporal cortex (Felleman & Van Essen, 1991) and the spikes needed for the information to step through all these areas suggest that fast categorization is performed in a single feed-forward pass of information (Thorpe et al., 1996; VanRullen & Thorpe, 2001a,b).

Our results give support to this view as they show a first early categorization of meaningful pictures starting at $90 - 120$ms. Consistent with studies showing that a visual scene can be rapidly detected (Thorpe et al., 1996; Fei-Fei et al., 2002), the presentation of a meaningful picture produced a rapid widespread activation throughout the cortex as compared to the meaningless scrambled pictures. In our data identifiable targets of animals or
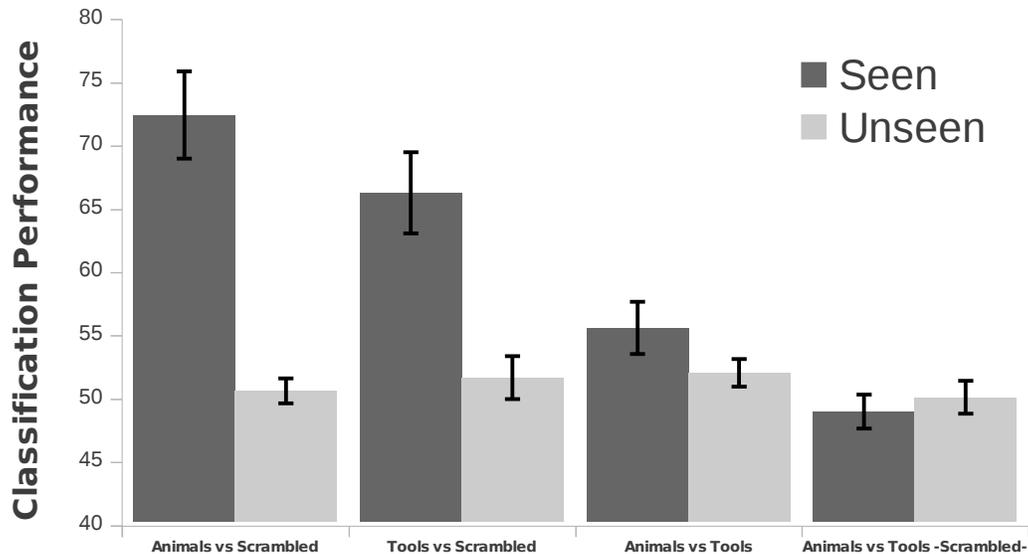
Figure 3.7. Single trial classification performance. Multivariate pattern analysis was used to discriminate between experimental conditions. The classifier was well above chance level for the discrimination of seen animals and seen tools against their scrambled controls ($p < 0.0001$). Also, the classifier found suggestive evidence of a discrimination between seen animals and seen tools categories but the final classification performance was not significant at the confidence level of 0.01 that we adopted in this work ($p = 0.0518$). The classifier was at chance level at discriminating scrambled animals from scrambled tools ($p > 0.05$). Seen animals versus seen tools was higher than the discrimination of seen scrambled animals versus seen scrambled tools ($p < 0.01$). This implies that low-level image statistics cannot account for the decoding of animals versus tools. For all the non-conscious stimuli comparisons the classification performance was at chance level. The classifier was run on each subject separately and the final classification performance was obtained from the average across subjects. Error bars depict one s.e.m.
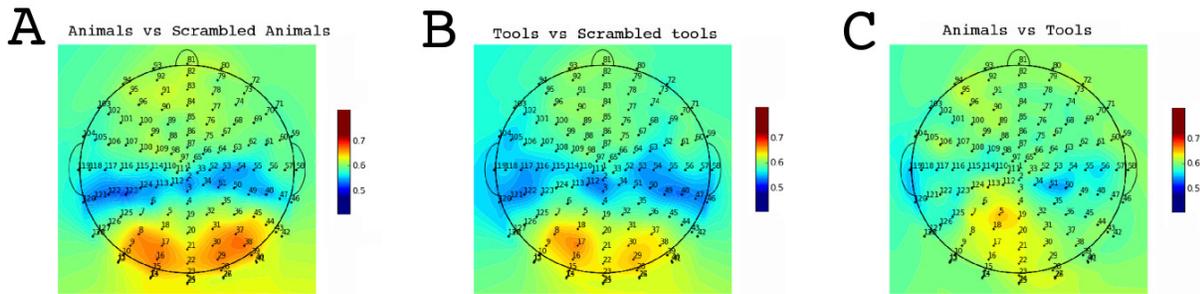
Figure 3.8. Single Trial Channel Sensitivity. Classification accuracy for each channel for the conditions with conscious targets. Each color represents the cross-validated accuracy of the classifier specific to each channel. For the comparisons of meaningful pictures against meaningless pictures (A & B) the occipital electrodes were of most importance. These occipital electrodes were not determinant for subtler semantic categorizations (C).

tools generated an early event-related component as early as 100ms, suggesting that initial visual categorization might originate from the first pass of processing in visual cortex. These early processes could not be attributed in our data to spatial frequency or mean luminance differences between targets and scrambled controls.

The absence of a difference in ERPs between seen animals and tools along with the low single trial classification performance suggests that finer semantic categorization takes place at a later stage of the processing hierarchy. This idea is in accordance with the latency of the N400 ERP component, usually in the time window of $200 - 500$ms after stimuli onset, associated with semantic processing as reported in previous studies (Kiefer, 2001; Kutas & Hillyard, 1980; Dehaene, 1995; Pulvermuller et al., 1996). Recent studies employing single trial analysis have shown better classification performances at discriminating between seen animal and tool categories (Murphy et al., 2009, 2010; Chan et al., 2011; Simanova et al., 2010) and animals versus vehicles (VanRullen & Thorpe, 2001b). Our results are slightly different from these previous studies as our classifier only found suggestive evidence of a discrimination between these two categories but a classification performance at the limit of chance level. We can only speculate that these differences might have occurred due to the

additive noise effect of the low luminance Mondrians accompanying the targets, to the lower number of trials or to possible biases in the feature selection and classification process.

Some theories state that visual awareness is linked to late stages of processing in the ventral stream (Bar & Biederman, 1999; Koch, 1996; Milner & Goodale, 1995). If this is the case, is there a preliminary categorization process for non-conscious stimuli? Backward masking studies have shown that for non-conscious stimuli the second stage of processing of information around 250ms is eliminated while the first pass of information survives suppression (Schiller & Chorover, 1966; Dehaene et al., 2001; Bacon-Macé et al., 2005; Melloni et al., 2007).

Models of binocular suppression propose that neural competitive interactions occur at several levels of the visual processing hierarchy (Blake & Logothetis, 2002; Tong, 2001; Tong et al., 2006). The idea that interocular suppression starts very early in visual processing (Wunderlich et al., 2005; Tong & Engel, 2001; Haynes et al., 2005) and that there exists an almost complete suppression of the information conveyed by the non dominant stimuli in ventral areas of the visual cortex is supported by psychophysics (Alais & Melcher, 2007; Moradi et al., 2005), fMRI (Hesselmann & Malach, 2011; Tong et al., 1998; Pasley et al., 2004), single-cell recordings in monkeys (Sheinberg & Logothetis, 1997) and single-cell recordings in human beings(Kreiman et al., 2002, 2005).

On the other side, recent experiments have shown that during interocular competition complex suppressed stimuli can nonetheless generate behavioral effects, suggesting invisible processing beyond striate cortex (Kovács et al., 1996; Alais & Parker, 2006; Andrews & Blakemore, 1999; Jiang et al., 2006; Stein et al., 2011). Also, it has been proposed that weak category-specific neural activity could be detected during CFS using MEG/EEG (Sterzer et al., 2009; Jiang et al., 2009) and multivariate analysis of fMRI data (Sterzer et al., 2008).

Our results suggest that CFS suppresses information even for the first pass and that non-conscious animal and tool categories are suppressed early in visual cortex. Previous reports on CFS have found residual processing of information in the dorsal stream for non-conscious

tool pictures but not for non-conscious animal pictures (Fang & He, 2005; Almeida et al., 2008). In these studies the results were explained in terms of the "graspability" nature of tool pictures and by the difference in interocular suppression for the ventral and the dorsal stream (Almeida et al., 2010). We were not able to corroborate this hypothesis as we did not observe any evidence of cortical activity in the parietal channels associated with the perception of manipulable objects, a result in agreement with a recent study by Hesselmann & Malach (2011).

An important reason for the discrepancies between previous studies and our results might be related to differences in depth of suppression (Tsuchiya et al., 2006; Alais & Melcher, 2007). In the studies by Fang & He (2005) and Almeida et al. (2008) the authors presented the target stimuli on the screen for 200ms. Target pictures were made invisible by presenting two flashes of Mondrians in each trial, the minimal set of Mondrian flashes for a paradigm to be considered *continuous* flash suppression. This fact might have bring their paradigms closer to backward masking than to classical continuous flash suppression (Tsuchiya & Koch, 2005) in terms of depth of suppression (Tsuchiya et al., 2006). In our study, however, we presented a continuum of flashes before and after picture targets appeared on the screen, which rendered suppression stronger (but see Jiang et al. (2006) for a design with several mondrian presentation). Under these conditions both non-conscious animal and tool targets were equally suppressed. Alternatively, it could also be argued that the our results arise from the differences in nature and temporal dynamics of EEG and fMRI recordings, that the small changes in BOLD signal generated by non-conscious tools in the parietal cortex that were reported by Fang & He (2005) might not have any correlate in any ERP component and would therefore go undetected.

Our results suggest that rapid categorization is suppressed under CFS. The fact that these processes can be cancelled by deep binocular suppression suggests a competition even within the first pass of visual recognition. Under some conditions, with only minimal competition, some weak categorization might occur, but our results question the robustness of these

unconscious processes to strong suppression. Thus, even target detection is not completely automatic, but can be intercepted by competitive interactions in early vision.

Chapter 4

Visual awareness across saccades

Backward masking and trans-saccadic vision

Humans make several eye movements every second, and thus a fundamental challenge in conscious vision is to maintain continuity by matching object representations in constantly shifting retinal coordinates (Melcher & Colby, 2008). One possible mechanism for visual stability is the remapping of receptive fields around saccade onset, combining pre- and post-saccadic information (Colby & Goldberg, 1999). The mislocalization of stimuli briefly flashed near the time of saccades (MacKay, 1970; Morrone et al., 2005; Lappe et al., 2000; Ross et al., 2001) has been taken as evidence for remapping. Yet the relationship between remapping, mislocalization, and trans-saccadic integration remains unclear. We asked participants to identify a target stimulus presented around the time of saccade onset, which was immediately visually masked by a postsaccadic stimulus presented in the same spatial location (backward masking). Presenting two rapidly occurring events across separate fixations allowed us to investigate how the visual system reconstructs what happens during a saccade. We show

that saccadic remapping resulted in perception of target and mask as either spatially segregated or integrated, depending on the exact timing of saccade onset. During segregation, the target was unmasked because it was perceived as displaced from the mask; during integration, the postsaccadic stimulus masked the presaccadic target (spatiotopic masking). Thus, segregation and integration may work together to yield continuity in conscious vision.

