Functional Hierarchy and Temporal Dynamics of Conscious and Unconscious Processes in Human Vision

A Dissertation

Presented to

the Faculty of the Department of Electrical and Computer Engineering

University of Houston

In Partial Fulfillment of

the Requirements for the Degree of

Doctor of Philosophy

in

Electrical and Computer Engineering

by

Alpay Koç

December 2005

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To Münise and Abdülbaki Koç

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ABSTRACT

Despite the fact that the human visual system is one the most extensively studied sensory systems, very little is known about its functional architecture and temporal dynamics. The broad, long term goal of our research is to understand the mechanisms and dynamics underlying conscious and unconscious registration of a visual stimulus. In order to address this question, we have used three paradigms where the degree of conscious registration of a stimulus can be controlled systematically: 1) Binocular rivalry, 2) Visual masking, and 3) Visual attention. In each paradigm, the strategy was either to suppress or enhance the conscious registration of a stimulus by a secondary stimulus and to probe the functional hierarchy or the dynamics of this interaction by varying stimulus parameters. Our results identify a functional hierarchy of unconscious processes in the brain starting with disinhibition in metacontrast followed by binocular rivalry, which in turn is followed by metacontrast masking. Moreover, our electroencephalography (EEG) results suggest that the parietal areas constitute one of the neural loci where metacontrast interactions take place during a period of 200-400 ms after stimulus onset. Under the framework of a model of masking (RECOD; Ogmen et al., 2003), our results suggest that the transient activity of a stimulus is suppressed mainly by inter-channel inhibition. Our results also suggest that a peripheral cue, which facilitates conscious registration of a stimulus through the deployment of attention mechanisms, also generates feature-based priming. Taken together, these results reveal a functional hierarchy of conscious and unconscious processing in the visual system and characterize some of the dynamics taking place within this hierarchy.

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Introduction

1.1. Specific Aims

Despite the fact that the human visual system is one the most extensively studied sensory systems, very little is known about its functional architecture and temporal dynamics. One of the aspects that we know so far is that conscious visual perception happens only after the visual information has been processed automatically and unconsciously in several stages. The broad, long term goal of the proposed research is to understand the mechanisms and dynamics underlying the conscious and unconscious registration of a visual stimulus. In order to address this question, we used three paradigms where the degree of conscious registration of a stimulus can be controlled systematically: 1) Binocular rivalry, 2) Visual masking and 3) Visual attention. In each paradigm, the strategy was either to suppress or enhance the conscious registration of a stimulus by a secondary stimulus and to probe the functional hierarchy or the dynamics of this interaction by varying stimulus parameters.

The specific aims of this dissertation are: 1) To further locate the substrates and stages of visual masking by using the binocular rivalry technique, 2) To investigate the electrophysiological correlates of visibility in visual masking, 3) To understand the mechanisms of target recovery under the hypothesis of a modified dual channel (RECOD) model of visual masking (Ogmen, 1993; Ogmen et al., 2003), 4) To investigate the mechanisms whereby transient focal attention is triggered by a visual peripheral cue.

1.2. Specific Research Questions

The specific research questions that will be addressed in this dissertation are as follows:

1) Is there any or how strong is visual masking before binocular rivalry?

Visual masking refers to the reduction in visibility of a stimulus, called the target, by another visual stimulus, called the mask (Breitmeyer, 1984). Binocular rivalry refers to the rivalry for conscious registration between two dissimilar stimuli separately presented to two eyes (dichoptic view). Several unconscious processing stages may contribute to the conscious registration of a visual stimulus (Kanwisher, 2001). Masking possibly occurs by interruption of processing of a stimulus in some of these stages. Nevertheless, a secondary mask can inhibit the masking effect of a mask (disinhibition), thus cause a recovery in the visibility of the masked target. Disinhibition studies show that masking of the target is not affected even when the awareness of the mask is reduced and moreover target recovery occurs while preserving awareness of the mask (Breitmeyer et al., 1981; Ogmen et al., 2004). When the target and the mask are presented to separate eyes, metacontrast masking is observed (e.g., Kolers, 1960; Schiller, 1965; Schiller & Smith, 1968). This finding suggests that the mechanisms of masking occur after binocular convergence. However, the functional hierarchy of metacontrast with respect to binocular rivalry is not known. We study this question through the following hypothesis. *<u>Hypothesis 1</u>: The stages of processing before binocular rivalry are not responsible for metacontrast masking.* In order to test this hypothesis, we use the binocular rivalry technique to suppress the visibility of the mask during metacontrast. Our hypothesis will be supported if we see substantial recovery from dichoptic masking when the mask is suppressed. It has been shown that binocular rivalry does not occur immediately after binocular convergence but becomes prominent while ascending to higher areas (Blake, 2001). Different neuronal correlate studies of masking show that LGN, V1, V4, IT cells are subject to masking (Kondo & Komatsu, 2000; Kovacs et al., 1995; Lamme et al., 2002; Macknik & Livingstone, 1998; Macknik & Martinez-Conde, 2004; Macknik et al, 2000; Rolls et al., 1999). Results of this study will also be informative in locating the substrates of masking. Since the metacontrast mechanism itself occurs at unconscious levels of processing, our results can also provide a means of establishing a functional hierarchy of unconscious visual processing.

2) What are neural correlates for the conscious registration of a visual stimulus?

We investigate neural correlates for the conscious registration of a visual stimulus by combining masking and electroencephalography (EEG) methods. We use the mask stimulus to suppress the visibility (hence conscious registration) of a target stimulus and measure correlated changes in the EEG signals. While earlier studies showed a correlation between changes in visual evoked potentials (VEPs) and masking functions (Andreassi et al., 1976; Vaughan & Silverstein, 1968), further studies were needed to understand better the relationship between the temporal dynamics at the perceptual and EEG levels. It has been shown that the VEP in response to a paired target-mask stimulus with a SOA is not equal to linear summation of the VEPs in response to the target-only stimulus and the mask-only stimulus shifted with the same SOA (Schiller & Chorover, 1966). Therefore, the approach that the previous studies used (Andreassi et al., 1976; Vaughan & Silverstein, 1968), which is the comparison of VEPs in response to the target-only stimulus with the VEPs in response to a paired target-mask stimulus, may not directly reflect correlates of masking. A better experimental design is needed by which we can clearly distinguish the masking effect on VEPs. *Hypothesis 2: The absolute amplitude differences in late VEPs [200-400ms] related to task related information in parietal areas reflect brain activities correlated with masking.* To test this hypothesis, a pair of disk and an annulus stimulus will be presented to the left and right of a fixation point. On one side (left or right, selected randomly in each trial), the disk will contain a small gap. The gap will be subject to masking when it is located close to the contour of the mask. The visibility of the gap remains unimpaired when the gap is presented at the center of the disk. The rationale behind this approach is that the masking strength decreases rapidly as the separation between the contours of the target and the mask increases (Breitmeyer, 1984). Observers will be asked to indicate which if the two disks, the one on the left or the on right, contains the gap. Our hypothesis will be supported if the differences between the contralateral and the ipsilateral VEPs with respect to the visual field that the gap will be presented correlate with the visibility functions of the target containing the gap.

3) Can the mechanisms of the dual channel (RECOD) model explain increase of reaction times in response to a stimulus during paracontrast masking?

The visibility of a stimulus which is reduced by a primary mask (masking) can be recovered by a secondary masking stimulus (target recovery or disinhibition). Previous studies showed that the timing of the secondary mask for target recovery depends on the type of masking produced by the primary mask (e.g., Robinson, 1966; Breitmeyer et al., 1981). The dual-channel model of masking (Breitmeyer & Ganz, 1976) proposes that interactions between transient and sustained responses generated by a paired stimulus cause the reduction in visibility mainly by suppressing the target's sustained response (see Breitmeyer, 1984 and Breitmeyer & Ogmen, 2000 for reviews). Recently, it has been shown that this model can account for target recovery in *metacontrast*, where a non-overlapping mask follows the target (Ogmen et al., 2004). We investigated further the mechanisms leading to target recovery in metacontrast using the following framework. Assumption 1*: The visibility of a stimulus is a function of its sustained activity*. Target recovery (disinhibition) studies show that in metacontrast, there is a double dissociation between the masking effectiveness and the visibility of the mask, which are associated with transient and sustained responses of the mask, respectively (Breitmeyer et al., 1981; Ogmen et al., 2004). *Assumption 2: The masking effectiveness of a stimulus in metacontrast is a function of its transient activity*. According to this model, the transient response generated by a stimulus is associated with its rapid localization and the suppression of this response causes reaction-times (RTs) in response to the onset of the stimulus to increase during forward masking (paracontrast). Simulations of the RECOD model account for the psychophysical data and support this approach (Ogmen et al., 2003). However we do not know which mechanisms are involved in the inhibition of the transient response. *Alternatives: Suppression of the transient response of the target can be caused by (i) the sustained response of the mask, or (ii) the transient response of the mask, or (iii) a combination of (i) and (ii).* We will evaluate these alternatives and assumptions by carrying out RT experiments using the disinhibition paradigm. *Corollary 1: If assumption 1 and alternative (i) are true, then we should see a correlation between RT to the target and the visibility of the mask. Corollary 2: If assumption 2 and alternative (ii) are true, then we should see a correlation between RT to the target and the metacontrast masking effect of the mask.* By comparison of RTs obtained from the target-mask pair and disinhibition conditions, we will investigate to what extent these corollaries hold.

3) What are the dynamics of visual attention triggered by a peripheral cue?

Visual attention is a very distinguished characteristic of the visual system such that depending on the present needs of the organism, the brain enhances the visual information by selecting it over time and space and filtering the unwanted information. Visual attention is very closely related to visual awareness. For example, inattentional and change blindness paradigms suggest that unattended stimuli are not consciously identified (Chun & Wolfe, 2001). The mechanisms of attention affecting the processing of visual information which leads to conscious registration can be better understood by investigating the temporal dynamics of attention. Time course of attention can be measured by varying the duration between the cue and the following search item (cue lead time, CLT). A symbolic central cue, which triggers voluntary control of attention, generates facilitation of accuracy monotonically (e.g., Cheal & Lyon, 1989, 1991; Müller & Rabbitt, 1989). However, previous studies employing an abrupt peripheral cue to draw involuntary attention showed that as CLT increases, performance improves and reaches a peak value at a CLT of approximately 100 ms. For long CLTs, performance declines to a lower plateau value (Müller & Findlay, 1988; Nakayama & Mackeben, 1989). These findings led to the suggestion that the dynamics of extrinsic attention consists of a rapid transient and a slower sustained component. However, the peripheral cue stimuli used in these studies can potentially act as a paracontrast mask reducing the visibility of the target. This is consistent with the paracontrast suppression observed in Ogmen et al. (2003). <u>*Hypothesis 3*</u>*: The dynamics of extrinsic involuntary attention is monotonic and that the decline in performance at long CLTs is due to paracontrast masking.* In order to test this hypothesis, the temporal course of involuntary attention is measured by varying the masking strength of the cue as an independent factor. Our hypothesis will be supported if we obtain a more monotonic function as the masking strength of the cue decreases. On the basis that masking is stronger at larger eccentricities, our hypothesis can also explain why the non-surrounding peripheral cue used by Cheal and Lyon (1991) generated "peak-plateau functions" at relatively large eccentricities. Furthermore, our preliminary studies suggest that figural interactions between the cue and the target also affect temporal course of attention. <u>*Hypothesis 4:*</u> *Feature-based priming is also evoked when the attention is drawn by an abrupt peripheral visual cue.* This hypothesis will be tested by manipulating systematically figural relationships between the cue and the target. Our hypothesis will be supported if we observe more attentional enhancement when the target and the cue have similar figural properties.

1.3. Background and Significance

One of the questions which have not been fully answered yet is what consciousness is. Although this problem has been discussed mainly by philosophers and psychologists, recently scientific advances in biological systems led people to think of the problem from a different perspective. Moreover, there have been studies to integrate the solutions offered by different schools (Noë & Thompson, 2004; Wilber, 1997). By introspection or from the first-person view of the mind, consciousness manifests itself in different aspects such as qualia (being aware of redness of red), mental unity (body is controlled by one entity) and free-will. However the third-person view of the mind and science see consciousness occurring in a localized physical organ, brain, by the electrochemical activities of the billions of cells in it. This discrepancy seen from different views has been termed as the mind-body problem by philosophers (Smith, 2001).

Leaving the discussions of consciousness from other schools aside, science approaches the problem by the method of reduction, i.e. trying to understand each neuron’s functionality, and by the method of emergence, i.e. how these neurons act as a whole. As a framework for consciousness, it has been quested that as a scientist it is nonsense to discuss consciousness until all its neural correlates are found (Crick & Koch, 1995, 2003).

There are many tools to investigate the neural correlates of perceptual awareness. The first one might be to study bistable stimuli, such as Rubin’s famous face/vase (Rubin, 1915) or a Necker cube (Necker, 1832). These stimuli ensure that the sensorial input is not changing, yet different perceptual awareness of the same stimulus occurs in time. Similarly as a second tool, bistability also occurs during the binocular rivalry of the two different stimuli presented to each eye (Wheatstone, 1838). Another approach can be to use the masking paradigm to impair the visibility of a stimulus. Other helpful studies might be to study attention, sub-threshold stimuli, motion perception, feature binding problem, imagery, patients having specific brain damages, and micro-stimulation of the neurons without presenting any stimuli.

Results of these studies suggest that correlations between neural activities and perceptual awareness occur in different areas of the brain (Kanwisher, 2001). Although this does not necessarily mean that a single mechanism might not be the real cause of consciousness, it can only be understood by studying more about the sufficiency and necessity of those correlations in generating a conscious experience. It has also been suggested that the awareness for vision is a series of static snapshots with motion painted on them generated by the coalition and competition of neurons in different perceptual epochs (e.g., Breitmeyer & Ogmen, in press; Crick & Koch, 2003; Grossberg & Mingolla, 1985; Ogmen, 1993; Ogmen et al., in press). Comparison of a conscious perceptual representation with an unconsciousness one also gave rise to different hypotheses (Kanwisher, 2001 for a review). The activation strength hypothesis merely states that consciousness gets stronger as neural representations get more active. However, the informational access hypothesis states that not only strong neural representations but also access to that information from other parts of the brain is needed for awareness of perceptual information. In this dissertation, we focus more on attention, binocular rivalry and visual masking paradigms for studying perceptual awareness. By using these three paradigms, visibility of a stimulus can be reduced or enhanced.

As one can see in our daily life, our visual environment contains a huge amount of visual information. Our visual system is faced with the challenge of processing this information in real-time with limited processing resources. Attention and similar mechanisms are used to selectively allocate processing resources to relevant parts of visual inputs. As a result only a small fraction of the incoming information reaches our awareness. The rest of the information is either filtered out at early levels of processing or processed unconsciously. Many engineering systems face a similar problem, namely a mismatch between the amount of input or data and the extent of processing resources. Therefore, learning how the human visual system allocates its processing resources to inputs and thereby selects which information is processed at unconscious or conscious levels can help us design artificial systems with similar capabilities.

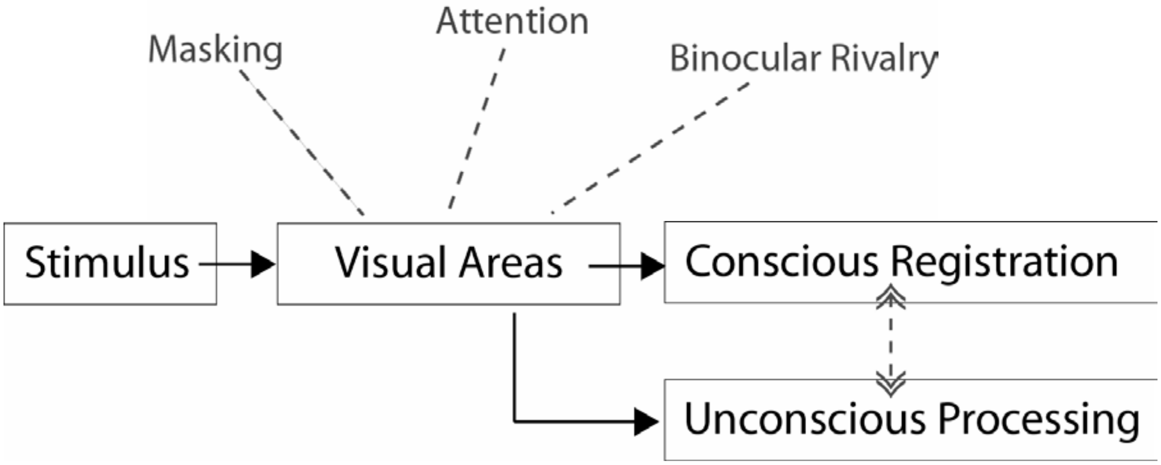


Fig. 1.1. The visibility of a stimulus can be reduced in the visual areas of the brain through interaction of another stimulus' information by using masking, attention and binocular rivalry paradigms.

Contrast is one of the factors that determine if a stimulus reaches conscious awareness. For example if the stimulus is very low contrast lower than a threshold value, it may be reported as invisible meaning that it does not reach to conscious registration. When we increase the contrast of a stimulus, its level or degree of conscious registration increases and it becomes more visible. We know that a visual stimulus is first processed by neurons in the eye and then in the visual areas and finally it is registered unconsciously or consciously. We can study the underlying mechanisms leading to conscious registration by reducing or enhancing the visibility. We can do that by increasing the light energy at the input level. Or more interestingly, the visibility can be reduced even by keeping the stimulus energy constant at the input level. For example in visual masking paradigm, when a stimulus is followed by another stimulus in time, its visibility is reduced. Therefore, when we understand the mechanisms of visual masking, we can also gain insight to the underlying mechanisms of conscious registration. Similarly, by using binocular rivalry and attention paradigms we can reduce or enhance the visibility of a stimulus by interacting with the stimulus information in the visual areas (Fig. 1.1).

1.3.1. Visual Masking

Visual masking refers to the reduction of the visibility of a briefly presented stimulus, called the target, in presence of a second stimulus, called the mask (Bachmann, 1994; Breitmeyer, 1984; Breitmeyer & Ogmen, 2000 for reviews). If the mask stimulus follows the target stimulus it is called backward masking, and if it is followed by the target it is called forward masking. There are two types of visual masking: 1) Masking by light and 2) Masking by pattern (Breitmeyer, 1984). Masking by light can be further splitted into two parts: masking light by light or masking pattern by light. In both cases, a second mask flash reduces the visibility of the test flash. Pattern masking can have several stimuli variants, three of which are: 1) Paracontrast and metacontrast, 2) Pattern masking by noise, 3) Pattern masking by structure (Breitmeyer, 1984). In the first variant, mask and target stimuli are spatially non-overlapping and usually the mask is an annulus and the target is chosen as a disk. Temporally metacontrast and paracontrast correspond to backward and forward masking, respectively. Usually, the second and the third stimuli variants are used for backward masking and as a methodological tool where the researchers are not interested in masking per se (e.g., Cheal & Lyon, 1991; Dehaene et al., 1998; Nakayama & Mackeben, 1989). The noise mask consists of random elements having different contrasts. In pattern masking by structure, the mask has similar features as the target and it covers the whole field like the noise mask. We investigate the mechanisms that produce paracontrast and metacontrast in this dissertation.

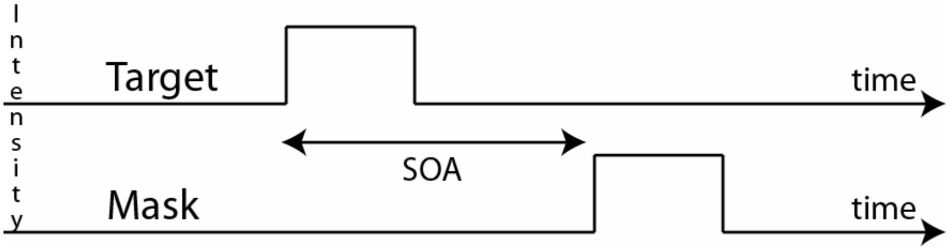


Fig. 1.2. This figure illustrates backward masking where SOA is positive. The horizontal and vertical axes are time and stimulus intensities, respectively.

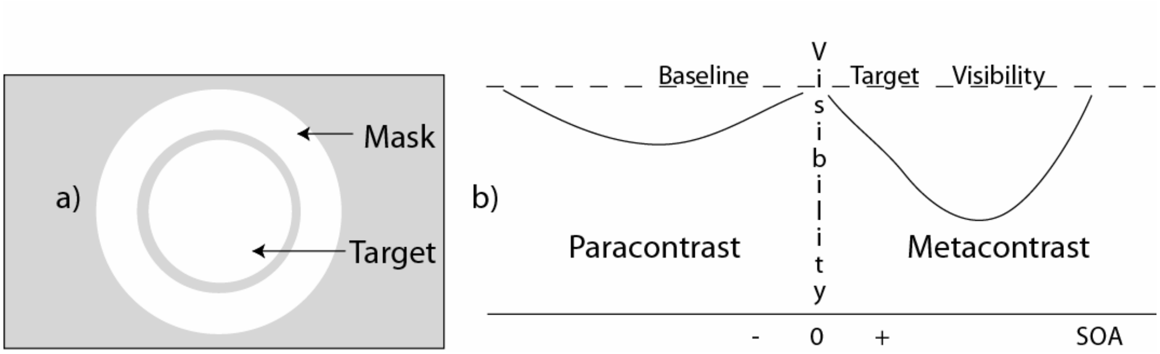


Fig. 1.3. Typical stimuli (a) and the corresponding U-shaped masking functions (b) for paracontrast and metacontrast. Masking functions are obtained by measuring the perceived visibility of the target while presenting the mask stimulus at different SOAs. For comparison purposes, perceived visibility of the target is also measured in absence of the mask which is indicated as the baseline target visibility.

The delay between the onsets of the target and the mask is called stimulus onset asynchrony (SOA) (Fig. 1.2). Usually, the visibility of the target is quantified and it is plotted against various SOA values (Fig. 1.3). This is called masking function. There are three types of masking functions: 1) Type-A, 2) Type-B (U-shaped), 3) Oscillatory (Breitmeyer, 1984; Prushothaman et al., 2000) (Fig. 1.4). Visibility of the target stimulus reduces monotonically while SOA gets closer to 0 ms in a type-A masking function. Type-B functions have an optimum SOA other than zero where the masking magnitude is the highest. Hence they are also called U-shaped functions. Masking functions showing oscillatory behavior are called oscillatory masking functions. Typically, type-A functions are generated when the mask stimulus has higher energy than the target or the mask is noise (Breitmeyer, 1984). When their energies are close, they produce type-B masking function. Oscillatory masking functions have not been studied widely because it necessitates the use of spatio-temporally localized very bright stimuli and a dense sampling of SOAs (Purushothaman et al., 2000). Mostly, the backward masking is preferred in studies because it produces much clear U-shaped masking function than forward masking.

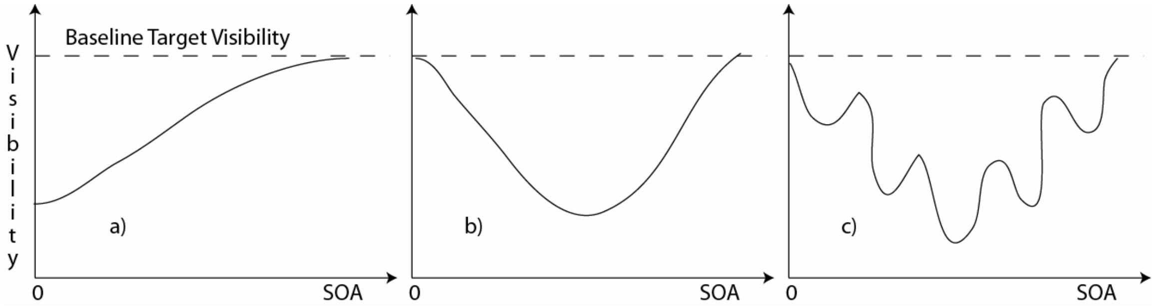


Fig. 1.4. Masking functions: a) Type-A, b) Type-B, c) Oscillatory.

The type of masking functions obtained in masking mostly depends on the following variables: 1) Task parameters and criterion content, 2) Stimulus intensity and contrast, 3) Spatial variables such as stimulus orientation, size, separation and location, 4) Viewing conditions such as monoptic and dichoptic, 5) Wavelength parameters such as chromatic and rod-cone interactions (Breitmeyer, 1984). For example, if the task of the observer changes from the judgment of the perceived brightness of the target stimulus to its simple detection or reaction time (RT) to its onset, we obtain a different masking function (e.g., Fehrer & Raab, 1962; Schiller & Smith, 1966). As the contrast of the mask stimulus increases while keeping the target contrast constant, the masking function changes from type-B to type-A function. Spatial variables also affect the strength of masking. For example the more the stimuli are in periphery or the more their contours are close to each other, the more masking we observe. There are also some studies showing that the viewing condition and the color of the stimuli generate different masking functions (Breitmeyer, 1984).

1.3.2. Theoretical Models of Visual Masking

Theoretical models of masking focus on mainly accounting for the U-shaped masking function obtained from psychophysical experiments. But only a few of them are biologically inspired. Even a simple differential equation having a few parameters can produce a U-shaped function (Francis, 2000, 2003a). Other computational models that can be simulated in a short time analyzed in Francis (2000, 2003b) include the ones that were proposed in Weisstein (1972), Bridgeman, (1978), Anbar and Anbar (1982), Francis (2000) and Di Lollo (2000). Francis' analysis (Francis, 1997) of the elaborated boundary contour system model (BCS) proposed by Grossberg and Mingolla (1985) for accounting other perceptual data showed that this model also can account for the masking data. Among all the aforementioned models, the dual channel sustained-transient model, which was first proposed in Breitmeyer and Ganz (1976) and further developed and named as retino-cortical dynamics (RECOD) model (Ogmen, 1993), is the only one that can explain the double-dissociation phenomenon in masking. Because this double-dissociation is critical to our studies, we use the RECOD model as a theoretical framework to study the disinhibition results in this dissertation. Since the RECOD model is a biologically inspired model, we will provide a brief review of the neurophysiology of the visual system.