Behavioral measures and eye movement recordings

Two authors and seven naive observers took part in the study (five males, age range $22-38$). All participants gave informed consent according to guidelines set by the University of Trento Ethical Committee. Participants sat on an adjustable chair in a dimly lit room. They placed their heads in a chinrest and forehead rest to help minimize their head movements. Stimuli were presented on a Mitsubushi Diamond Pro 2070 monitor with a refresh rate of 85 Hz (80 cm distance). Mean monitor luminance was 16.4 cd/m2.

After running practice trials to familiarize themselves with the task, each participant completed two control blocks with no saccades After the two control blocks participants completed two saccade conditions (filled and unfilled shapes). Each saccade condition was made up of 8 blocks of 96 trials each. Examples of saccadic trials for each condition are illustrated in Figures 4.1 A and 4.1 B. In these trials, participants first fixated a yellow cross (0.7° at the center of a black screen (80 cm viewing distance) for a variable period (2, 2.5, or 3 s). Fixation disappeared briefly (blank of 24 ms), and then a yellow cross (saccade cue) appeared at 8.3° left or right of center. After a brief delay (150 ms), a white target stimulus (size 0.7°; filled square or diamond for condition 1, unfilled square or diamond for condition 2) appeared ipsilaterally to the cue 2.8° to the left or right of the center for 11.7 ms. After a variable ISI (12, 118, or 212 ms for condition 1; 12, 118, or 352 ms for condition 2), the mask (size 1°; white unfilled square or diamond for both conditions) was presented for 188 ms on the same location as the target for the specific trial. The lateralized cross remained

visible until participant's response or for a maximum of 5.9 s. Eye movements were recorded during each session (see *Eye Movement Analysis* below).

Filled and empty shape trials in the main experiment were run in separate blocks, in which three different possible ISIs between target and mask were presented randomly across trials. The maximum ISI differed for the filled and empty shape conditions, based on pilot studies showing stronger masking in the empty shape target condition. In all experiments stimuli were presented using the psychophysical software package ASF ("A Simple Framework", available from jens.schwarzbach@unitn.it), running under Psychtoolbox-3 (Brainard, 1997)) in MATLAB. Participants pressed one of six buttons (on a keyboard, the "z", "x", or "c" key with their left hand, or the "m", ",", or "." key with their right hand) to indicate target identity (mapped onto separate hands: left for diamonds and right for squares) and location (mapped onto three fingers of each hand: left, right, or same location of the mask).

Mislocalization Control Experiment. Two control blocks were performed for each condition (one at the beginning and one at the end of each filled/empty shape condition; 48 trials per block see Figures 4.2 and 4.4). Trials were identical to the main (saccadic) condition, except that the fixation point remained stationary at the center throughout each trial.

Masking Control Experiment. Five subjects (2 authors and 3 naïve) were tested in 4 blocks (96 trials each) which were identical to the empty shape condition of the main experiment, except that: (1) the target/mask ISI was kept fixed at 48 msec (to ensure strong masking); (2) on half of the trials the mask was shown in the same spatial location as the target (as in the main experiment), but in the other half of the trials the location of the mask was offset vertically of 4° (to ensure that it could not act properly as a mask). Trials in which either there was a displacement or in which the saccade onset did not occur during the interval between the target and the mask were excluded from the analysis (45% in total)

Eye movement analysis. Eye movements were recorded using a video-based eye tracking system (EyeLink 1000) which tracks the pupil of one eye (the right eye in our experiment) at a sampling rate of 1000 Hz. At the start of each block of trials, gaze calibration was

performed, which required fixating targets that appeared on a 3 by 3 grid. A validation procedure followed which repeated the calibration with the same 9 points in a different order. If gaze position during validation deviated from the initial calibration measurements by more than 0.5 degrees, then calibration was repeated. We discarded from analysis (a) trials with saccade onsets shorter than 100 msec and longer than 300 msec (b) trials in which participants failed to make a saccade in the correct direction; or (c) trials with a saccade landing shorter than 6° (i.e., saccades landing closer to the target/mask than to the saccadic cue). Additional filters on the data were used in the accuracy analyses, in order to specifically examine trials in which the saccade was made during the blank interval between the target and the mask. See Figure 4.3.

Unmasking targets

To explore trans-saccadic vision, we adopted backward metacontrast masking, an experimental procedure in which the conscious perception of a briefly flashed stimulus (target) is reduced or eliminated by the subsequent occurrence in the same location of a larger stimulus (mask) (Breitmeyer, 1984) that fits around the contours of the target without touching it. Critically, targets were presented before or during a saccade, whereas the mask could appear after the saccade in the same spatial, but different retinal, position. Targets were either easily distinguishable from the masks (filled shapes) or identical to the masks but smaller in size (unfilled, or empty shapes). In the former condition, target and mask could be perceived as separate spatiotemporal objects: participants could see something before the mask, even though they could not say exactly what (Mattler, 2003). In the latter condition, in contrast, masking was generally so complete that participants were entirely unaware that the target had been presented at all.