1.3.3. Neurophysiology of the Visual System

There are three types of ganglion cells in the retina. These are called magnocellular, parvocellular and konicellular (Merigan, 1993). The first two types are about 90% of all the ganglion cells. The responses of the magnocellular cells are transient and fast but parvocellular cells produce a longer duration and slower response (Kaplan & Benardete, 2001). Magnocellular cells are more sensitive to contrast but their responses saturate at around 15% contrast and responses of parvocellular cells show linear behavior especially at lower contrasts (Kaplan & Benardete, 2001; Purpura et al., 1998). These two types of cells project their outputs distinctively first to the lateral geniculate nucleus (LGN), then to the primary visual cortex, V1 (Fig. 1.5). About ten percent of the signals from the retina go to superior colliculus (SC), which is involved in the control of eye movements (Merigan, 1993). The LGN is a region in the thalamus in the deep brain and has many more feedback connections than feedforward connections (Goldstein, 1999). Starting with the cortical area V1, responses of magnocellular and parvocellular cells interact (Merigan, 1993).

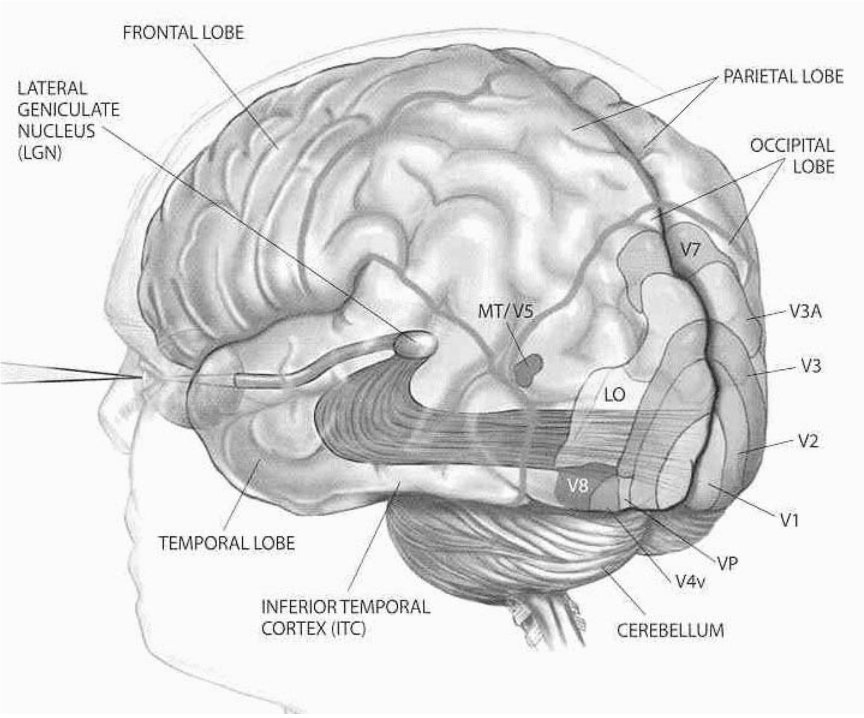


Fig. 1.5. Human visual pathway. Major brain areas processing visual information of a stimulus starting from its presentation up to its perception and recognition are shown. Adapted from Logothetis (1999).

According to their connections, it has been suggested that there are two different cortical pathways (1-dorsal or parietal and 2- ventral or temporal) (Merigan, 1993) (Fig. 1.6). The dorsal pathway mostly receives its inputs from the fast signals produced by the magnocellular cells and the ventral pathway mostly from signals produced by slow parvocellular cells. According to many studies, there is a double dissociation between the functions of these two pathways (Milner & Goodale, 1995). The dorsal pathway is called "where" or "action" pathway which determines the location of the visual input and how it can be reached. The ventral pathway is called "what" or "perception" pathway, which is responsible for the perception of visual objects (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). The knowledge of the actual connections in the brain is very limited. There are extensive feedforward and feedback connections between different layers and areas of the brain (van Essen, 1992). The neurons in V1 act like filters, which are sensitive to specific directions and spatial frequencies (Lamme & Roelfsema, 2000). As signals go to the higher areas (V2, V3, V4, medial temporal cortex-MT, inferotemporal cortex-IT), the size of the receptive fields of the neurons increases and the neurons become activated by more complex stimuli (Lamme & Roelfsema, 2000).

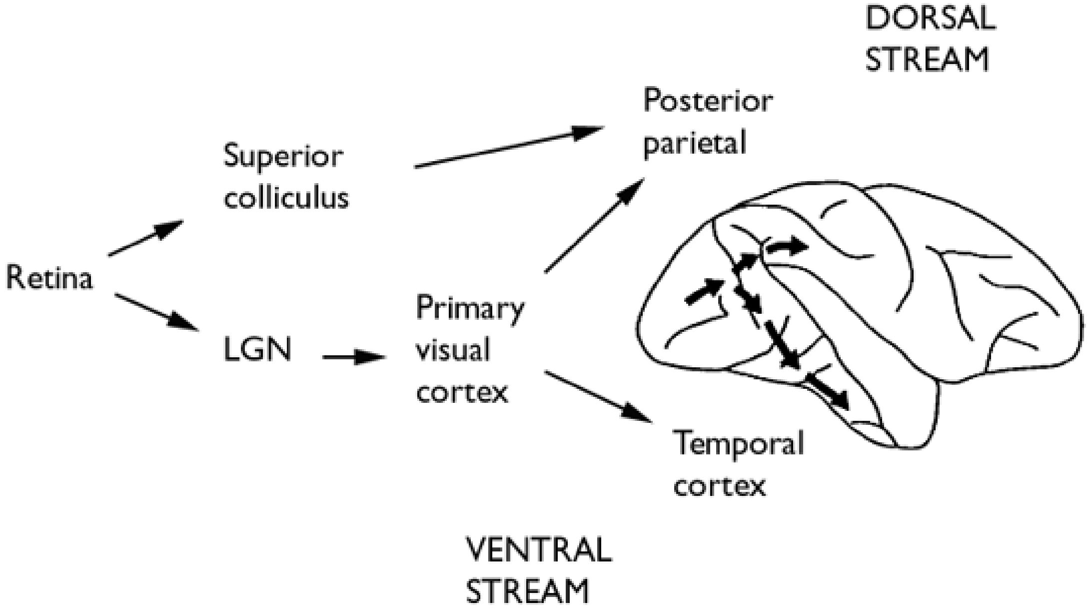


Fig. 1.6. Dorsal and ventral pathways. From Gazzaniga (2000).

1.3.4. REtino-COrtical Dynamics (RECOD) Model

Retinal neural processing is included in the RECOD model (Ogmen, 1993; Ogmen et al., 2003). Visual light input is copied and processed in parallel by two different neuron types (transient and sustained), which are analogous to magnocellular and parvocellular cells (Fig. 1.7). Accordingly, the model uses the physiological properties of these cells such as their receptive-field characteristics and gain controls. These neurons produce transient and sustained responses to a visual stimulus. The transient response is a short latency brief burst activity. The activity of the sustained response exhibits an initial overshoot but then decays in time. The latency and duration of the sustained response is higher than that of the transient response. The post-retinal part of the model consists of two channels that receive their primary inputs from parvocellular (sustained, S, channel) and magnocellular pathways (transient, T, channel). These channels are analogous to the dorsal and the ventral pathways, respectively. There are reciprocal inhibitions between the post-retinal T and S channels and reentrant connections in the S channel. In the post-retinal S channel, the first transient response resets the ongoing activity (reset phase), and then the overshoot part of the sustained response triggers the activities (feedforward dominant phase). While the sustained response loses its strength, feedback connections become dominant (feedback dominant phase). Visibility and RT in detection tasks in the model are correlated with the activities of the S channel and T channel, respectively. The RECOD model made a novel prediction that the reset phase initiates the readiness of the following perception. There is evidence from physiological studies for the dynamics of the model such as different temporal activations of the brain by magnocellular and parvocellular cells (Baseler &

Sutter, 1997), feedforward and feedback dominant phases in V1 neurons (Lamme & Roelfsema, 2000; Lamme et al, 2002), correlation between the late components and perception or awareness in the higher areas of the temporal pathway (Milner & Goodale, 1995).

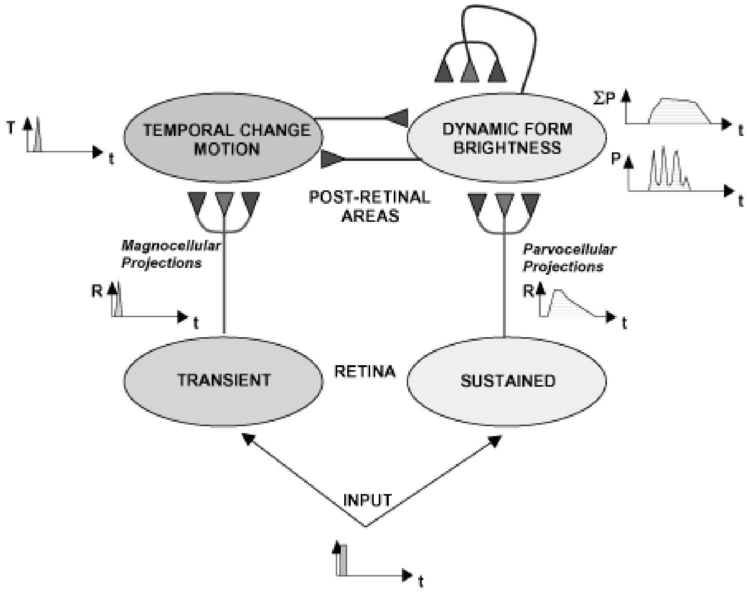


Fig. 1.7. The RECOD model. Adapted from Ogmen et al. (2003).

In its original form, the dual-channel model proposes that the sustained response of the target is inhibited and as a result the visibility of the target is modified (Breitmeyer, 1984; Breitmeyer & Ganz, 1976) (Fig. 1.8). There are two main inhibitory mechanisms to account for the shape of masking functions: 1) inter-channel (transient-on-sustained) and 2) intra-channel (sustained-on-sustained). In metacontrast, both mechanisms are effective; however the dominant one is transient-on-sustained inhibition. In paracontrast, only intra channel sustained-on-sustained inhibition is effective. Therefore, the masking magnitude is higher in metacontrast than in paracontrast. In type-A forward and backward masking, within-channel (sustained-with-sustained) integration causes the mask to override the target visibility. Integration is dominant especially when the mask overlaps with the target. As the energy of a non-overlapping mask increases with respect to the target, sustained-on-sustained inhibition causes the optimum masking SOA to shift to zero. At SOA=0, sustained responses of the target and the non-overlapping mask compete for common spatial-frequency analyzers, and thus type-A masking occurs. These mechanisms explaining the U-shapes of masking functions are realized in feedforward manner in the RECOD model.

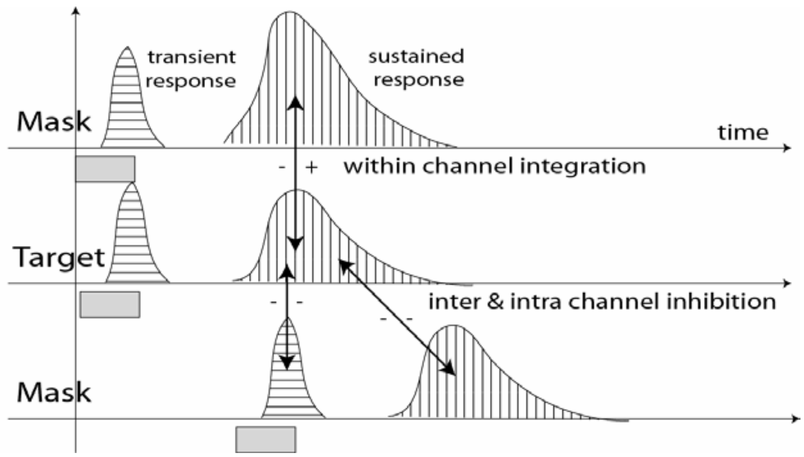


Fig. 1.8. Interactions between the responses of the target and the mask stimuli according to the dual channel model.

1.3.4.1. RECOD Model Accounts for Paracontrast and Metacontrast

Ogmen et al. (2003) investigated reaction times in response to the target stimulus along with its visibility during paracontrast and metacontrast. RTs were measured by presenting the target on one side of the observer while showing the mask on both sides. Since observers were asked to respond as fast and as accurately as possible, RTs reflect the localization performance of the observer which relies more on the transient response of the stimulus. They found that the masking magnitude in metacontrast was higher than that of in paracontrast which confirms the previous findings (Fig. 1.9) (e.g., Breitmeyer, 1984; Cavonius & Reeves, 1983). Similar to the findings of Fehrer and Raab (1962), and Schiller and Smith (1966), they found that RTs during metacontrast were about constant which means that there is no masking effect on RTs. However RTs gradually increased with SOA approaching 0 ms during paracontrast. They hypothesized that there is also an additive interference effect in RTs other than masking effect because of rapid presentation of stimuli (Meyer et al., 1988; Sanders, 1998; Wellford, 1980). Hence, they also measured RTs by using a “pseudo-mask” which would cause minimum masking. The difference between RTs (ΔRTs) obtained by using a real-mask and a pseudo-mask would give then an estimate of RTs caused by masking effects. ΔRTs produced an inverse U-shaped function during paracontrast but were about constant during metacontrast (Fig. 1.9). They showed that RECOD model simulations also well account for the visibility and ΔRT functions for both paracontrast and metacontrast.