We presented targets near the onset of saccades in order to examine the time course of perisaccadic perception. Numerous studies have shown that neurons involved in visual-
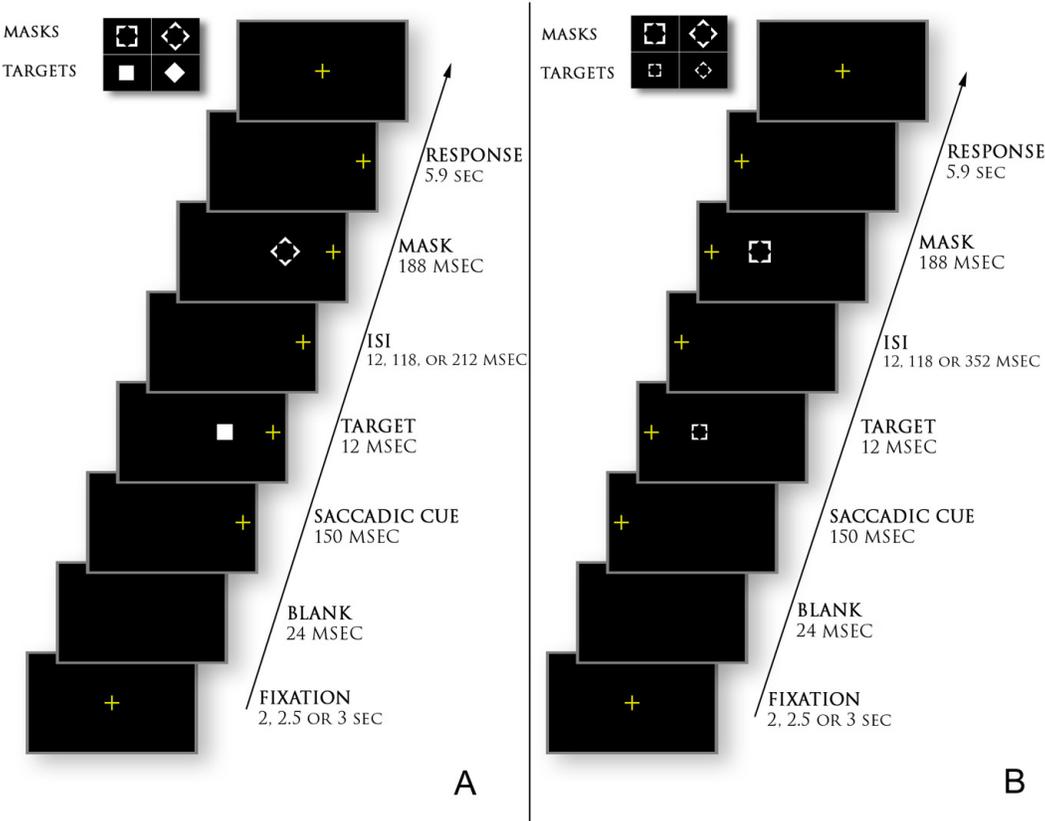
Figure 4.1. Experimental Design during Saccadic Blocks. Participants fixated a yellow central cross and then, after a variable blank delay, were presented with a lateral saccadic cue indicating the new fixation location. Prior to or during their actual eye movement, a target was briefly shown on the screen ipsilaterally to the requested saccade (white filled square or diamond in condition 1 [A]; white empty square or diamond for condition 2 [B]). After a variable interstimulus interval (ISI), a larger mask (white empty square or diamond) appeared in the same location as the target. We varied the ISI between the target and mask in order to directly manipulate the influence of the mask. The background was black throughout the experiment.
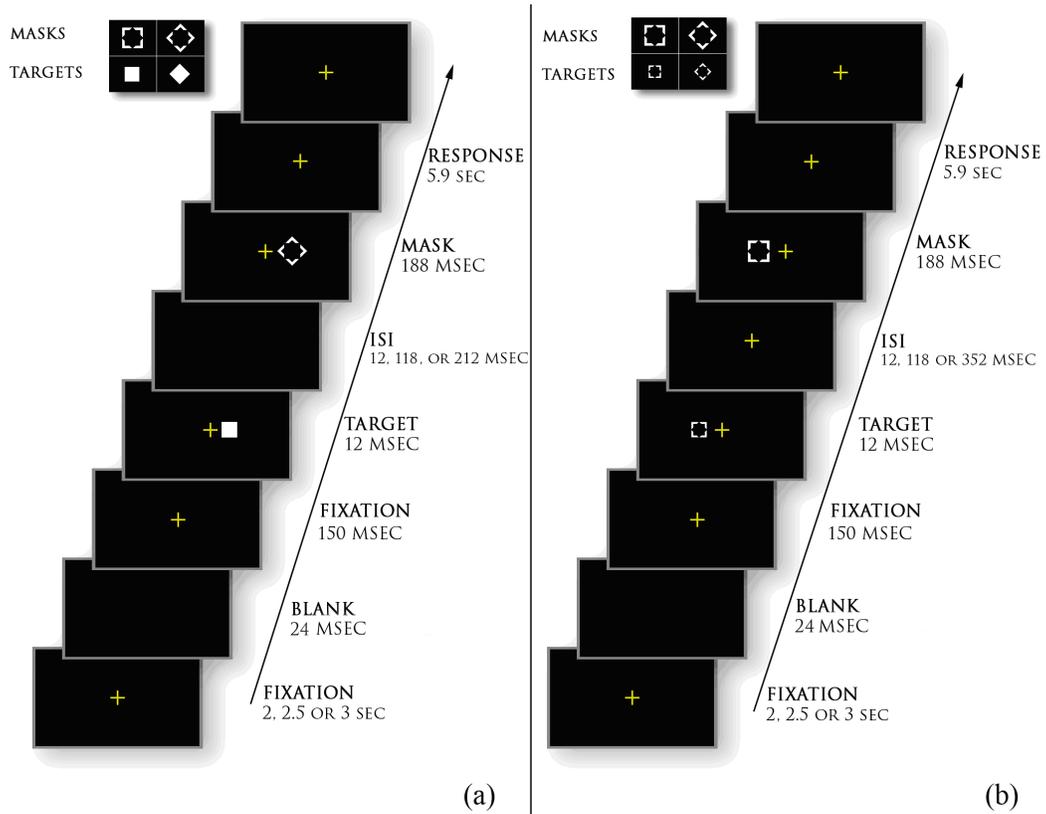
Figure 4.2. Experimental design for the control condition with no saccadic eye movements, showing filled shapes (a) and empty shapes (b)
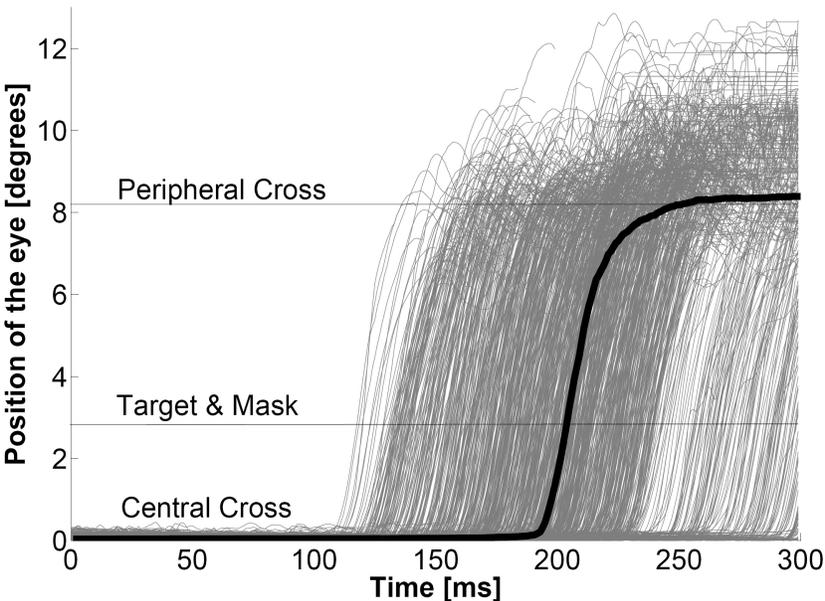
Figure 4.3. Each grey line shows the eye position trace recorded on an individual trial in the main experimental conditions (for 3 representative subjects). The thick black line shows the average saccade across the entire group of trials. For the accuracy analyses, trials in which the saccadic onset occurred less than 140 msec after the displacement of the fixation cross were excluded, in order to ensure that the test and mask stimuli were not presented at the same retinal location.
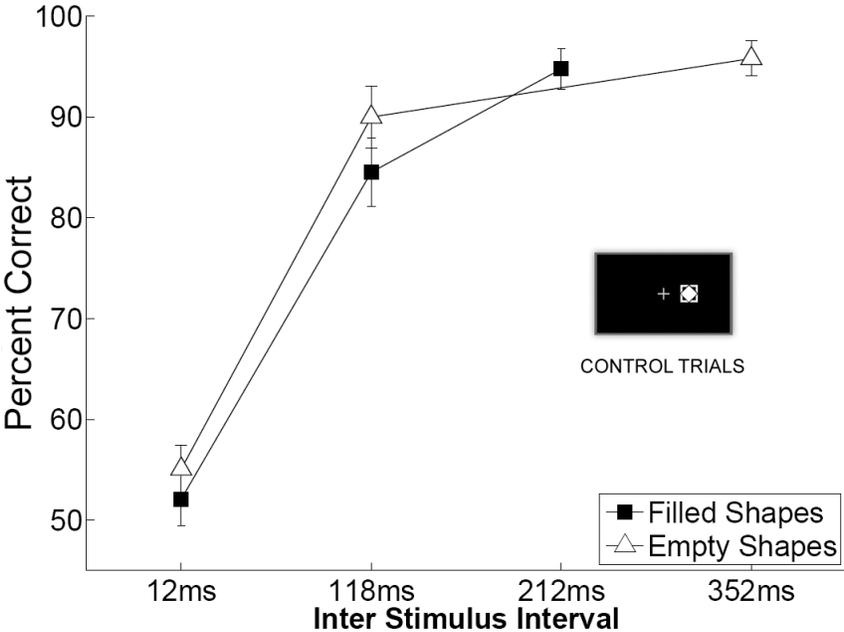
Figure 4.4. Performance in discriminating the target shape as a function of the inter-stimulus interval. The internal panel depicts how participants invariably perceived the target and the mask as located in the same spatial location.

spatial representation change their receptive fields based on the anticipated outcome of the saccade, a phenomenon known as remapping (Colby & Goldberg, 1999). The activity of these remapping neurons is not discretely tied to single fixations, but instead these neurons respond based upon information from the future, or even past, receptive field. If the remapping of receptive fields serves as a bridge for conscious perception, as we suggest, then this leads to the following predictions about the influence of saccades on backward masking: (1) when perisaccadic mislocalization occurs, the target should be unmasked and appear as segregated from the mask, thus increasing its visibility; and (2) when trans-saccadic integration occurs, the target should be hidden by the mask, even when the target and mask have different retinotopic coordinates.

Participants were cued to make saccades either to the left or to the right. Just before saccade onset, a target stimulus was briefly flashed and then, after a variable interstimulus interval (ISI), masked by a larger stimulus (the mask) shown at the same location. After the saccadic eye movement, participants reported the identity of the target (square or diamond) and where they perceived it compared to the mask (same location, to the left, or to the right; Figure 4.1).

Consistent with theories of remapping as an explanation for perisaccadic mislocalization (Ross et al., 2001), the proportion of displaced trials was greatest around the time of saccadic onset (Figures 4.5 A and 4.5 B). When the target was shown more than 100 ms before the saccade, it was typically perceived in the correct location, whereas around the time of saccadic onset, the target was displaced toward the saccadic target on a majority of trials. The fact that mislocalization occurred so frequently might be considered surprising, given previous studies showing that the presence of a longer visual reference (in this case, the mask) can reduce mislocalization (Honda, 1999; Georg & Lappe, 2009). Despite the presence of the visual reference, participants reported displacements of the target, particularly in the perisaccadic time period.

Moreover, the displacement perceptually unmasked the target (main effect of displace-

ment across both filled- and empty-shapes conditions: F = 9.29, p < 0.05). In the filledshapes condition (Figure 4.6 A), displacement of the target in the direction of the saccade dramatically improved the ability to correctly report the target shape (F = 11.79, p < 0.01). This benefit of displacement was found even with the shortest ISI, in which only one blank frame of 12 ms separated target and mask (t = 2.75, p < 0.05). Participants were unable to correctly discriminate the target identity at the shortest ISI, for which d' (Wickens, 2001) was near zero (d' = 0.84, standard deviation [SD] = 0.75) for filled shapes perceived veridically but equal to 1.9 (SD = 0.75) for displaced trials. As expected, accuracy generally increased for longer ISIs between target and mask (main effect of ISI: F = 39.56, p < 0.0001). Best performance in the strong-masking condition (ISI of 12 ms) was found near the time of the saccade (Figure 4.6 C), consistent with the hypothesis that displacement made the target more visible.

The empty-shapes condition allowed us to test the case in which the target and mask tended to be perceptually fused into a single object, showing stronger masking (main effect of filled versus empty shape: F = 7.73, p < 0.05). With these unfilled targets and no perceived target displacement, backward masking could completely eliminate any awareness of the presence of the target stimuli, especially at the shortest ISI (d' = 0.37, SD = 0.41), with only gradual improvement with longer ISIs (Figure 4.6 B). Performance was better on trials in which the target was perceived as displaced, compared to when the target was perceived at its actual location (F = 5.55, *p* < 0.05), even for the shortest ISI (mean d' = 1.22, SD = 1.5). As in the filled-shape condition, best performance was found in the perisaccadic time period (Figure 4.6 D).

The empty-shape condition also provided the opportunity to test whether masking might continue even when the target and mask were separated by a saccadic eye movement. Previous studies have suggested that metacontrast masking occurs mainly in retinotopic coordinates (Breitmeyer et al., 1982). When looking at trials in which the target was shown before the saccade and the mask shown after the saccade (Figure 4.7 A), however, we found
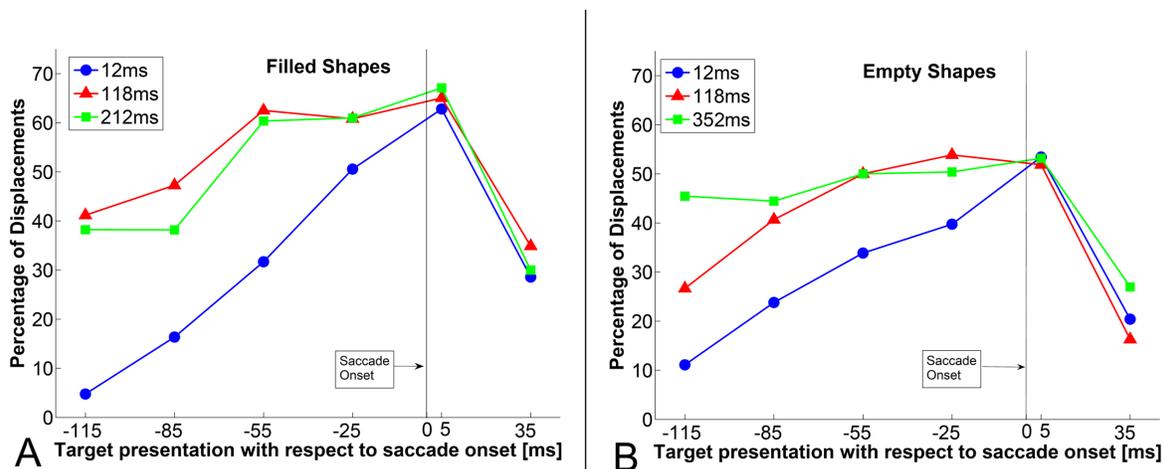
Figure 4.5. Percentage of Displacements as a Function of the Presentation Time of the Target with Respect to the Saccade Onset. In these panels, we report the percentage of perceived displacements for each ISI, respectively, for filled (A) and empty (B) shapes. Each data bin represents the average inside a 30 ms time period as a function of target presentation with respect to the initiation of the saccade. The data points are positioned at the center of the 30 ms interval. The vertical black line indicates the saccade onset time. The proportion of displacements varied across the bins (F = 23.4, $p < 0.0001$ for filled shapes; F = 17.7, $p < 0.0001$ for empty shapes). To further investigate the relationship between saccade onset and the perception of displacement, we performed multiple comparison tests. We used the 2130 ms to 2100 ms bin as baseline, because the targets appeared prior to the perisaccadic time period. There was a significant difference from the baseline for the bins ranging from 270 ms to 20 ms for the filled shapes and from 240 ms to 20 ms for the empty shapes, showing that perception of displacement is tightly related to the timing of the presentation of the target with respect to saccade initiation. There was a trend for displacements in the shortest ISI conditions to be more strictly constrained to the perisaccadic time period than with longer ISIs. For bins to the left of saccadic onset of 225 ms, the saccade onset was initiated after the disappearance of the target, thus suggesting that a remapping process accounts for the perception of displacement.
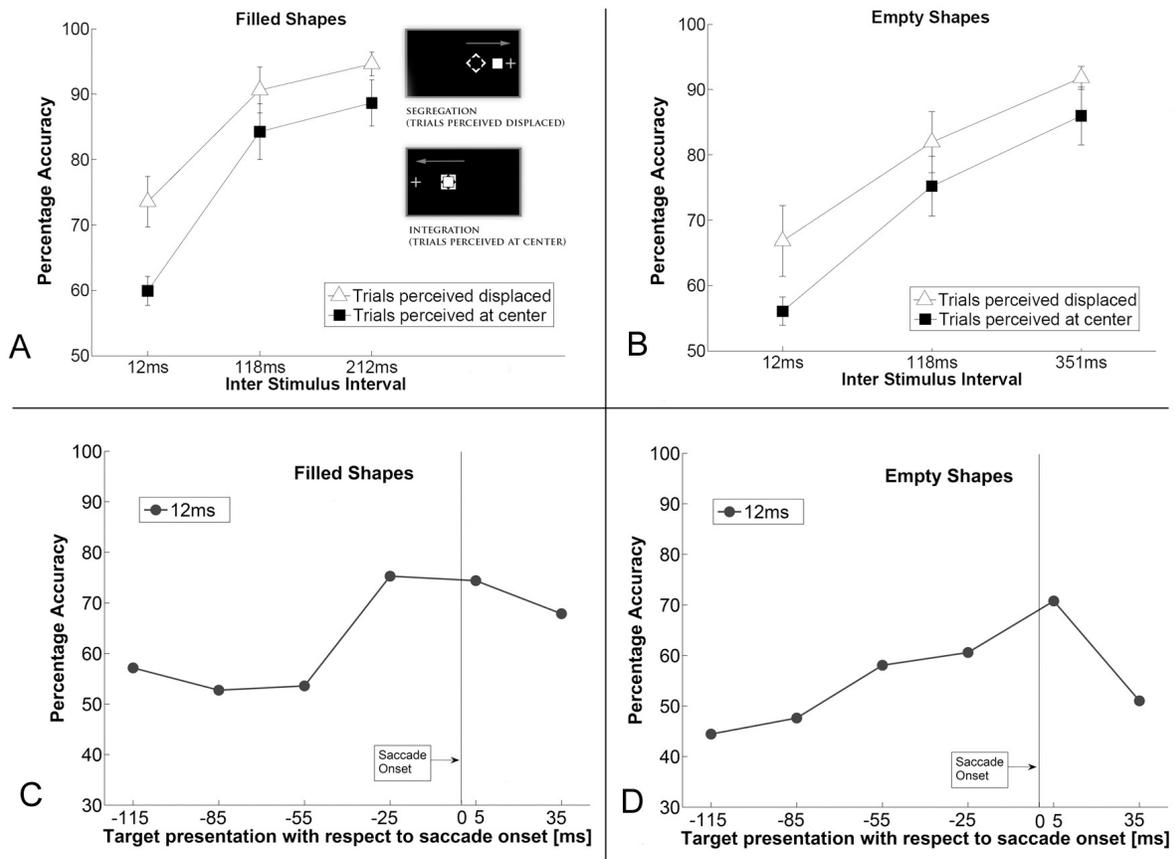
Figure 4.6. Target Discrimination Accuracy. The top row shows the percentage of trials in which the target shape was correctly reported as a function of ISI, whereas the second row shows performance in the shape discrimination task as a function of the timing of the target with respect to saccade onset (left panels for filled shapes, right panels for empty shapes).
(A and B) In the insets of panel A, we depict how participants subjectively perceived the target and mask locations in the filled-shape condition. The target and mask were always shown in the same spatial location on the screen, but the location of the target was not always perceived veridically. Observers reported seeing the target and mask in the same location when integrating (bottom inset) but in different locations when segregating (top inset). Notice how segregation increased the visibility of the target, even at the smallest ISI between target and mask. Error bars indicate standard error of the mean. (C and D) Target detection accuracy as a function of target presentation with respect to saccade onset. Data is shown for trials with the shortest target/mask ISI (i.e., 12 ms). Accuracy for the other ISIs, where masking was weaker, remained relatively high (above 75%) and thus are not depicted.

evidence for trans-saccadic masking in spatial coordinates. First, performance was worse ($t = 2.75$, $p < 0.05$) when the mask was shown shortly after the saccade (ISI = 118 ms), compared to trials in which the mask was shown late in the trial (ISI = 352 ms) (Figure 4.7 B). Overall, the postsaccadic mask had a greater influence when it was shown nearer in time to the target (main effect of postsaccadic ISI across filled and empty shapes: $F = 11.94$, $p < 0.01$). Second, there was a consistent trend for displacement to improve performance, even on trials in which the mask was shown postsaccadically (main effect of displacement across filled and empty shapes: $F = 6.22$, $p < 0.05$). Because the postsaccadic mask was shown at a different retinal location, we might have expected that performance on these trials would have been unaffected by ISI or displacement; instead, the main effects of displacement and ISI continued across the saccade.

To confirm that the decrement in performance on trials with the postsaccadic mask was due to masking rather than to a failure to see the target, we conducted a second experiment (see Supplemental Experimental Procedures available online) in which the strength of the masking was increased by reducing the blank interstimulus interval between the target and mask. If there was trans-saccadic masking, then we would predict strong masking when the mask and target locations were matched across the saccade, which is what we found (Figure 4.7 C, left bar). In contrast, performance remained high when the mask location was vertically offset from the target (Figure 4.7 C, right bar) ($t = 3.53$ $p < 0.05$). Thus, the inability to discriminate the target shape was neither due to the act of making a saccade nor to the mere presence of a postsaccadic stimulus. Instead, these results show that trans-saccadic masking can occur when the postsaccadic mask is shown in the same spatial coordinates as the target.
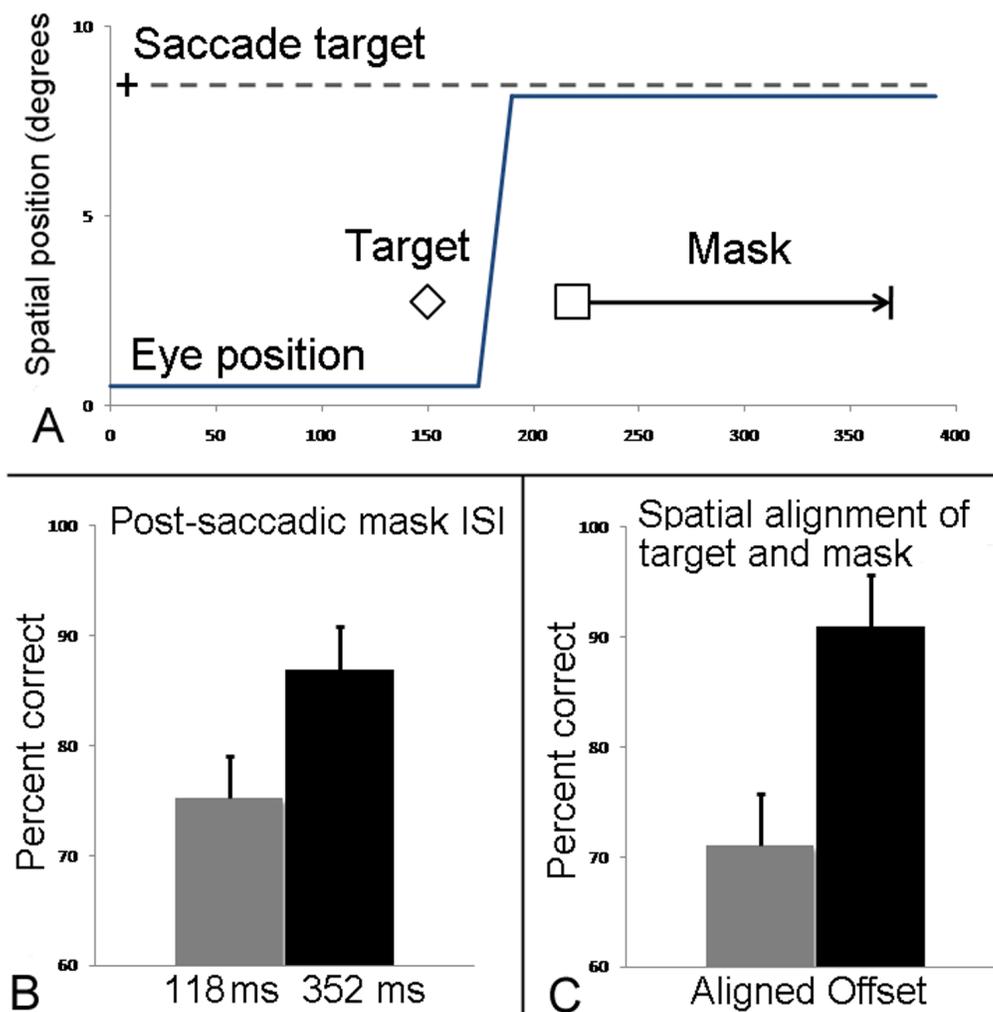
Figure 4.7. Trans-saccadic Masking in Spatiotopic Coordinates.
(A) Trials were examined in which the saccade was made during the blank interval between the test and the mask stimulus. Note that this means that the target and mask were shown at different retinal positions (different visual hemifields) but at the same spatial location on the screen.
(B) In experiment 1, the masking continued across the saccade. Here, performance at discriminating the empty target shape for the two different postsaccadic ISIs of 118 ms (left bar) and 352 ms (right bar) is shown. The percentage correct on trials in which the mask was presented shortly after the saccade (ISI = 118 ms) was lower than on trials in which the mask was shown later in the trial (ISI = 352 ms), consistent with the predictions of trans-saccadic masking.
(C) Performance in experiment 2 (see Supplemental Experimental Procedures) in which the ISI was reduced to 48 ms in order to increase the strength of the masking. The mask was either shown in the same spatial location on the screen (left bar) or was slightly displaced vertically (right bar). Although performance with the spatially offset mask was near perfect, a consistent decrement in performance was found on trials in which the spatiotopic location of test and mask was matched across the saccade. Error bars in (B) and (C) indicate standard error of the mean.