According to the model, the increase in ΔRT is explained by the inhibition of the target’s transient component (Ogmen et al., 2003). This study shows that there is dissociation between the visibility and the localization of a masked stimulus in metacontrast (Fig. 1.10). In other words, ΔRT in response to the onset of the masked stimulus does not change but its visibility is reduced. In paracontrast, there is lack of dissociation such that both the visibility and localization performance is reduced. This finding suggests that there are two discernible components followed by in time in response to a visual stimulus which supports the dual channel model. When the contrast ratio between the mask and the target was set to M/T=3, Ogmen et al. (2003) showed that

ΔRTs produce an inverse-W shaped function. Magnitude of ΔRTs obtained from M/T=3 condition were also higher than that of M/T=1 condition including the range around SOA=0. Their results suggest that two mechanisms might be effective in increase of ΔRT observed during paracontrast: 1) sustained-on-transient (SonT) and 2) transient-on-transient inhibition (TonT). In this dissertation, we investigate these two mechanisms to determine whether they are effective or not and in the affirmative the SOA range of their action. Using the predictions of the model for masking, many experiments have been carried out and accounted for the psychophysical data (Breitmeyer, 1984; Breitmeyer & Ogmen, 2000). The RECOD model also accounts for other experimental data in perception such as deblurring in static and moving images, and oscillations in brain activities (Azizi et al., 1996; Prushothaman et al., 2000, 2002).

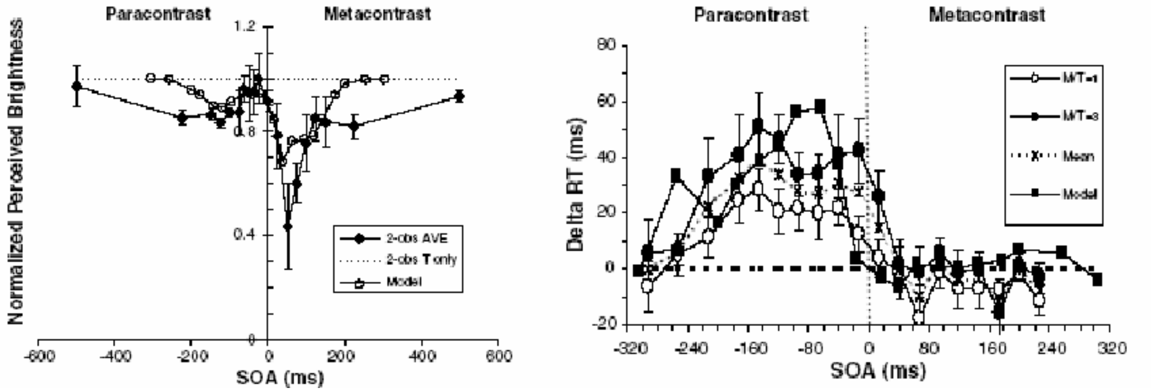


Fig. 1.9. Dissociation between the visibility and the localization of the target in metacontrast but not in paracontrast. Both the visibility and ΔRT are impaired during paracontrast. Although masking magnitude is higher in metacontrast, ΔRTs are not affected. Adapted from the experimental results reported in Ogmen et al. (2003).

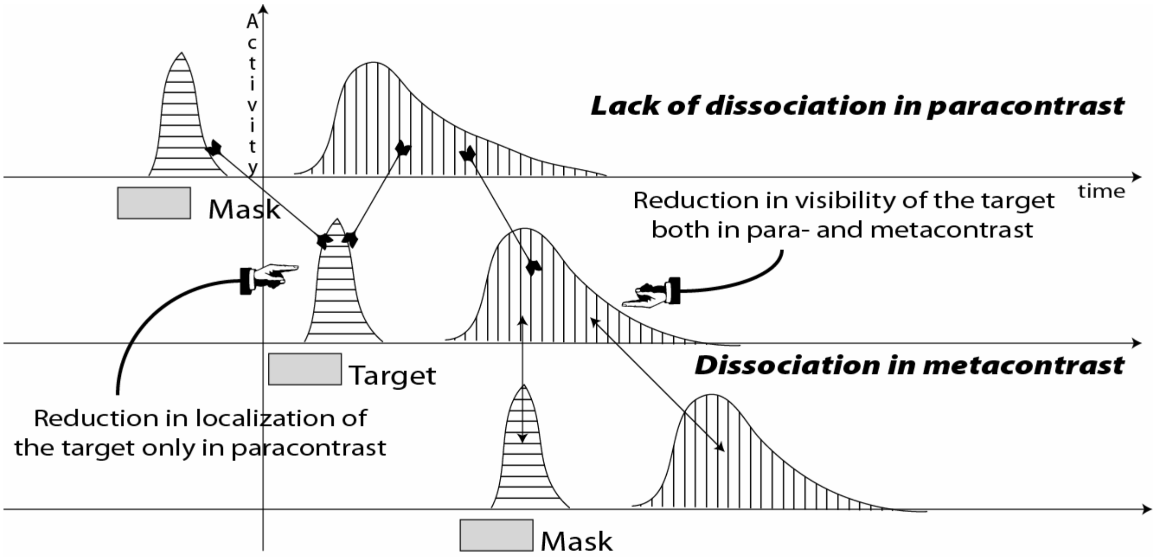


Fig. 1.10. Dissociation between the visibility and the localization of the target in metacontrast but not in paracontrast according to the RECOD model.

1.3.5. Target Recovery (Disinhibition)

The reduction in visibility of the target can be recovered by introducing a third stimulus (Barry & Dick, 1972; Breitmeyer, 1978; Breitmeyer et al., 1981; Briscoe et al., 1983; Bryon & Banks, 1980; Dember & Purcell, 1967; Dember et al., 1978; Kristofferson et al., 1979; Long & Gribben, 1971; Purcell & Stewart, 1975; Purcell et al., 1982; Robinson, 1966, 1968; Schiller & Greenfield, 1969; Tenkink, 1983; Tenkink & Werner, 1981). This phenomenon is called target recovery or disinhibition. Target recovery can be observed in various stimuli configurations. The target (T) stimulus can be a uniformly illuminated disk (e.g., Robinson, 1966, 1968), a pattern such as a letter or a digit (e.g., Dember & Purcell, 1967; Purcell & Stewart, 1975; Tenkink & Werner, 1981) or a vernier (Breitmeyer, 1978). The primary (M1) and secondary (M2) masks can be overlapping disks (e.g., Long & Gribben, 1971; Robinson, 1966) or patterns (Breitmeyer, 1978;

Bryon & Banks, 1980; Dember et al., 1978; Tenkink & Werner, 1981) but also non-overlapping rings (e.g., Breitmeyer et al., 1981; Dember & Purcell, 1967). Target recovery can occur when T-M1 or M1-M2 sequences produce either type-A or type-B masking functions (e.g., Breitmeyer et al., 1981; Briscoe et al., 1983; Robinson, 1966). The disinhibition effect of M2 on M1 can be observed when M2 either follows (e.g., Kristofferson et al., 1979; Robinson, 1966) or precedes M1 (Breitmeyer et al., 1981; Purcell & Stewart, 1975;). No study has reported target recovery in paracontrast condition. Target recovery can be so apparent such that masked target can be substantially recovered without any facilitation effect of M2 on T (Dember et al., 1978; Kristofferson et al., 1979). Other than binocular viewing of stimuli, Robinson (1968) presented T and M1 to one eye and M2 to the other eye. They observed disinhibition significantly when M2-M1 SOA is 10 or 20 ms in binocular viewing, but they did not in dichoptic viewing of M2. However, they reported that disinhibition is observable in some observers at higher M2-M1 SOAs in dichoptic viewing.

1.3.5.1. RECOD Model Accounts for Disinhibition in Metacontrast

Although Barry and Dick (1972) argues that suppression of M1 is required for target recovery, Breitmeyer et al. (1981) study showed that *in metacontrast* there is a double dissociation between the visibility and the masking effectiveness of a non-overlapping ring stimulus M1 during disinhibition of a disk target in presence of a non-overlapping ring stimulus M2.

Target recovery (or decrease in masking effectiveness of M1) occurs when M1’s visibility does not change but there is no target recovery when the visibility of M1 is reduced (Fig. 1.11). This suggests that reduction in visibility is because of the inhibition of the sustained response of T by the transient response of M1. In other words, masking effectiveness of M1 is a function of its transient response and target recovery occurs because M2 inhibits M1’s transient response (Fig. 1.12). This finding has been further tested by increasing the contrast of M2 with respect to M1 while keeping the contrast of T constant (Ogmen et al., 2004). Since the transient magnocellular channels saturate at low contrasts (Purpura et al., 1988), the idea in this study was to increase the sustained response of M2 much more than its transient response. This study found that target recovery effect increases with M2’s contrast without saturation but the reduction in visibility of M1 saturates rapidly. This finding also supports the hypothesis that the masking effectiveness of M1 is a function of its transient response. In addition, what we can say from this study is that the sustained-on-transient inhibition by M2 on M1 is effective for target recovery but we cannot rule out the possibility that the transient-on-transient inhibition by M2 on M1 might be also effective. In fact, observation of target recovery when the SOA between M2 and M1 is close to 0 ms especially supports this possibility.

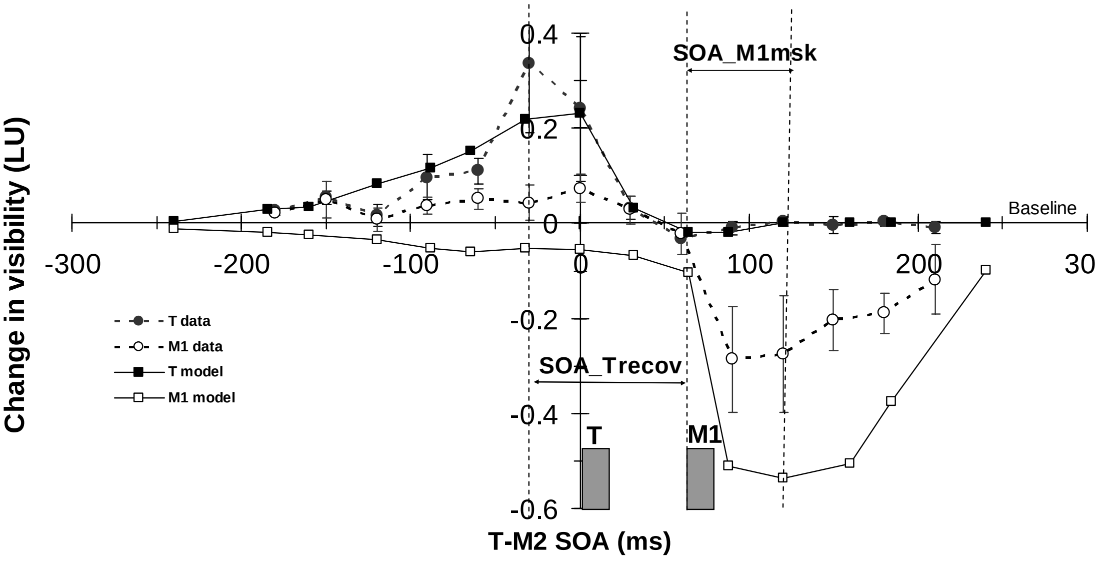


Fig. 1.11. In order to observe whether there is any target recovery, the SOA between M2 and T is varied by keeping the SOA between M1 and T constant. The SOA between M1 and T is chosen to make the visibility of T minimum and the visibility of T at this SOA also provides a baseline value to see the affect of additional M2 on the target's visibility. Baseline visibility of M1 is measured without presenting M2 but T. Relative visibility functions of T and M1 with respect to their baselines are superimposed in this figure Maximum target recovery is at SOA_Trecov. Maximum masking of M1 is at SOA_M1msk. Durations of target recovery and visibility reduction in M1 does not overlap in time. This shows that there is a double dissociation between the visibility and the masking effectiveness of M1. Adapted from the experimental results reported in Ogmen et al. (2004).

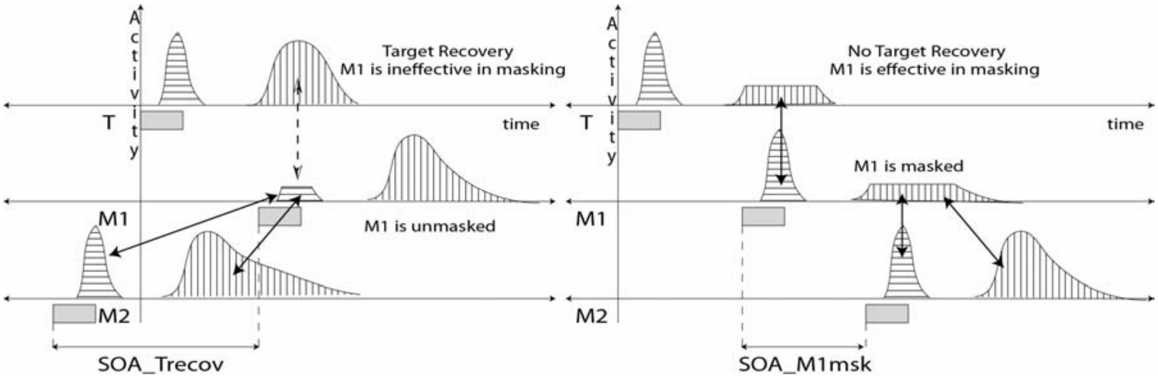


Fig. 1.12. Double dissociation between the visibility and the masking effectiveness of M1 according to the RECOD model. See text for details.