Summary and conclusions

Our main finding is that presaccadic targets were effectively unmasked by the saccade, even when the postsaccadic mask followed the target at the shortest ISI. This overall pattern of results is consistent with previous reports of perisaccadic mislocalization of flashed targets but also shows that mislocalized stimuli can be perceived, in the case of masking, more accurately than their correctly localized counterparts. Thus, mislocalization in our task was likely related to saccadic remapping rather than to confusion or guessing about the target (Chapman et al., 2007; Ostendorf et al., 2007). Our results suggest that eye movements increased the ability of the visual system to segregate target and mask as separate perceptual objects. Although saccades are often viewed as a problem for the visual system, our results suggest that the brain may take advantage of saccades to make perception more effective (Ross & Ma-Wyatt, 2004; Melloni et al., 2009; Rajkai et al., 2008).

In addition, the strong masking found with unfilled targets led to trans-saccadic masking across the eye movement. This spatiotopic masking provides further evidence that the visual system interprets perceptual events as continuing across the saccade rather than beginning anew with each fixation (Jonides et al., 1983; O'Regan et al., 1999; Yarrow et al., 2001; Watson & Krekelberg, 2009). Indeed, trans-saccadic integration can improve performance on some tasks (Melcher & Colby, 2008; Melcher & Morrone, 2003). Previous studies have shown that when the identity or location of the stimulus is changed across the saccade, the presaccadic stimulus may be essentially overwritten by the postsaccadic one (Tatler, 2001; Triesch et al., 2003), consistent with the idea of postsaccadic masking. Our results suggest that postsaccadic masking can also be interpreted in terms of integration of the pre- and postsaccadic information. When there is conflicting information about the object across saccades, the visual system is likely to give preference to the more recent and thus more reliable postsaccadic information.

In addition, our findings have implications for theories about the circuits of consciousness. These results suggest that remapping can either route target information toward awareness

when the target is identified as a unique object or hide the target from awareness when it is masked. Because remapping has been shown to be strongest in areas of posterior parietal cortex, where nearly 100% of neurons show remapping (Duhamel et al., 1992), our results support models in which visual awareness is mediated by recurrent signals from frontal-parietal to posterior visual areas (Edelman, 1993; Crick & Koch, 1995; Lamme, 2000). Our results are consistent with the proposal that visual awareness of object location across saccades depends critically on the remapping of object pointers in sensorimotor location maps in parietal cortex (Melcher & Colby, 2008; Ross et al., 2001) that are part of the network of conscious perception.

Chapter 5

Discussion

The relationship between attention and awareness, and the processing of visual information outside of attention and awareness, remain controversial issues. In chapter 2 we employed the motion aftereffect (MAE) illusion and continuous flash suppression (CFS) to study the behavioral effects of non-conscious and unattended visual motion. The main finding was that either withdrawal of attention or the lack of visual awareness on the adaptors did not eliminate the formation of translational MAEs, spiral MAEs or the interocular transfer of the MAE. However, no spiral MAE was generated when attention was diverted from the non-conscious spiral adaptors. Interestingly, all MAEs that arose in the absence of awareness or in the absence of attention were reduced in size. The pattern of results is consistent with suggestions that the magnitude of visual motion adaptation depends both on attention and awareness.

The operations and processes that the human brain employs to achieve fast visual categorization remain a matter of debate. A first issue concerns the timing and place of rapid visual categorization and to what extent it can be performed with an early feed-forward pass of information through the visual system. A second issue involves the categorization of stimuli that do not reach visual awareness. There is disagreement over the degree to which these stimuli activate the same early mechanisms as stimuli that are consciously per-

ceived. In chapter 3 we have shown the results that we obtained employing continuous flash suppression, EEG recordings and machine learning techniques to study visual categorization of conscious and non-conscious stimuli. Our classifiers were able to predict from the EEG recordings the category of stimuli on conscious trials but not on non-conscious trials. Rapid categorization of conscious images could be detected around 100 ms on the occipital electrodes, consistent with a fast, feed-forward mechanism of target detection. For the invisible stimuli, however, continuous flash suppression eliminated all traces of early processing. Our results support the idea of a fast mechanism of categorization and suggest that this early categorization process plays an important role in later, more subtle categorizations and perceptual processes.

In chapter 4 we used visual masking along with saccadic eye movements to study how the process of remmaping can induce an otherwise masked stimuli to gain access to consciousness. Our experiments have shown that the interplay between the integration or segregation of visual information across saccades determines what percepts enter consciousness. Stimuli that are masked under conditions of fixation can be unmasked and gain access to consciousness due to remmaping. When a target is identified as a unique and separable object from its mask remmaping can route it towards consciousness. Considering that neurons in parietal cortices show the strongest responses to remmaping (Melcher & Colby, 2008; Ross et al., 2001), our experiments support the idea that recurrent activity from parietal cortices is crucial for visual awareness. This fact is in line with the main proposal of the global workspace framework and with models that hypothesize that recurrent signals from a fronto-parietal network to posterior areas are crucial for visual awareness.

During the past three decades of research in visual neuroscience a number of physiological experiments studying the properties of visual neurons have demonstrated an intriguing fact: most neurons in the visual cortex respond to what is physically being projected to the retina at a certain moment in time while only a proportion of neurons fire in correlation with the reported perception of subjects. The proportion of cells whose firing rate correlates

with visual awareness varies across different areas of visual cortex, being small in early visual areas and increasing considerably in higher visual areas such as the middle temporal lobes (Logothetis & Schall, 1989; Logothetis, 1998; Kreiman et al., 2005). How does the activity of these neurons relate to behavioral responses is still under study. The results of studying the behavioral and physiological consequences of processing non-conscious stimuli suggest that visual awareness plays an important functional role in the visual system. The study of the limits of non-conscious perception can shed light into this observation. Studying the limits of non-conscious processing we can start thinking about the function of visual awareness and its evolutionary meaning.

The limits to non-conscious processing

In most psychophysics experiments, non-conscious stimuli generate small behavioral differences across conditions, short-lasting behavioral effects and reduced neuronal responses as compared to conscious stimuli. Information processing in the brain is somehow degraded when it comes to non-conscious stimuli. Here we briefly review some of the experimental evidence that supports this view.

The magnitude of the behavioral responses to orientation processing (Blake et al., 2006) and for the generation of afterimages (Tsuchiya & Koch, 2005) are reduced when adaptors are non-conscious to the subjects. Similarly, inattention and/or the lack of visual awareness reduces the magnitude of visual motion adaptation (this was the main topic of study in chapter 2). Furthermore, face adaptation is abolished under both interocular suppression (Alais & Melcher, 2007; Stein & Sterzer, 2011; Amihai et al., 2011) and inattention (Moradi et al., 2005).

Repetition and semantic priming have been found with visual masking (Marcel, 1983; Dehaene et al., 2001). However, it is important to mention that the effects of subliminal priming are small (differences in reaction times in the order of $30 - 50$ms) and short-lived

(the effect disappears with an SOA between prime and target larger than 150-200ms). Interestingly, if interocular suppression is used instead of visual masking, semantic priming appears to be completely eliminated (Kang et al., 2011; Zimba & Blake, 1983). This fact seems to indicate that the mechanism of suppression differs for visual masking and binocular rivalry. Recent studies have shown semantic priming under continuous flash suppression for non-conscious images of tools in the dorsal stream (Fang & He, 2005; Almeida et al., 2008). The logic behind these experiments was that the "grasp-ability" of the images of tools would escape interocular suppression in dorsal areas but not in temporal areas. In chapter 3 we have further investigated this hypothesis but could not confirmed it. Our difficulties in replicating these results are in line with a recent fMRI study by Hesselmann & Malach (2011), which showed no differential suppression for images of animals and tools along the dorsal and ventral streams.

Perceptual learning provides another example of the limits of non-conscious perception: classical conditioning depends on being conscious of the relation between the two stimuli (Clark et al., 2002). When stimuli are invisible to the subject perceptual conditioning is heavily impaired. Thus, subjects under anesthesia or in a vegetative state do not show visual or auditory conditioning. Only patients in the minimal state of consciousness appear to have some preserved conditioning. Interestingly, it has been suggested that the responses of patients in a minimal state of consciousness in a conditioning task might be used as a test of consciousness (Bekinschtein et al., 2009). Neurofeedback is another example of how consciousness is necessary to generate motor and perceptual learning (Baars, 1988). In a recent study, patients with implanted electrodes learned to control the images they were presented on a screen by altering the firing rate of single neurons that were recorded at real-time from their brains (Cerf et al., 2010). In a similar experiments subjects wearing an EEG cap can learn, for example, to control the position of a ball on a screen by modifying their alpha rhythms. Thus, the brain can learn to control processes that are usually automatic, non-conscious and out of awareness. Importantly, all these tasks become impossible to achieve

without *conscious feedback* (Baars, 1988).

The evidence coming from studies of neglect patients points in a similar direction. The damage hemisphere of these patients can nonetheless process stimuli that are invisible to the subject (Vuilleumier et al., 2002). However, the question remains: what can these patients do with the non-conscious information that they perceive? What is the functional role of this information? Again, it seems that the non-conscious information has very little impact on the general behavior. Up to date, almost no therapy was able make use of non-conscious information to help in the rehabilitation of patients suffering from neglect syndrome.

Finally, executive control and planning require awareness. Non-conscious stimuli are usually unable to yield long-lasting modification in executive control. Even though subjects can proficiently extract statistical relations among stimuli and use them to exploit different strategies, these operations require awareness (Posner & Rothbart, 1998). If stimuli are masked or unattended these strategies fail to deploy (Vandenbussche et al., 2008; Merikle & Joordens, 1997). Besides, when errors are unconscious to subjects they do not produce the typical effect of slowing down responses, which is a typical effect of being aware of errors (Kunde, 2003; Nieuwenhuis et al., 2001).