Breitmeyer et al. (1981) investigated both sustained-on-transient and transient-on-transient inhibition effects by varying the spatial separation between M2 and M1 in disinhibition and masking. The rationale behind varying spatial separation was that the magnocellular neurons have larger receptive fields than parvocellular cells (Kaplan & Benardete, 2001). So the expectation was to observe the inhibition effect of sustained channels in a short range of spatial separation compared to that of transient channels. In order to avoid the transient response, M2 was continuously presented in a disinhibition experiment and sustained-on-transient inhibition was observed up to 17’ of spatial separation. Since the sustained response cannot be avoided, masking magnitude on M1 by M2 and the target recovery magnitude with M1 and M2 were compared. Masking magnitude on M1 which is caused by the transient-on-sustained inhibition and target recovery magnitude which may be caused both by sustained-on-transient and transient-on-transient inhibitions dropped monotonically up to 68’ separation. Thus this finding shows that intra-channel transient-on-transient inhibition by M2 on M1 might be also effective in target recovery.

1.3.6. Visual Masking as a Tool to Understand Conscious Registration

In this section, we briefly review the literature in which visual masking is used a methodological tool to understand the unconscious processing of a visual stimulus. A target stimulus that cannot be perceived consciously during masking may still be processed unconsciously. With this idea, the effects of masked stimulus on masking stimulus have been studied in the literature. For example, it has been shown that when the mask and the target stimuli are congruent, i.e. if they have similar features, reaction time to the masking stimulus is less when compared to the case that they are incongruent (e.g., Ansorge et al., 1998; Dehaene et al., 1998; Eimer & Schlaghecken, 2003; Fecteau & Munoz, 2003). Other than motor preparation, priming effects on semantic and perceptual processing have been reported (Dehaene et al., 1998; Dolan, 2002; Herzog & Koch, 2001). Therefore, the priming effects on various information processing levels can be identified by visual masking. A recent study shows that color priming occurs at stimulus (wavelength) but not at percept dependent levels (Breitmeyer, Ro, & Singhal, 2004). Moreover, form priming occurs at a higher level than color priming (Breitmeyer, Ogmen, Ramon, & Chen, in press). As parts of a form in a stimulus become more primitive, the priming effect decreases (Breitmeyer, Ogmen, & Chen, 2004). Effects of top-down settings on priming have also been investigated (Ansorge et al., 1998; Naccache et al., 2002; Scharlau & Neumann, 2003). It has been reported that the priming effect occurs even when the locations of the masking stimuli and the response are incompatible (Leuthold, 2003). Another important finding suggests that attention can change unconscious processing by showing that masked priming depends on temporal attention (Naccache et al., 2002).

Although visual masking is used in many studies as a methodological tool, the neural mechanisms of visual masking have not been fully identified yet. Since masking can be observed by different stimuli variants and the masking functions associated with them change accordingly, different neural substrates for visual masking have been reported. Psychophysical experiments on masking by pattern show that neural substrates might be cortical, because when the mask and the target stimuli are presented to separate eyes (dichoptic presentation); masking by pattern still occurs (Breitmeyer, 1984). However, masking by light only occurs in monoptic presentation (both stimuli presented to one eye only), therefore it was claimed that the most likely neural substrate for masking by light is sub-cortical or retinal (Breitmeyer, 1984; Schiller, 1965; Turvey 1973).

Studies on monkeys reported that there are neuronal correlates of visual masking in V1 (Lamme et al., 2002; Macknik & Livingstone, 1998; Macknik & Haglund, 1999; Macknik & Martinez-Conde, 2004), V4 (Kondo & Komatsu, 2000), IT (Kovacs et al., 1995; Rolls et al., 1999), in frontal eye visual field (FEF) (Thompson & Schall, 1999) and LGN cells (Fehmi et al., 1969; Macknik et al, 2000; Macknik & Martinez-Conde, 2004). The aforementioned studies used different stimuli variants for visual masking. The studies of Macknik with his colleagues used a vertical bar as a target and flanking bars as masks and obtained U-shaped masking functions from human observers in paracontrast and metacontrast conditions. During their neural activity recordings from the monkey brain, they presented target and mask stimuli one after the other so as to make paracontrast and metacontrast masking effects of the mask on the target. Macknik and Livingstone (1998) study found that the stimuli in their backward masking experiment cause a reduction of transient offset discharge while the forward masking causes suppression of onset response in macaque V1 neurons. Macknik and Martinez-Conde (2004) found that responses in LGN and V1 monocular cells are inhibited during both forward and backward masking in monoptic presentation. Responses in binocular cells however are both affected in both monoptic and dichoptic masking. Fehmi et al. (1969) used a test flash followed by a very bright flash and reported that responses to the test flash in the early visual areas including optic nerve, LGN and visual cortex are attenuated in monkey. Correlates of metacontrast in single cells of the cat visual system have also been reported as an attenuation of the late responses in early visual areas (Bridgeman, 1975). At higher levels of the brain, such as in IT, backward masking caused by overlapping pattern masks which yielded type-A masking functions on human observers affects late responses by decreasing their duration and peak firing rates (Kovacs et al., 1995; Rolls et al., 1999). Another study in which overlapping pattern mask was employed, also showed that masking affects only the late responses of V1 cells (Lamme et al., 2002) when V1 cells become activated by the visual stimuli presented outside of their classical receptive fields (Lamme & Roelfsema, 2000). Thus they claimed that masking interrupts recurrent interactions between V1 and higher visual areas (Lamme et al., 2002).

Neuroimaging studies on humans revealed that masked stimuli having priming effects on emotional (Whalen et al., 1998) and motor response (Dehaene et al., 1998) can be measured with functional magnetic response imaging (fMRI) technique. Higher visual areas such as late occipital cortex (LO) and fusiform gyrus have been found to be important for object recognition by employing masking paradigm (Bar et al, 2001; Grill-Spector et al., 2000). A recent study found correlates of masking in LO inferior parietal, pulvinar and anterior cingulate (Green et al., 2005). They suggested that LO is the main neuronal substrate for visual masking and the other areas are more likely activated by attentional effects on visual stimuli. A recent fMRI study showed that visibility change during metacontrast masking correlates with the signals in the higher brain areas (such as fusiform gyrus [FS], posterior cingulated cortex [PCC], temporaparietal junction [TPJ], V5/MT) but not in the retinotopic areas (such as V1, V2, V3, V4) (Haynes, Driver, & Rees, 2005). They found that coupling between V1 and FG, i.e. the correlation coefficients between V1 and FG signals at different SOAs, correlate also with the U-shaped visibility function. This suggests that there is an effective connectivity between these two areas when the visibility of a stimulus increases.

In a study of categorization task employing visual masking, it was reported that two distinct stages in VEP could be identified (van Rullen & Thorpe, 2001). One is a perceptual stage occurring 70-80 ms after the onset of a visual stimulus relating to its low-level properties, and the other one is a task-related stage correlated with the subject’s decision starting after 150 ms (Thorpe, 1996; van Rullen & Thorpe, 2001). They suggested that a feedforward sweep of visual information up to higher areas may be enough for object recognition (van Rullen & Koch, 2003), but also added that late stages of processing because of feedback connections cause the perception of complex stimuli and produce conscious registration (Crick & Koch, 1995; Lamme & Roelfsema, 2000; Milner & Goodale, 1995; Pollen, 1999; Thorpe & Fabre-Thorpe, 2001). A magnetoencephalography (MEG) study also reported that backward masking is effective between 70 ms and 160 ms after the presentation of the target stimulus (Rieger et al., 2002). In a forced choice letter identification task, single pulse transcranial magnetic stimulation (TMS) (Hallett, 2000; Walsh & Cowey, 2000) has been applied over occipital regions on healthy subjects (Corthout et al., 1999). It was observed that TMS pulses impaired the identification task when it was applied before 50 ms and after 100 ms of the target presentation. This shows that TMS can be used as a mask. Ro et al. (2003) have utilized TMS in a metacontrast masking paradigm. They found that target recovery occurs while TMS is suppressing the visibility of the mask. Moreover, when the target is present, TMS reduces the visibility of the mask much more than when it is not present. The first finding resembles to a disinhibition experiment in which M2’s role is served by TMS. They concluded that TMS interrupts mainly feedback signals from higher visual areas to V1.

1.3.7. Electroencephalography (EEG) as a Technique in Neuroscience

There are many techniques in neuroscience. But, several of them are forbidden to be used on human subjects because of ethical reasons. Hence, researchers focused on risk free evoked potential (EP) and neuro-magnetic studies (Regan, 1989). The physiological basis of neural network models that aim at describing the dynamics of the visual system can be probed by examining electrical recordings of the brain. Because of its low cost and ease of use, the electroencephalograph (EEG) has been extensively used as a research tool in recent decades (Regan, 1989). While the EEG technique offers limited spatial resolution for source localization, it is a technique of choice for temporal resolution and correlation studies compared to the other techniques (Walsh & Cowey, 2000).

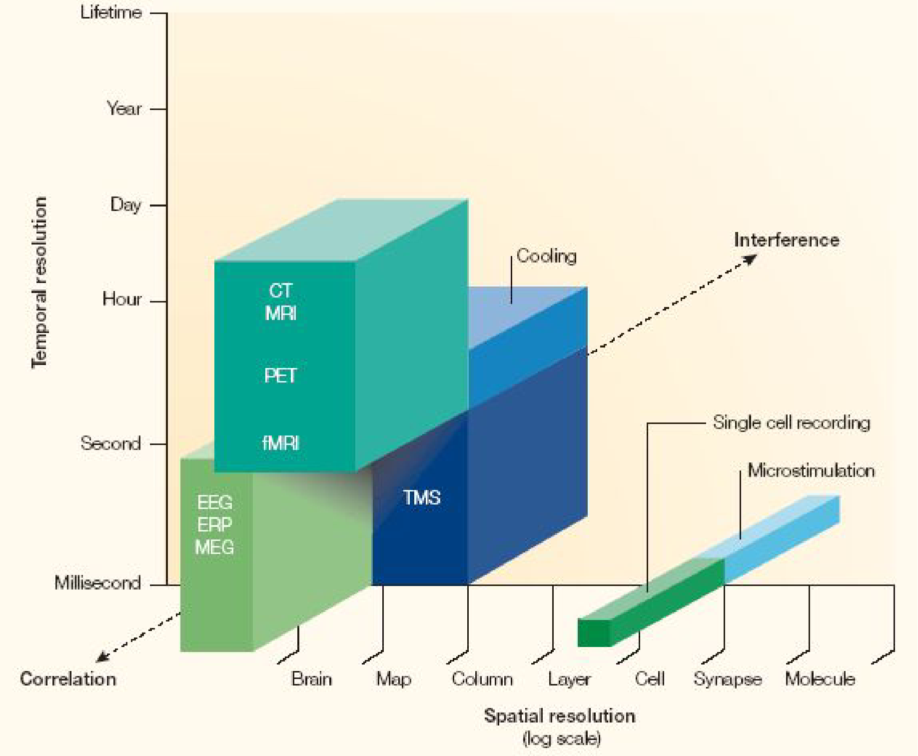


Fig. 1.13. Several techniques in neuroscience are compared in the dimensions of correlation, interference, spatial and temporal resolution. CT, computerized tomography; MEG, magneto-encephalography; fMRI, functional magnetic resonance imaging; EEG, electroencephalography; PET, positron emission tomography; ERP, event-related potential. EEG is a technique of choice especially for temporal resolution and correlation studies (From Walsh & Cowey, 2000).

It has been well known that the brain outperforms high-speed digital computers in many simple tasks. How the brain can process so much information in a short time can be understood at least in part by considering the fact that the brain possesses parallel pathways. This led researchers to investigate the brain by focusing on specific tasks done in specific parts of the brain. Like other sensory pathways, the visual pathway is considered to have functional units that process visual information in parallel (Regan, 1989). Therefore, the visual stimulus has to be simple but capable enough to probe hypothesized functional unit without probing other functional units in the visual system. This has led people to use flashes as stimuli in visual evoked potential (VEP) studies (Regan, 1989). In addition, to advance the understanding of human recognition of objects, pattern stimuli have also been used (Regan, 1989). Although EEG signals which have been produced by activities of millions of neurons look like ambiguous voltage fluctuations, a careful visual inspection shows that EEG signals vary depending on the state of the brain. For example the EEG signals change whether the observer is sleepy or in an attentive mode. Likewise, cognitive processing in the brain may also evoke detectable voltage changes across the surface of the scalp. The changes in EEG between different conditions may be reported by different properties of the signals, for instance amplitude, frequency or power of the signals computed from a time range may differ. Since the brain is always working no matter whether the stimulus is presented or not and thus emits endogenously evoked potentials, the potentials evoked by the experimented external stimulus can be enhanced with respect to the ongoing EEG activity by presenting the stimulus many times and then taking the ensemble average of EPs. Although there is variability between EPs obtained from different trials, examining the ensemble averaged EP is almost a standard in EEG studies as a first step before continuing further the investigated study.