We would like to take note of an important fact here. Even though perception is generally impaired for non-conscious stimuli, the visual brain can still achieve important tasks without visual awareness. Twenty years ago, Milner & Goodale (1995) proposed the hypothesis of the existence of a visuomotor system which is independent of visual awareness of the target's object form. They called this system "vision for perception" as opposed to the "vision for action" system. Their claim of the existence of these two system was initially based on a case study of the agnosic patient D.F. This patient, who suffered a kind of visual agnosia due to brain damage, had surprising visuomotor abilities in spite of being unable to consciously report the form of the targets he was observing: she could grasp objects in front of her quite accurately, walk around her own, step over blocks placed in front of her and she could appropriately insert a card into a slot of different orientations. She could do all this even

though she was unable to report the orientation of the slot nor recognize objects by sight. Her grasping abilities were preserved (her posture reflected the size, shape or orientation of the stimuli) but she was not able to recognize the objects by visual inspection.

This study demonstrated that automatic visuomotor routines can be performed without being aware of certain aspect of the stimuli. However, these visuomotor routines, though valid, had a limited range of action. Citing Westwood & Goodale (2011): "Her performance sharply deteriorates for objects defined by second-order contrast, objects whose principal axis of orientation is ambiguous, objects removed from view before the onset of the action, and objects seen without cues to absolute distance". Therefore, only certain routines of the vision for action system are independent of awareness of form. Furthermore, one should notice that these studies point to the independence of the visual routines of the vision from action system from awareness of the *form* of an object. Still, visual awareness intended as detection of an object cannot be discarded as necessary to start any visual process.

Final Remarks

Two questions address the issue of the function of visual awareness: what is/are the function/s of visual awareness for the sensory system? And how did they appeared during evolution? Undoubtedly, to answer these questions further studies are needed. For now we can only assert that, as we have outlined in the previous review, the lack of visual awareness has important consequences for sensory perception.

In chapter 1 we have introduced the idea of the hard and easy problems proposed by David Chalmers. In simple terms, the reasoning put forward by Chalmers is that for one particular neuronal activity it is *logically possible* to reach to two subjective states: one conscious and one non conscious (the famous philosophical zombie agents). Even though this line of reasoning cannot be refuted, we believe that it is important to stress that the majority of the empirical evidence on conscious and non-conscious processing shows that

visual awareness *serves a purpose in functional terms.*

The fact that non-conscious processing is usually diminished and degraded in nature suggests that the origins of visual awareness might be tightly related to an evolutionary advantage for the visual system (and hypothetically for the brain in general). It seems as though our brains could have evolved without being aware of the external world but they simply did not. If consciousness serves a purpose (if it is not just a simple epiphenomenon) and if it determines how the visual system evolved, then we should consider it as a natural and intrinsic part of our visual system.

One open question is whether the neural correlates of visual awareness can be found across species. Another is whether awareness serves one or many purposes (such as visual adaptation, perceptual learning or priming) in visual perception. The only partial answer we can give here is that achieving normal levels of motion (as shown in chapter 2) and face adaptation requires consciousness.

As we gain knowledge on the operations of the visual brain, we will get closer to know the NCC. In Christoph Koch's own words: "Progress in the study of the Neural Correlates of Consciousness on one hand, and of the neural correlates of non-conscious behaviors on the other, will hopefully lead to a better understanding of what distinguishes neural structures or processes that are associated with consciousness from those that are not" (Koch & Mormann, 2007). When that time arrives we will be in the position to say whether by knowing the work of millions of neurons in the visual cortex will be enough to explain the mystery of our visual conscious sensations.

References

Aghdaee, M. M. & Zandvakili, A. (2005). Adaptation to spiral motion: global but not local motion detectors are modulated by attention. Vision Research, 45, 1099–1105.

Aghdaee, S. M. (2005). Adaptation to spiral motion in crowding condition. Perception, 34, 155–162.

Alais, D. & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. Nature Neuroscience, 2, 1015–1018.

Alais, D. & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. Vision Research, 47, 269–279.

Alais, D. & Parker, A. (2006). Independent Binocular Rivalry Processes for Motion and Form. Neuron, 52, 911–920.

Almeida, J., Mahon, B. Z., & Caramazza, A. (2010). The Role of the Dorsal Visual Processing Stream in Tool Identification. Psychological Science, 21, 772–778.

Almeida, J., Mahon, B. Z., Nakayama, K., & Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. Proceedings of the National Academy of Sciences of the United States of America, 105, 15214–15218.

Amihai, I., Deouell, L., & Bentin, S. (2011). Conscious awareness is necessary for processing race and gender information from faces. Consciousness and Cognition, 20, 269–279.

Andrews, T. J. & Blakemore, C. (1999). Form and motion have independent access to consciousness. Nature Neuroscience, 2, 405–406.

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

Bacon-Macé, N., Macé, M. J. M., Fabre-Thorpe, M., & Thorpe, S. J. (2005). The time course of visual processing: Backward masking and natural scene categorisation. Vision Research, 45, 1459–1469.

Bahrami, B., Carmel, D., Walsh, V., Rees, G., & Lavie, N. (2008). Unconscious orientation processing depends on perceptual load. Journal of Vision, 8, 1–10.

Bar, M. & Biederman, I. (1999). Localizing the cortical region mediating visual awareness of object identity. Proceedings of the National Academy of Sciences of the United States of America, 96, 1790–1793.

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

Bekinschtein, T. A., Shalom, D. E., Forcato, C., Herrera, M., Coleman, M. R., Manes, F. F., & Sigman, M. (2009). Classical conditioning in the vegetative and minimally conscious state. Nature Neuroscience, 12, 1343–1349.

Biederman, I. (1972). Perceiving real-world scenes. Science, 177, 77–80.

Blake, R., Ahlström, U., & Alais, D. (1999). Perceptual priming by invisible motion. Psychological Science, 10, 145–150.

Blake, R. & Logothetis, N. K. (2002). Visual competition. Nature Reviews Neuroscience, 3, 13–21.

Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. Proceedings of the National Academy of Sciences of the United States of America, 103, 4783–4788.

Brainard, D. H. (1997). The psychophysics toolbox. Spatial Vision, 10, 433–436.

Breitmeyer, B. G. (1984). Visual Masking: An Integrative Approach. (Oxford University Press, USA).

Breitmeyer, B. G., Kropfl, W., & Julesz, B. (1982). The existence and role of retinotopic and spatiotopic forms of visual persistence. Acta Psychologica, 52, 175–196.

Cajal, S. R. (1995). Histology of the Nervous System of Man and Vertebrates. (Oxford University Press, USA), 1st edn.

Cavanagh, P. & Alvarez, G. (2005). Tracking multiple targets with multifocal attention. Trends in Cognitive Sciences, 9, 349–354.

Cerf, M., Thiruvengadam, N., Mormann, F., Kraskov, A., Quiroga, R. Q., Koch, C., & Fried, I. (2010). On-line, voluntary control of human temporal lobe neurons. Nature, 467, 1104–1108.

Chalmers, D. J. (1995). Facing up to the problem of consciousness. Journal of Consciousness Studies, 3, 200–219.

Chan, A. M., Halgren, E., Marinkovic, K., & Cash, S. S. (2011). Decoding word and category-specific spatiotemporal representations from MEG and EEG. Neuroimage, 54, 3028–3039.

Chapman, C. S., Hunt, A. R., & Kingstone, A. (2007). Squeezing Uncertainty from Saccadic Compression. Journal of Eye Movement Research, 1, 1–5.

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. Nature, 344, 60–62.

Chun, M. M. & Potter, M. C. (1995). A two-stage model for multiple target detection in rapid serial visual presentation. Journal of Experimental Psychology. Human Perception and Performance, 21, 109–127.

Clark, R. E. E., Manns, J. R. R., & Squire, L. R. R. (2002). Classical conditioning, awareness, and brain systems. Trends in Cognitive Sciences, 6, 524–531.

Colby, C. L. & Goldberg, M. E. (1999). Space and attention in parietal cortex. Annual Review of Neuroscience, 22, 319–349.

Crick, F. & Koch, C. (1995). Are we aware of neural activity in primary visual cortex? Nature, 375, 121–123.

Crick, F. & Koch, C. (2003). A framework for consciousness. Nature Neuroscience, 6, 119–126.

De Pisapia, N., Turatto, M., Lin, P., Jovicich, J., & Caramazza, A. (2011). Unconscious Priming Instructions Modulate Activity in Default and Executive Networks of the Human Brain. Cerebral Cortex, in press.

Dehaene, S. (1995). Electrophysiological evidence for category-specific word processing in the normal human brain. Neuroreport, 6, 2153–2157.

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

Dehaene, S. & Changeux, J.-P. P. (2011). Experimental and theoretical approaches to conscious processing. Neuron, 70, 200–227.

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

Delorme, A. & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134, 9–21.

Dennett, D. C. (1996). Commentary on Chalmers "Facing Backwards on the Problem of Consciousness".

Dennett, D. C. (2004). Consciousness Explained. (Gardners Books).

Desimone, R. & Duncan, J. (1995). Neural Mechanisms of Selective Visual Attention. Annual Review of Neuroscience, 18, 193–222.

Duhamel, Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. Science, 255, 90–92.

Edelman, G. (1993). Neural Darwinism: Selection and reentrant signaling in higher brain function. Neuron, 10, 115–125.

Fabre-Thorpe, M., Delorme, A., Marlot, C., & Thorpe, S. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. Journal of Cognitive Neuroscience, 13, 171–180.

Fang, F. & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. Nature Neuroscience, 8, 1380–1385.

Fei-Fei, L., VanRullen, R., Koch, C., & Perona, P. (2002). Rapid natural scene categorization in the near absence of attention. Proceedings of the National Academy of Sciences, 99, 9596–9601.

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

Finkbeiner, M. & Palermo, R. (2009). The Role of Spatial Attention in Nonconscious Processing. Psychological Science, 20, 42–51.

Freud, S. (1901). The Psychopathology of Everyday Life. (Digireads.com).

Georg, K. & Lappe, M. (2009). Effects of saccadic adaptation on visual localization before and during saccades. Experimental Brain Research, 192, 9–23.

Gilroy, L. A. & Blake, R. (2005). The Interaction between Binocular Rivalry and Negative Afterimages. Current Biology, 15, 1740–1744.

Grimes, J. (1996). On the failure to detect changes in scenes across saccades. In Perception (Vancouver Studies in Cognitive Science), K. Akins, ed. (New York: Oxford University Press), chap. 2, pp. 89–110.