A typical averaged EP consists of peaks and troughs following each other in response to a stimulus. Mostly peaks or troughs are named indicating their sign in amplitude and the time they occur after the presentation of the stimulus (Coles & Rugg, 1995). Specific to an experimental paradigm, the evoked potentials may differ from the normal conditions which are then can be considered a specific component produced by specific neural generators even though the peaks or troughs that can always be observed in response to a stimulus are also called components. So far there have been many specific components reported in cognitive studies (Fabiani et al., 2000). Some of them are related to movement related potentials such as: 1) Lateralized readiness potential (LRP) occurring prior to voluntary movements of the hand and observed maximally on central sites contralateral to the responding hand (Coles, 1989; Kornhuber & Deecke, 1965). 2) Contingent negative variation (CNV) which is negativity in potential before the occurrence of a stimulus that is to be responded to and expected to occur because of a previous warning signal (Walter et al., 1964). 3) Error-related negativity (ERN) occurring when observers make errors in sensorimotor or choice reaction-time tasks (Dehaene et al., 1994; Falkenstein et al., 1990). Some of the cognitive components produced by the so-called endogenous potentials occurring around 100-500 ms post-stimulus are: 1) Early negativities around N1 and P1 components in selective attention tasks requiring attention focusing on the left or the right spatial locations with respect to a fixation stimulus (Hillyard, 1973). 2) Mismatch negativity (MMN) occurring in response to a rare stimulus while the task of the observer is not related to the presented stimuli (Naateen et al., 1978). 3) Late positive activities caused by the novelty of the stimuli or memory-related resources of the brain which are a family of P300 occurring in response to a rare relevant stimulus (Duncan-Johnson & Donchin, 1979; Sutton et al, 1965). 4) Semantic related N400 component occurring when a sentence is ended with an unexpected semantic error

(Kutas & Hillyard, 1980). 5) N2 posterior contralateral (N2pc) or posterior contralateral negativity (PCN) which reflects attention-controlled selection of contralateral stimuli (Eimer, 1996; Luck & Hillyard, 1994; Shedden & Nordgaard, 2001).

1.3.8. Correlates of Masking in VEP Studies

Donchin et al. (1963) recorded VEPs in response to paired test and mask flashes. They found that the mask flash which was very much brighter than the test flash completely suppressed the VEP in response to the test flash at very short SOAs when the test flash was not identified. They concluded that the origin of interference between the flashes was before the primary visual cortex. Jeffreys (1971) reported that there were two main components called C1 and C2 in VEP recordings in response to a brief stationary pattern. Metacontrast effects on these components were investigated by Jeffreys and Musselwhite (1986). They used patterns for the target and the non-overlapping mask to obtain U-shaped metacontrast masking functions. According to their findings, since no significant effect was observed in amplitudes and latencies of C1 and C2 components, they concluded that there would not be any inhibition of target visibility in early cortical levels. However, Breitmeyer and Ogmen (2000) in their review paper suggested that their findings cannot be conclusive evidence for a lack of inhibition in early cortical levels because of the fact that the underlying neural activity cannot be exactly identified by scalp potential distribution. Also Bridgeman’s (1988) reanalysis of Jeffreys’ and Musselwhite’s results show that there are correlates of metacontrast in late components.

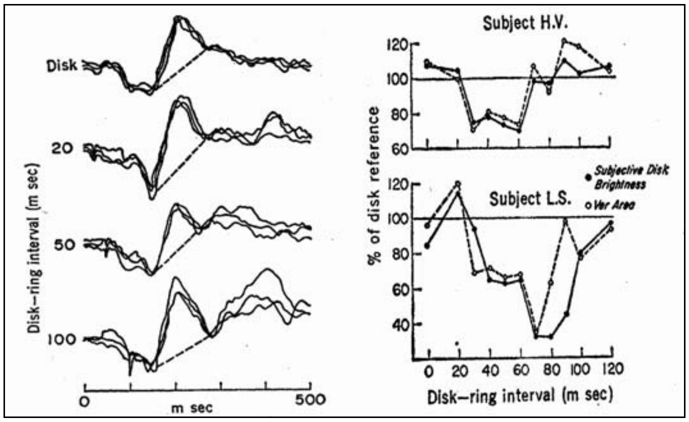


Fig. 1.14. Left panel: VEP recordings of subject H.V. Right panel: Plots of VER area and subjective brightness for subjects H.V. and L.S. Values are expressed as a percentage of the disk VER area and of the comparison disk brightness to the disk, i.e. target (From Vaughan & Silverstein, 1968).

Schiller and Chorover (1966) investigated whether the brightness reduction observed in metacontrast has any correlates in VEP and they concluded that VEP does not necessarily reflect changes in subjective brightness. However, Vaughan and Silverstein (1968) reported that the reason why Schiller and Chorover failed to detect the changes in VEP under metacontrast conditions was because of the parafoveal stimulus they used. According to them, light falling on the fovea overcomes the effects of parafoveal stimulation. Therefore they used both foveal and parafoveal stimuli in their metacontrast experiments. The stimuli they used were a disk as a target and a non-overlapping ring as a mask by which they obtained U-shaped metacontrast visibility functions. Like Schiller and Chorover, they also found no correlates of metacontrast in VEPs when parafoveal stimulus was used. However their study showed that there are changes in visual evoked response components to the foveal stimulus during metacontrast masking (left panel; Fig. 1.14). The amplitude of the component at about 200 ms after the first stimulus is reduced at SOA values at which masking are observed. They plotted the response component area (VER) at 200 ms and subjective brightness as a function of SOA (right panel; Fig. 1.14) for two subjects. Their results showed that there was a high correlation between VEP recordings and associated metacontrast masking function. Other studies employing patterns as target and non-overlapping mask also found that backward masking causes amplitude decrease in late components of VEP (Andreassi et al., 1976; Andreassi, 1984).

Kaitz et al. (1985) investigated paracontrast masking effects on VEP signals by using a disk as a target and an annulus as a mask. As they pointed out that VEPs evoked by temporally disparate stimuli do interact and the interaction varies with the time interval between the stimuli, they reported that the masking profile from the psychophysical and the VEP data are not identical. As already discussed by Schiller and Chorover (1966), because of the nonlinearity of brain signals, VEP in response to a paired-stimulus is not equal to summation of VEPs in response to stimuli presented alone. Therefore, the reduction in amplitudes of late VEP components observed in some of the previous studies may not be directly because of masking but partly maybe due to the overlapping of positive and negative components of the VEPs evoked by the target and the mask. In this dissertation, we design an EEG experiment in order to investigate more clearly the correlates of masking. For this purpose, we adopt “contralateral-ipsilateral” approach. We present visual stimuli to both visual fields of the observers. The stimulus presented to the left visual field projects to the right hemisphere and vice versa.

Consequently, the VEP signal recorded at the side contralateral to the relevant stimulus was compared with the VEP signal recorded at the side ipsilateral to the relevant stimulus which is contralateral to the irrelevant stimulus. Thus, the comparison reveals directly the task relevant information, which is the visibility of the stimulus in our experimental design.

The contralateral-ipsilateral approach in EEG studies has been used especially in attention studies. The effect of shifts of attention on VEPs can be observed by using multi-element displays and balancing the stimuli across two sides of the visual field. It has been shown that the EEG signals obtained from the contralateral side of the attended stimulus shows more negativity especially 200-250 ms after the onset of the stimulus on parietal areas compared to the ipsilateral EEG signals (Woodman & Luck, 1999). This relative negativity is called N2pc (N2-posterior-contralateral) component (Eimer, 1996; Luck & Hillyard, 1994).

Woodman and Luck (2003) investigated whether N2pc is observed during a newly termed object-substitution (four-dot) masking (Enns & Di Lollo, 1997). They used three different shapes as target stimuli: triangle, square and circle. One of them was chosen as a distractor in a block of trials and a number of distractors balanced across two sides of the visual field were presented randomly at different locations from trial to trial. One of the other two shapes of target stimuli was chosen as a relevant stimulus for an observer and each of them was presented randomly on one of the visual fields accompanied by a common onset surrounding four-dot mask. They varied the offset asynchrony between the target and the mask. When they had common offsets (co-termination condition), visibility of the target was around 85% and as expected they observed N2pc. Even though visibility of the target was reduced to around 65% in the delayed-offset condition, N2pc was not significantly different than the co-termination condition. When they used overlapping noise mask to obtain the same amount of target visibility as in the delayed-offset condition, they did not observe N2pc component. They also compared the VEPs obtained from the trials when the target is correctly identified or not in the delayed-offset condition. Although the contralateral-ipsilateral difference seems to be high in correct trials especially 400 ms onward of the target presentation as they also pointed out and attributed to a possible post-perceptual effect, the N2pc component did not differ statistically between correct and erroneous trials. Based on their findings, they concluded that attentional N2pc component can be evoked even when the visibility of the stimulus is reduced suggesting a degree of dissociation between awareness and attention.

Jaskowski et al. (2002) investigated whether N2pc is observed in a priming study employing metacontrast masking. They presented target and mask stimuli to two visual fields of the observers. They used two different shapes for target and mask. During EEG recording, there were three conditions. In the neutral condition, both of the targets were irrelevant. The shapes of target and mask presented on the same side were the same and different in the congruent and incongruent condition, respectively. In all conditions, different mask shapes were presented randomly to two sides. One of the shapes was chosen as relevant stimulus for an observer. During EEG recording, observers indicated the side of the relevant mask stimulus. They used two SOAs to change the visibility of the target and subsequently to see the effect on VEPs. In the incongruent and neutral conditions, as expected they observed N2pc in response to the mask. But in the congruent condition, N2pc in response to the mask was not observed whether the target visibility was reduced or not suggesting the priming effect of the target on both cases. Interestingly, N2pc in response to the target was observed only when the visibility of the target was high with the longer SOA. Based on this finding, they suggested that N2pc can be a good correlate for visual awareness. Eimer and Mazza (2005) also suggested that N2pc can determine the visibility of a stimulus based on the results they found by employing change detection paradigm.

1.3.9. Binocular Rivalry

The fact that having two eyes located symmetrically on the left and on the right sides of our head leads to different retinal images, with relative displacement of objects (disparities) in the two monocular views. However, we automatically merge both monocular views and combine a single fused cyclopean view (Henkel, 2003). When dissimilar images are presented to the two eyes (dichoptic presentation), we see only one of the images at a time rather than seeing a combination of them. In other words, dissimilar images compete for conscious registration. This phenomenon is called binocular rivalry. Interestingly, dominance of the left-eye stimulus and the right-eye stimulus oscillate in time and their exact durations are unpredictable. However, the suppression durations of one image can be shortened if it is biased to become a stronger competitor, for example by increasing its contrast (Blake & Logothetis, 2001). Although voluntary attention can increase the dominance period of an image, it cannot avoid being suppressed during binocular rivalry. If the images are relatively large, different portions of both images may become dominant (Blake & Logothetis, 2001). Also the establishment of dominance does not occur instantaneously, but starts from a region and expands to the whole field (Blake & Logothetis, 2001). We used binocular rivalry paradigm as a tool to suppress the visibility of a masking stimulus in this dissertation.

There are two main competing theories of binocular rivalry: 1) Interocular competition theory (Blake, 1989; Lehky, 1988; Levelt, 1965), 2) Pattern competition theory (Dayan, 1998; Leopold & Logothetis, 1996; Logothetis et al., 1996). While the first one claims that competition occurs between monocular neurons in early visual areas, the second one suggests that competition is only because of the incompatible patterns and occurs well after area V1. Other theories of rivalry (Lumer et al., 1998; Miller et al., 2000) reflect top-down selection by executive mechanisms or switching mechanisms between two hemispheres. However they are in a development stage and supporting evidence for them is not as much as the first two ones (Tong, 2001).

Single unit recordings from alert monkeys found relatively increasing correlations of rivalry while going upper areas starting from V1 up to inferior temporal cortex (IT) (Leopold & Logothetis, 1996; Logothetis, 1998; Lumer et al., 1998). However fMRI studies found robust correlation in blood oxygen level dependent (BOLD) signals from human V1 visual area during binocular rivalry (Lee & Blake, 2002; Polonsky et al., 2000; Tong & Engel, 2001). While the neuronal studies support the theory of pattern competition, fMRI studies suggest that binocular rivalry is resolved fully in V1 (Tong et al., 1998; Tong & Engel, 2001, 2003). VEP studies also show that binocular rivalry is partly resolved in early visual areas (Kaernbach et al., 1994; Roeber & Schroger, 2004). Although these types of unresolved issues are the focus of ongoing studies and the reevaluations of single cell studies support the theory of interocular competition

(Polonsky et al., 2000), it has been also suggested that there may be different mechanisms located in different regions of the brain, which modulate binocular rivalry (Blake, 2001).

1.3.10. Loci of Metacontrast Masking and Binocular Rivalry

Several unconscious processing stages may contribute to the conscious registration of a visual stimulus (Kanwisher, 2001). Masking possibly occurs by interruption of processing of a stimulus in some of these stages. Disinhibition studies show that masking of the target is not affected even when the awareness of the mask is reduced and moreover target recovery occurs while preserving awareness of the mask (Breitmeyer et al., 1981; Ogmen et al., 2004). Nevertheless, another study which reduced the visibility of the mask by transcranial magnetic stimulation (TMS) technique caused target recovery (Ro et al., 2003), which suggests a functional specificity of target recovery between using TMS and a secondary visual mask. When the target and the mask are presented to separate eyes (dichoptic view), metacontrast masking is observed (e.g., Kolers, 1960; Schiller, 1965; Schiller & Smith, 1968). This suggests that the mechanisms of masking occur after binocular convergence.