Gross, J., Schmitz, F., Schnitzler, I., Kessler, K., Shapiro, K., Hommel, B., & Schnitzler, A. (2004). Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. Proceedings of the National Academy of Sciences of the United States of America, 101, 13050–13055.

Hanke, M., Halchenko, Y. O., Sederberg, P. B., Olivetti, E., Fründ, I., Rieger, J. W., Herrmann, C. S., Haxby, J. V., Hanson, S. J., & Pollmann, S. (2009). PyMVPA: a unifying approach to the analysis of neuroscientific data. Frontiers in Neuroinformatics, 3, 1–13.

Haynes, J.-D., Deichmann, R., & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. Nature, 438, 496–499.

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. Nature, 383, 334–337.

Hesselmann, G. & Malach, R. (2011). The Link between fMRI-BOLD Activation and Perceptual Awareness Is âĂİ Stream-InvariantâĂİ in the Human Visual System. Cerebral Cortex, doi:10.1093/cercor/bhr085.

Honda, H. (1999). Modification of saccade-contingent visual mislocalization by the presence of a visual frame of reference. Vision Research, 39, 51–57.

Hung, C. P., Kreiman, G., Poggio, T., & DiCarlo, J. J. (2005). Fast readout of object identity from macaque inferior temporal cortex. Science, 310, 863–866.

Jiang, Y., Costello, P., Fang, F., Huang, M., & He, S. (2006). A gender- and sexual orientation-dependent spatial attentional effect of invisible images. Proceedings of the National Academy of Sciences, 103, 17048–17052.

Jiang, Y., Shannon, R. W., Vizueta, N., Bernat, E. M., Patrick, C. J., & He, S. (2009). Dynamics of processing invisible faces in the brain: automatic neural encoding of facial expression information. Neuroimage, 44, 1171–1177.

Jonides, J., Irwin, D. E., & Yantis, S. (1983). Failure to integrate information from successive fixations. Science, 222.

Kanai, R., Tsuchiya, N., & Verstraten, F. (2006). The Scope and Limits of Top-Down Attention in Unconscious Visual Processing. Current Biology, 16, 2332–2336.

Kang, M.-S., Blake, R., & Woodman, G. F. (2011). Semantic Analysis Does Not Occur in the Absence of Awareness Induced by Interocular Suppression. Journal of Vision, 11, 321–13545.

Keliris, G. A., Logothetis, N. K., & Tolias, A. S. (2010). The Role of the Primary Visual Cortex in Perceptual Suppression of Salient Visual Stimuli. The Journal of Neuroscience, 30, 12353–12365.

Kiefer, M. (2001). Perceptual and semantic sources of category-specific effects: Event-related potentials during picture and word categorization. Memory & Cognition, 29, 100–116.

Kim, C.-Y. Y. & Blake, R. (2005). Psychophysical magic: rendering the visible 'invisible'. Trends in Cognitive Sciences, 9, 381–388.

Koch, C. (1996). Towards the neuronal correlate of visual awareness. Current Opinion in Neurobiology, 6, 158–164.

Koch, C. (2003). The quest for consciousness: a neurobiological approach. (Englewood, Colorado 80111: Roberts & Company Publishers).

Koch, C. & Mormann, F. (2007). Neural correlates of consciousness ,. Scholarpedia, 2, 1740+.

Koch, C. & Tsuchiya, N. (2007). Attention and consciousness: two distinct brain processes. Trends in Cognitive Sciences, 11, 16–22.

Kovács, I., Papathomas, T. V., Yang, M., & Fehér, A. (1996). When the brain changes its mind: Interocular grouping duringâĂŁbinocularâĂŁrivalry. Proceedings of the National Academy of Sciences, 93, 15508–15511.

Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., & Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. Neuroimage, 24, 704–714.

Kreiman, G., Fried, I., & Koch, C. (2002). Single-neuron correlates of subjective vision in the human medial temporal lobe. Proceedings of the National Academy of Sciences, 99, 8378–8383.

Kreiman, G., Fried, I., & Koch, C. (2005). Responses of single neurons in the human brain during flash suppression. In Binocular Rivalry, D. Alais & R. Blake, eds. (Cambridge, MA: MIT Press.), chap. 12, pp. 213–230.

Kunde, W. (2003). Sequential modulations of stimulus-response correspondence effects depend on awareness of response conflict. Psychonomic Bulletin & Review, 10, 198–205.

Kutas, M. & Hillyard, S. A. (1980). Reading senseless sentences: brain potentials reflect semantic incongruity. Science, 207, 203–205.

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

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

Lankheet, M. J. & Verstraten, F. A. (1995). Attentional modulation of adaptation to two-component transparent motion. Vision Research, 35, 1401–1412.

Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic compression of space. Nature, 403, 892–895.

Lehmkuhle, S. W. & Fox, R. (1975). Effect of binocular rivalry suppression on the motion aftereffect. Vision Research, 15, 855–859.

Levitt, H. (1971). Transformed up-down methods in psychoacoustics. The Journal of the Acoustical Society of America, 49, 467–477.

Lin, Z. & He, S. (2009). Seeing the invisible: the scope and limits of unconscious processing in binocular rivalry. Progress in neurobiology, 87, 195–211.

Ling, S., Liu, T., & Carrasco, M. (2009). How spatial and feature-based attention affect the gain and tuning of population responses. Vision research, 49, 1194–1204.

Liu, H., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, timing, timing: fast decoding of object information from intracranial field potentials in human visual cortex. Neuron, 62, 281–290.

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

Logothetis, N. K. (1998). Single units and conscious vision. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 353, 1801–1818.

Logothetis, N. K. & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. Science, 245, 761–763.

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

MacKay, D. M. (1970). Mislocation of test flashes during saccadic image displacements. Nature, 227, 731–733.

Macknik, S. L. & Martinez-Conde, S. (2004). Dichoptic visual masking reveals that early binocular neurons exhibit weak interocular suppression: implications for binocular vision and visual awareness. Journal of Cognitive Neuroscience, 16, 1049–1059.

Marcel, A. J. (1983). Conscious and unconscious perception: Experiments on visual masking and word recognition. Cognitive Psychology, 15, 197–237.

Marois, R., Yi, D. J., & Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. Neuron, 41, 465–472.

Maruya, K., Watanabe, H., & Watanabe, M. (2008). Adaptation to invisible motion results in low-level but not high-level aftereffects. Journal of Vision, 8.

Mather, G., Verstraten, F., & Anstis, S. (1998). The motion aftereffect: a modern perspective. (The MIT Press).

Mattler, U. (2003). Priming of mental operations by masked stimuli. Perception & Psychophysics, 65, 167–187.

Maunsell, J. H. & Cook, E. P. (2002). The role of attention in visual processing. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 357, 1063–1072.

Melcher, D. & Colby, C. L. (2008). Trans-saccadic perception. Trends in Cognitive Sciences, 12, 466–473.

Melcher, D. & Morrone, C. C. (2003). Spatiotopic temporal integration of visual motion across saccadic eye movements. Nature Neuroscience, 6, 877–881.

Melcher, D., Papathomas, T. V., & Vidnyánszky, Z. (2005). Implicit attentional selection of bound visual features. Neuron, 46, 723–729.

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.

Melloni, L., Schwiedrzik, C. M., Rodriguez, E., & Singer, W. (2009). (Micro)Saccades, corollary activity and cortical oscillations. Trends in Cognitive Sciences, 13, 239–245.

Meng, M. & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. Journal of Vision, 4, 539–551.

Meng, X., Chen, Y., & Qian, N. (2004). Both monocular and binocular signals contribute to motion rivalry. Vision Research, 44, 45–55.

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

Milner, D. & Goodale, M. (1995). The visual brain in action. (Great Clarendon Street, Oxford OX2 6DP: Oxford University Press), 2nd edn.

Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. Nature, 429, 410–413.

Moradi, F., Koch, C., & Shimojo, S. (2005). Face adaptation depends on seeing the face. Neuron, 45, 169–175.

Moran, J. & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. Science, 229, 782–784.

Morrone, C. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. Nature Neuroscience, 8, 950–954.

Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. Nature, 376, 507–509.

Moutoussis, K., Keliris, G., Kourtzi, Z., & Logothetis, N. (2005). A binocular rivalry study of motion perception in the human brain. Vision Research, 45, 2231–2243.

Murphy, B., Baroni, M., & Poesio, M. (2009). EEG responds to conceptual stimuli and corpus semantics. In Proceedings of the 2009 Conference on Empirical Methods in Natural Language Processing: Volume 2 - Volume 2, EMNLP '09, pp. 619–627. (Stroudsburg, PA, USA: Association for Computational Linguistics).

Murphy, B., Poesio, M., Bovolo, F., Bruzzone, L., Dalponte, M., & Lakany, H. (2010). EEG decoding of semantic category reveals distributed representations for single concepts. Brain and Language, 117, 12–22.

Naccache, L., Blandin, E., & Dehaene, S. (2002). Unconscious Masked Priming Depends on Temporal Attention. Psychological Science, 13, 416–424.

Nieuwenhuis, S., Ridderinkhof, K. R., Blom, J., Guido, & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task. Psychophysiology, 38, 752–760.

Nishida, S. & Ashida, H. (2000). A hierarchical structure of motion system revealed by interocular transfer of flicker motion aftereffects. Vision Research, 40, 265–278.

Olivetti, E., Mognon, A., Greiner, S., & Avesani, P. (2010). Brain decoding: biases in error estimation. First Workshop on Brain Decoding: Pattern Recognition Challenges in Neuroimaging, pp. 40–43.

Ooi, T. L. & He, Z. J. (1999). Binocular rivalry and visual awareness: the role of attention. Perception, 28, 551–574.

Oram, M. W. & Perrett, D. I. (1992). Time course of neural responses discriminating different views of the face and head. Journal of Neurophysiology, 68, 70–84.

O'Regan, J. K., Rensink, R. A., & Clark, J. J. (1999). Change-blindness as a result of 'mudsplashes'. Nature, 398.

Oshea, R. & Crassini, B. (1981). Interocular transfer of the motion after-effect is not reduced by binocular rivalry. Vision Research, 21, 801–804.

Ostendorf, F., Fischer, C., Finke, C., & Ploner, C. J. (2007). Perisaccadic compression correlates with saccadic peak velocity: differential association of eye movement dynamics with perceptual mislocalization patterns. Journal of Neuroscience, 27, 7559–7563.

Pashler, H. (1994). Dual-task interference in simple tasks: data and theory. Psychological Bulletin, 116, 220–244.

Pasley, B. N., Mayes, L. C., & Schultz, R. T. (2004). Subcortical Discrimination of Unperceived Objects during Binocular Rivalry. Neuron, 42, 163–172.

Penfield, W. (1978). Mystery of the Mind: A Critical Study of Consciousness and the Human Brain. (Princeton Univ Pr).

Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. Experimental Brain Research, 47, 329–342.

Pessoa, L. & Ungerleider, L. G. (2004). Neural Correlates of Change Detection and Change Blindness in a Working Memory Task. Cerebral Cortex, 14, 511–520.

Plato, Cooper, J. M., & Hutchinson, D. S. (1997). Plato Complete Works. (Hackett Pub Co).

Popper, K. R. (1992). Conjectures and Refutations: The Growth of Scientific Knowledge. (Routledge), 5th edn.

Posner, M. I. (1994). Attention: the mechanisms of consciousness. Proceedings of the National Academy of Sciences of the United States of America, 91, 7398–7403.

Posner, M. I. & Rothbart, M. K. (1998). Attention, self-regulation and consciousness. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 353, 1915–1927.

Potter, M. C. & Faulconer, B. A. (1975). Time to understand pictures and words. Nature, 253, 437–438.

Pulvermuller, F., Preissl, H., Lutzenberger, W., & Birbaumer, N. (1996). Brain rhythms of language: nouns versus verbs. The European Journal of Neuroscience, 8, 937–941.

Rajimehr, R. (2004). Unconscious orientation processing. Neuron, 41, 663–673.

Rajkai, C., Lakatos, P., Chen, C.-M. M., Pincze, Z., Karmos, G., & Schroeder, C. E. (2008). Transient cortical excitation at the onset of visual fixation. Cerebral Cortex, 18, 200–209.

Raymond, J. (1993). Complete interocular transfer of motion adaptation effects on motion coherence thresholds. Vision Research, 33, 1865–1870.

Reddy, L., Reddy, L., & Koch, C. (2006). Face identification in the near-absence of focal attention. Vision Research, 46, 2336–2343.

Rees, G. (2007). Neural correlates of the contents of visual awareness in humans. Philosophical Transactions of the Royal Society B: Biological Sciences, 362, 877–886.

Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. Science, 278, 1616–1619.

Rodman, H. R. & Albright, T. D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). Experimental Brain Research, 75, 53–64.

Ross, J. & Ma-Wyatt, A. (2004). Saccades actively maintain perceptual continuity. Nature Neuroscience, 7, 65–69.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. Trends in Neurosciences, 24, 113–121.

Rousselet, G. A., Macé, M. J., Thorpe, S. J., & Fabre-Thorpe, M. (2007). Limits of Event-related Potential Differences in Tracking Object Processing Speed. Journal of Cognitive Neuroscience, 19, 1241–1258.

Schiller, P. H. & Chorover, S. L. (1966). Metacontrast: Its Relation to Evoked Potentials. Science, 153, 1398–1400.

Schlkopf, B. & Smola, A. J. (2002). Learning with kernels: support vector machines, regularization, optimization, and beyond (adaptive computation and machine learning). (Cambridge, Massachusetts London, England: MIT Press), 1st edn.

Schmid, M. C., Mrowka, S. W., Turchi, J., Saunders, R. C., Wilke, M., Peters, A. J., Ye, F. Q., & Leopold, D. A. (2010). Blindsight depends on the lateral geniculate nucleus. Nature, 466, 373–377.

Schmid, M. C., Panagiotaropoulos, T., Augath, M. A., Logothetis, N. K., & Smirnakis, S. M. (2009). Visually Driven Activation in Macaque Areas V2 and V3 without Input from the Primary Visual Cortex. PLoS ONE, 4, e5527+.

Schmidt, F. & Schmidt, T. (2010). Feature-based attention to unconscious shapes and colors. Attention, Perception & Psychophysics, 72, 1480–1494.

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.

Seth, A. K. (2007). Models of Consciousness. Scholarpedia, 2, 1328+.

Shapiro, K., Raymond, J., & Arnell, K. (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, 94, 3408–3413.

Shin, K., Stolte, M., & Chong, S. C. (2009). The effect of spatial attention on invisible stimuli. Attention, Perception, & Psychophysics, 71, 1507–1513.

Simanova, I., van Gerven, M., Oostenveld, R., & Hagoort, P. (2010). Identifying object categories from event-related EEG: toward decoding of conceptual representations. PLoS ONE, 5, e14465.

Simons, D. J. & Chabris, C. F. (1999). Gorillas in our midst: sustained inattentional blindness for dynamic events. Perception, 28, 1059–1074.

Sincich, L. C., Park, K. F., Wohlgemuth, M. J., & Horton, J. C. (2004). Bypassing V1: a direct geniculate input to area MT. Nature Neuroscience, 7, 1123–1128.

Smith, A. T. & Hammond, P. (1985). The pattern specificity of velocity aftereffects. Experimental Brain Research, 60, 71–78.

Sperling, G. (1960). The information available in brief visual presentations. Psychological Monographs, 74, 1–29.

Srinivasan, N. (2008). Interdependence of attention and consciousness. Progress in Brain Research, 168, 65–75.

Stein, T., Senju, A., Peelen, M. V., & Sterzer, P. (2011). Eye contact facilitates awareness of faces during interocular suppression. Cognition, 119, 307–311.

Stein, T. & Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: Evidence from continuous flash suppression. Journal of Vision, 11.

Steiner, V., Blake, R., & Rose, D. (1994). Interocular transfer of expansion, rotation, and translation motion aftereffects. Perception, 23, 1197–1202.

Sterzer, P., Haynes, J.-D. D., & Rees, G. (2008). Fine-scale activity patterns in high-level visual areas encode the category of invisible objects. Journal of vision, 8, 1–12.

Sterzer, P., Jalkanen, L., & Rees, G. (2009). Electromagnetic responses to invisible face stimuli during binocular suppression. Neuroimage, 46, 803–808.

Suzuki, S. & Grabowecky, M. (2003). Attention during adaptation weakens negative after-images. Journal of Experimental Psychology. Human Perception and Performance, 29, 793–807.

Tanaka, K., Fukada, Y., & Saito, H. A. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. Journal of Neurophysiology, 62, 642–656.

Tatler, B. W. (2001). Characterising the visual buffer: real-world evidence for overwriting early in each fixation. Perception, 30, 993–1006.

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

Thorpe, S. J. & Fabre-Thorpe, M. (2001). Seeking Categories in the Brain. Science, 291, 260–263.

Tong, F. (2001). Competing Theories of Binocular Rivalry: A Possible Resolution. Brain and Mind, 2, 55–83.

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

Tong, F. & Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. Nature, 411, 195–199.

Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. Trends in Cognitive Sciences, 10, 502–511.

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. (2008). Consciousness as Integrated Information: a Provisional Manifesto. The Biological Bulletin, 215, 216–242.

Tononi, G. & Edelman, G. M. (1998). Consciousness and Complexity. Science, 282, 1846–1851.

Treue, S. & Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. Nature, 399, 575–579.

Triesch, J., Ballard, D. H., Hayhoe, M. M., & Sullivan, B. T. (2003). What you see is what you need. Journal of Vision, 3, 86–94.

Tsuchiya, N. & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. Nature Neuroscience, 8, 1096–1101.

Tsuchiya, N., Koch, C., Gilroy, L. A., & Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. Journal of Vision, 6, 1068–1078.

van Boxtel, J. J., Tsuchiya, N., & Koch, C. (2010a). Opposing effects of attention and consciousness on afterimages. Proceedings of the National Academy of Sciences of the United States of America, 107, 8883–8888.

van Boxtel, J. J. A., Knapen, T., Erkelens, C. J., & van Ee, R. (2008). Removal of monocular interactions equates rivalry behavior for monocular, binocular, and stimulus rivalries. Journal of Vision, 8, 13.

van Boxtel, J. J. A., Tsuchiya, N., & Koch, C. (2010b). Consciousness and Attention: On sufficiency and necessity. Frontiers in Psychology, 1, 1–13.

Van Der Zwan, R., Wenderoth, P., & Alais, D. (1993). Reduction of a pattern-induced motion aftereffect by binocular rivalry suggests the involvement of extrastriate mechanisms. Visual Neuroscience, 10, 703–709.

van Ee, R., van Dam, L. C., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. Vision Research, 45, 41–55.

Vandenbussche, E., Segers, G., & Reynvoet, B. (2008). Conscious and unconscious proportion effects in masked priming. Consciousness and Cognition, 17, 1345–1358.

VanRullen, R. & Thorpe, S. J. (2001a). Is it a bird? Is it a plane? Ultra-rapid visual categorisation of natural and artifactual objects. Perception, 30, 655–668.

VanRullen, R. & Thorpe, S. J. (2001b). The time course of visual processing: from early perception to decision-making. Journal of Cognitive Neuroscience, 13, 454–461.

Vuilleumier, P., Armony, J. L., Clarke, K., Husain, M., Driver, J., & Dolan, R. J. (2002). Neural response to emotional faces with and without awareness: event-related fMRI in a parietal patient with visual extinction and spatial neglect. Neuropsychologia, 40, 2156–2166.

Watson, T. L. & Krekelberg, B. (2009). The relationship between saccadic suppression and perceptual stability. Current Biology, 19, 1040–1043.

Weiskrantz, L. (1997). Consciousness lost and found: a neuropsychological exploration. (Oxford University Press).

Westwood, D. A. & Goodale, M. A. (2011). Converging evidence for diverging pathways: neuropsychology and psychophysics tell the same story. Vision Research, 51, 804–811.

Wickens, T. D. (2001). Elementary Signal Detection Theory. (Oxford University Press, USA), 1st edn.

Wiesenfelder, H. & Blake, R. (1990). The neural site of binocular rivalry relative to the analysis of motion in the human visual system. The Journal of Neuroscience, 10, 3880–3888.

Wiesenfelder, H. & Blake, R. (1992). Binocular rivalry suppression disrupts recovery from motion adaptation. Visual Neuroscience, 9, 143–148.

Wilke, M., Mueller, K.-M. M., & Leopold, D. A. (2009). Neural activity in the visual thalamus reflects perceptual suppression. Proceedings of the National Academy of Sciences of the United States of America, 106, 9465–9470.

Wunderlich, K., Schneider, K. A., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. Nature Neuroscience, 8, 1595–1602.

Yarrow, K., Haggard, P., Heal, R., Brown, P., & Rothwell, J. C. (2001). Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. Nature, 414, 302–305.

Zimba, L. D. & Blake, R. (1983). Binocular rivalry and semantic processing: Out of sight, out of mind. Journal of Experimental Psychology: Human Perception and Performance, 9, 807–815.