It has been shown that binocular rivalry does not occur immediately after binocular convergence and becomes more prominent while ascending to higher areas (Blake, 2001). Different neuronal correlate studies of masking also show that LGN, V1, V4, IT cells are subject to masking (Kovacs et al., 1995; Kondo & Komatsu, 2000; Lamme et al., 2002; Macknik & Livingstone, 1998; Macknik & Martinez-Conde, 2004; Macknik et al, 2000; Rolls et al., 1999). Results of this study are informative in locating the substrates of masking. In this dissertation, we combine binocular rivalry and metacontrast paradigms in order to find functional locus of metacontrast with respect to that of binocular rivalry. Since the metacontrast mechanism itself occurs at unconscious levels of processing, our results can also provide a means of establishing a functional hierarchy of unconscious visual processing.

1.3.11. Visual Attention

The amount of visual information provided by the optic nerves is estimated to be in the range of 10^8-10^9 bits per second (Koch, 2004). However the human brain is not capable of fully processing and assimilating such a huge amount of information into conscious experience. Therefore some parts of the incoming visual information are processed preferentially. This is called selective or focal visual attention. With attention, observers actively seek and process the “relevant” information in order to actively interact with their environments (Chun & Wolfe, 2001).

The most apparent characteristic of visual attention is to select visual information over space and time and filter out unwanted information. The spotlight metaphor (Posner, 1980) has been considered to be useful in understanding of deployment of attention to a specific location in visual field. According to this metaphor, attention is a beam of light that can be employed across space and time within which processing is enhanced in order to reveal what is hidden in the world. In order to study this metaphor, cueing experiments have been developed. A cue is presented before the presentation of a visual item that has to be attended. Studies support the spotlight metaphor such that visual attention loses its effectiveness as the distance between the visual item and the cue increases (e.g., Hoffman & Nelson, 1981; LaBerge, 1983). According to this metaphor, time to deploy attention from one location to another depends on the distance between the locations. However, the shift of visual attention is found to be instantaneous and the multiple spots can be processed at the same time, which is also called divided attention (e.g., Bichot et al., 1999; Krose & Julesz, 1989; Kwak et al., 1991).

Studies related to the spotlight metaphor also showed that the size of spots that are attended can be changed depending on the task and the visual item (Pashler, 1998). For this reason, a “zoom lens” model has been offered such that the attended information is selected and then zoomed (Eriksen & Yeh, 1985). Visual attention can also be considered as a filter, a skill, a selective attenuator or a resource because the perceptual load, difficulty of task or properties of the visual item alter the strength of visual attention across the observers (Wright, 1998). Visual attention can be selectively allocated to an object (e.g., Behrmann et al., 1998; Cave & Bichot, 1999). This is called object-based attention, which is different than spatial-based attention above. A good example for object-based attention is that an observer can attend and follow only one of the overlapping movies (Neisser & Becklen, 1975).

The visual search paradigm has been developed in order to study visual attention in a more realistic situation. For example, an image of nature can be presented and an observer can be asked to find an animal in the image according to visual search paradigm. Artificial simple stimuli such as letters, colored bars having different shapes can also be used. In visual search experiments, a fixation stimulus, for example a cross, stays during the experiment. The observer is asked to maintain his/her eyes fixed on the fixation stimulus and covertly, i.e. without moving his/her eyes, attend the stimuli in the search array. Usually RT and accuracy are measured. The search item that is asked to be attended is usually called the target and the other items around the target are called distractors.

Visual search studies show that the difficulty of finding the search item depends on the properties of the target and the distractors. For example, a white target can easily be located among the black bars. This is called “pop-out” effect or parallel search (Fig. 1.15a) because the number of distractors does not affect the time to correctly locate the search item (Pashler, 1998). The complexity of the target makes it difficult to find, for example searching for a horizontal black item among the vertical or horizontal black or white items. This is called serial search (Fig. 1.15b), because the time to correctly locate the target increases as the number of distractors increases (Pashler, 1998). Usually serial searches have been found when two or more features have been used such as combinations of orientation and color features. This is called conjunctive paradigm. Along with visual search experiments, dual task experiments, in which two stimuli have to be attended, are informative in revealing the attentional resources (van Rullen et al., 2004). In this dissertation, we use the conjunctive search paradigm to study the temporal dynamics of visual attention.

Treisman (1980) developed the “feature integration theory” (FIT) in order to explain the findings from visual search experiments. According to this theory, the target item can be processed in parallel or serial depending on the similarity between it’s and the distractors’ features. Attention is then required to bind multiple features into a single object. This theory triggered many studies in order to determine how a serial or parallel search is conducted. The guided-search model by Wolfe (1994) proposed a two-stage model. According to this model, attention is guided by the interaction of pre-attentive and attentive stages of stimulus processing. For example, a stimulus that can pop out produces the highest saliency in the pre-attentive stage. Several other models have been proposed to account the data from the visual search experiments (e.g., Heinke & Humphreys, 2005; Itti & Koch, 2003; Koch, 2004).

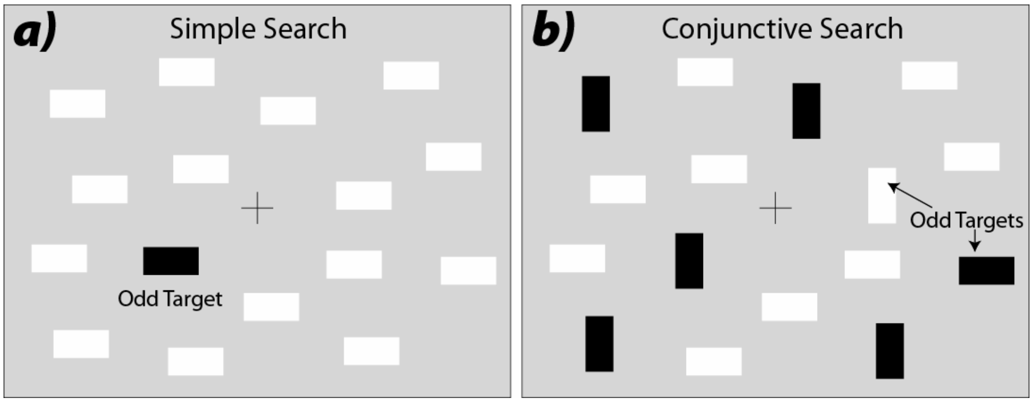


Fig. 1.15. a) Parallel or simple search in which the odd target pops out. b) Serial or conjunctive search in which both orientation and color describes the odd target.

Visual attention can be deployed endogenously or exogenously (Posner, 1980). The first one refers to the control of attention voluntarily, which is also known as the goal-directed, top-down, volitional control of attention. Exogenous attention is deployed by a physical stimulus involuntarily, for this reason it is known as the stimulus-driven, bottom-up, sensorial control of attention. There are two types of cues that can activate goal-directed and stimulus-driven attention. A central cue, which informs the observer where to attend, is called symbolic cue. This cue triggers voluntary, top-down attention because the cue has to be interpreted first. An abrupt peripheral cue involuntarily captures attention even when it is not informative about the search item. In a visual search task, these two domains of attentional control interact (Egeth & Yantis 1997; Folk et al., 1992; Theeuwes, 2004; Theeuwes & Burger).

The information about the location of the search item can be altered by changing the validity of the cue. For example, if it is a 100% valid cue, the search item always appears at the location indicated by the cue. In contrast, if the cue is a 100% invalid cue, this means that the observer must seek the search item at a location other than that indicated by the cue. Similarly a cue can be uninformative meaning that the probabilities of the search item to appear among possible locations are the same or at chance in a trial. Before starting the experiment, the observer is informed about the validity of the cue. Attentional benefits or costs on RT and accuracy can be identified by comparing the results obtained from the trials employing a valid and an invalid cue.

Psychophysical experiments show that attention alters appearance. Attention improves performance both at the decisional and perceptual levels (Carrasco et al., 2004). At the perceptual level, attention modulates the representation of the stimulus by signal enhancement (Carrasco et al., 2002) and external noise reduction (Lu & Dosher, 2000). The rate of visual information processing is also accelerated by covert attention (Carrasco & McElree, 2001). Speed of visual processing increases with eccentricity (Carrasco et al., 2003). Attention improves visual performance by increasing contrast and enhancing spatial resolution (Ciaramitaro & Glimcher, 2000; Yeshurun & Carrasco, 1998, 1999). However, transient spatial attention degrades temporal resolution (Yeshurun, 2004; Yeshurun & Levy 2003). The finding that attention improves spatial resolution while degrading temporal resolution led Yeshurun (2004) to suggest that attention favors parvocellular over magnocellular neurons. As she points out, an attentional facilitation of parvocellular neurons, which in turn inhibiting magnocellular neurons could also account the finding that attention reduces masking (Tata, 2002).

Modulation of neuronal activity by visual attention has been reported in V1, V2, V4 and MT areas of the monkey brain (Kastner & Ungerleider, 2000; Luck et al., 1997). The modulation occurs by increasing baseline activity, response enhancement and suppression of unattended stimuli by competition of the stimuli in the receptive field of neurons (Kastner & Ungerleider, 2000). Based on lesion, VEP and fMRI studies on humans, sources of goal-directed and stimulus-driven attention are found to be in the regions of frontal eye field (FEF), intraparietal sulcus/superior parietal lobe (IPs/SPL) and temporoparietal junction (TPJ) (Corbetta & Shulman, 2002). Event related potential (ERP) studies show that modulation of spatial attention starts within 100 ms of stimulus onset (Hillyard & Anllo-Vento, 1998; Hopf & Mangun, 2000; Luo et al., 2001; Martinez et al., 1999, 2001). ERP components of P1 and N1 have been reported to be larger in response to attended stimuli. By using multi-element stimuli balanced on the left and right sides of the observer, the N2pc component is observed around 200-300 ms after the onset of the stimuli (e.g., Woodman & Luck, 1999, 2003). This component is related to the shift of attention between the two hemispheres and the covert orienting of attention before the completion of object recognition. One recent VEP study reported that a fully masked stimulus does not evoke an attentional component during metacontrast masking (Jaskowski et al., 2002). Another study found that the attentional component in VEP is observed by using a four-dot mask but not by a noise mask (Woodman & Luck, 2003). But these two recent studies did not report any correlates of masking in VEP. Spatial attention has different effects on the magno- and parvocellular pathways (Di Russo &

Spinelli, 1999). Amplitude enhancement related to automatic gain control is observed for the stimuli that activate both magno- and parvocellular pathways. However, latencies of VEP components decrease in response to stimuli, which dominantly activate dorsal pathway (Di Russo et al., 2001).

1.3.12. Attention Affects Masking

It has been demonstrated in several studies that attention also affects the masking function (Di Lollo et al., 2000; Enns & Di Lollo, 1997, 2000; Ramachandran & Cobb, 1995; Shelley-Tremblay & Mack, 1999; Tata, 2002). When the focus of attention is diverted from the locus of the target stimulus, visual masking gets stronger (Ramachandran & Cobb, 1995). When the target's capability to draw attention increases, it is less vulnerable to masking and conversely when the mask stimulus' capability to draw attention is higher, masking of the target stimulus becomes stronger (Shelley-Tremblay & Mack, 1999). Furthermore, dividing attention by increasing the number of possible target locations or the distractors increases the masking (Tata, 2002). But masking decreases when a valid cue is presented which indicates the location of the target stimulus (Tata, 2002). Using a salient target stimulus that can pop out among the distractors also reduces masking (Tata, 2002). In order to study attentional effects on masking, Enns and Di Lollo (1997) used a four-dot mask surrounding the target. In their study, masking only occurred when the attention was divided across many spatial locations. The target and the mask stimuli may have common onsets and in this case masking is stronger if the mask has a delayed offset and also the four-dot mask may be used as a cue in a visual search experiment (Enns & Di Lollo, 1997; Woodman & Luck, 2003). Enns and his colleagues used a new term, object substitution masking, to describe the masking obtained under these conditions. This type of masking is compared with the aforementioned classical masking experiments and it was found that as attention decreases masking strength increases in all cases but the reduction of the visibility starts earlier in classical masking than that of the object substitution (Enns, 2004). This led the author to suggest that there are two distinct object formation and object substitution states and the classical masking occurs during object formation (Enns, 2004). These studies related to attentional effects on masking show that in fact, attention can be considered as a parameter in a masking experiment. However, it remains to be seen whether object-substitution masking is a fundamentally new form of masking or whether it can be explained by classical types of masking by using attention as a modulating factor (Breitmeyer & Ogmen, 2000). Therefore the results in these studies must be evaluated by considering the spatio-temporal properties of visual attention. For example, it is reasonable to expect higher masking when attention is divided away from the target because attention can alter the appearance of a stimulus by increasing its contrast and spatial resolution (e.g., Yeshurun & Carrasco, 1998, 1999). Since previous studies have shown that attention affects masking, it is reasonable to suggest that masking can also affect attentional performance. In this dissertation, we investigate the effect of masking on attentional performance.

1.3.13. Temporal Dynamics of Attention

Attention is a crucial mechanism that allows the visual system to deploy efficiently its processing resources according to ever-changing environmental needs.

Cumulating evidence suggests that attention manifests itself in both spatial and temporal domains to produce a relative enhancement of targets of interest and/or suppression of distractor items (Carrasco et al., 2000; Dosher & Lu, 2000; Kastner & Ungerleider, 2000; Luck et al., 1997). Deployment of attention to a location or an object differs in time depending on both spatial and temporal properties of the stimulus to be used for cueing. The duration between the cue and the search item (cue lead time, CLT) is varied in order to study temporal course of attention triggered by the onset of the cue. The facilitation generated on accuracy and RT by a symbolic valid cue, which triggers top-down control of attention, increases monotonically as a function of CLT (e.g., Cheal & Lyon, 1989, 1991; Müller & Rabbitt, 1989). An abrupt peripheral valid cue produces facilitation of RT and accuracy at short CLTs but the facilitation slightly decreases at long CLTs (e.g., Cheal & Lyon, 1991; Nakayama & Mackeben, 1989; Posner & Cohen, 1984).

Posner and Cohen (1984) found that RTs for previously cued targets are faster (slower) than for targets at novel, i.e. uncued, locations when the CLT is short (long) (Fig. 1.16). The cue they used was a peripheral surrounding square abruptly appearing at an eccentricity with respect to a fixation stimulus. In order to disengage attention from the cued location, they either used an uninformative cue or they flashed the fixation stimulus. They called inhibition of return (IOR) the surprising finding that RTs are longer in cued (attended) locations compared to uncued (unattended) locations at long CLTs. In other words, they suggested that there is an inhibitory mechanism in visual attention causing poorer performance in returning to the previously attended locations. IOR, however, is not observed when a central symbolic cue is used (Posner & Cohen, 1984; Rafal et al., 1989). These results suggest that there are two discernible components in temporal course of attention. These components can be called facilitation component (FC) and IOR component (IORC) causing faster and slower RTs for cued locations, respectively.

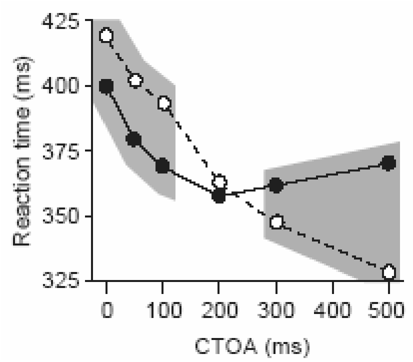


Fig. 1.16. Reaction-times to the target stimulus obtained from cued (filled circles) and uncued (open circles) trials. There is facilitation at short cue-target onset asynchronies (CTOAs) but inhibition of return (IOR) at long CTOAs. From the experimental data reported in Posner and Cohen (1984). See text for details.

Müller and Findlay (1988) observed components similar to FC and IORC when accuracies obtained from valid and invalid trials are compared. The peripheral surrounding square cue yielded both FC and IORC but the central cue produced only FC. Performance after around CLT=100 ms in valid trials also slightly decreased but it increased in invalid trials. They suggested that their and Posner and Cohen’s (1984) findings can be explained by a two-component model of spatial orienting (Jonides, 1981; Posner, 1980). They labeled the components automatic and controlled. The automatic component is a consequence of involuntary orienting of attention which is effective at short CLTs. The controlled component is caused by voluntary attention showing a monotonically increasing effect of facilitation. They suggested that IOR occurs when the automatic component fades and the controlled component becomes more dominant. Many researchers have studied the temporal and spatial properties of IOR since its discovery in 1984 (Klein, 2000 for a review).

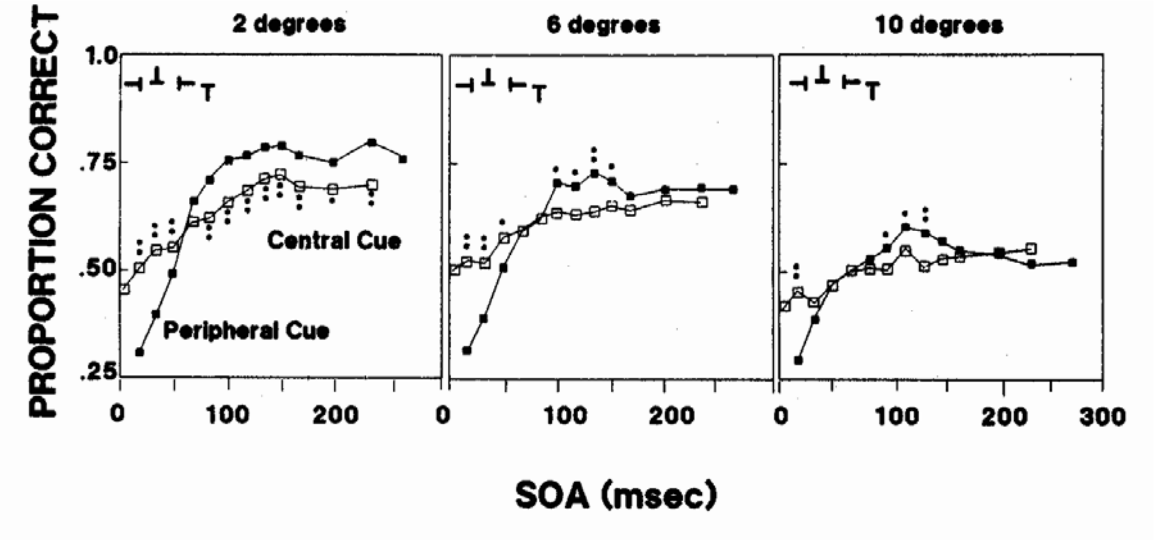


Fig. 1.17. Accuracy obtained by using a four-alternative forced choice procedure (4AFC) at different eccentricities. There is monotonic increase of accuracy for central cues (open squares). For peripheral cues, accuracy produces a peak around CLT=100 ms but then slightly decays especially at large eccentricities (filled squares). From the experimental data reported in Cheal and Lyon (1991). See text for details.

Cheal and Lyon (1991) investigated the time course of attention by measuring accuracy (Fig. 1.17). In their study, the spatial cue was always valid to avoid disengagement of attention from the cued locations. They presented an arrow indicating the location of the search item as a central cue and a non-surrounding square or an arrow as a peripheral cue. Like Müller and Findlay (1988), they presented local masking stimuli immediately after the search items disappeared. Either two-alternative (2AFC) or four-alternative forced-choice (4AFC) procedure was used to discriminate the search stimuli. They found monotonically increasing functions in facilitation of accuracy when the cue was central for both procedures and when the cue was peripheral only for the 2AFC procedure. However, accuracy peaked around CLT=100 ms and then slightly decreased at long CLTs when the cue was peripheral and the procedure was 4AFC. The decrease was more clearly observed when the eccentricity was increased. They suggested that there might be an inhibitory mechanism at long CLTs. Considering the findings about IOR as mentioned above, we can say that the same inhibitory mechanism might also be the cause of IOR; even though IOR is defined based on the discrepancy in performance between cued and uncued cases.

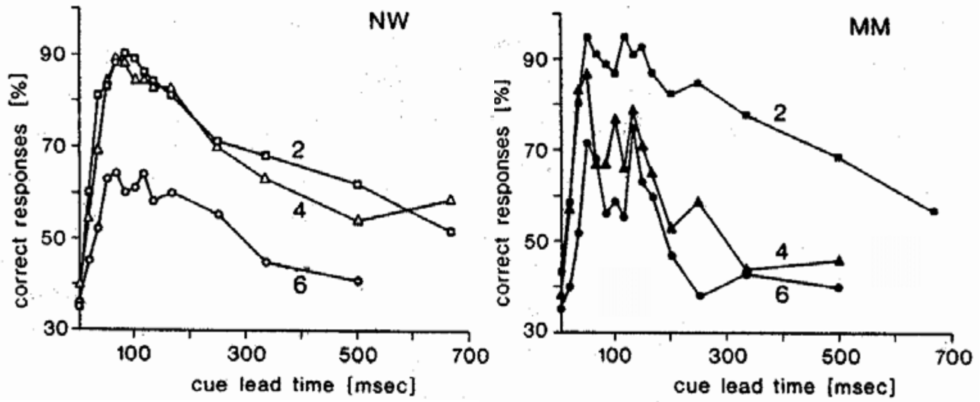


Fig. 1.18. Time course of attention up to CLT = 700 ms obtained from two observers (NW and MM) at three different eccentricities (2, 4 and 6 degrees). From Nakayama and Mackeben (1989).

In a similar study, Nakayama and Mackeben (1989) used a powerful global high energy post-stimulus mask to effectively curtail the persistence of the search items. They employed a conjunctive search paradigm and used a three-alternative forced-choice procedure (3AFC). A surrounding square was used as a peripheral cue but the cue in their study stayed until the disappearance of the search items. Their results showed a much stronger decay at long CLTs compared to the other studies (Fig. 1.18). Like Müller and Findlay (1988), they also suggested that there are two temporal components of attention: transient and sustained components. Further, they suggested that these two components reflect the involuntary, bottom-up and voluntary, top-down control of attention, respectively. Nakayama and Mackeben’s (1989) findings have been replicated using similar methodology in other experiments (Kristjansson et al., 2001, 2002; Kristjansson & Nakayama, 2002).

Temporal properties of attention have also been studied by presenting visual stimuli at rates of up to 20 items per second (rapid serial visual presentation, RSVP). A single target can be easily identified in RSVP (e.g., Potter, 1975; Sperling et al., 1971). If there are two consecutive targets to be detected, the first one can be correctly detected. However, the detection of the following target is severely impaired if it appears 200-500 ms after the onset of the first target. This is called attentional blink (Broadbent & Broadbent, 1987; Raymond et al., 1992). Weichselgartner and Sperling (1987) employed RSVP to study time-course of attention. While observers were fixating to a numeral RSVP stream in which a cueing frame is embedded, they asked observers to report the earliest four numerals they could remember. The cueing frame that the observers had to attend was either an outline square around a numeral or was a highlighted numeral. They found that the recalling probability distribution is bimodal, i.e. there are two peaks of performance in time. Performance starts to increase 100 ms before the onset of the cue and peaks at CLT=0 ms. After the first peak, performance decreases but starts to increase again at CLT=200 ms and peaks at around CLT=400 ms and thereafter gradually decreases until CLT=800 ms. This finding is very close to the attentional blink paradigm mentioned above. Weichselgartner and Sperling also studied time-course of attention by asking observers to shift their attention from one RSVP stream to another. While observers were fixating to a letter RSVP stream, they were asked to attend to the other numeral RSVP stream located two degrees to the right when the target letter, i.e. the cue, was detected and to report the earliest four numerals that they could remember. They found that probability distribution is no more bimodal; there was only one peak. Performance starts to increase at CLT=100 ms and peaks around CLT=400 ms and thereafter gradually decreases. Based on their findings, they suggested that time-course of attention consists of automatic and controlled components. The results of cueing and RSVP show very close resemblance of time-course of attention although they might probe different neural mechanisms of the brain.

Temporal and physical properties of the cue and the search item affect the strength and temporal characteristics of FC and IORC in experiments measuring RT, and these two components have been suggested to be occurring due to independent mechanisms (Maruff et al., 1999; Pratt et al. 2001). Maruff et al. (1999) only found FC when the cue overlapped in time with the search item, but only IORC when they did not overlap. However, other studies have found FC and IORC even when the cue and the search item do not overlap in time (e.g., Maylor, 1985; Pratt & Abrams, 1995). With spatially overlapping cues, IORC but not FC was observed (Pratt et al., 2001). However a spatially non-overlapping cue yielded both FC and IORC (Pratt et al., 2001). Facilitation but not IOR was observed even when the cue was presented below a threshold of awareness (McCormick, 1997). A masked cue also produces facilitation but not IOR when its presence or location is judged (Ivanoff & Klein, 2003). These studies suggest that temporal dynamics of attention might be modulated depending on the interactions between the spatial and temporal properties of the cue and the search item.

1.4. Organization

This introduction chapter explains how we study conscious registration of a visual stimulus. Three aspects of conscious registration are studied: 1) Temporal dynamics, 2) Neural Locus, and 3) Functional specificity. Functional specificity and neural locus aspects of conscious registration are studied in chapter 2 by combining masking and binocular rivalry paradigms. We use visual masking paradigm to investigate EEG correlates of conscious registration in chapter 3 to study the temporal dynamics and to some extent neural locus of conscious registration. In chapter 3, we study visual masking under the framework of the RECOD model by which we examine all three aspects of conscious registration. We study underlying mechanisms of visual attention and further examine temporal dynamics of conscious registration in chapter 4. We conclude the dissertation in chapter 5. Appendix A explains in more detail processing of EEG signals and the statistical analysis of the data.

Chapter 2

Functional Hierarchy of Visual Information Processes

It is well known that the brain shows to some extent modularity and hierarchy in processing of visual information. Some of processing in this hierarchy takes place at unconscious levels. We combined binocular rivalry and metacontrast masking phenomena to assess where, relative to the functional locus of binocular rivalry, visual processes responsible for target suppression during metacontrast masking occur. We found that the visibility of a masked stimulus substantially increased when the visibility of the masking stimulus was suppressed by using the binocular rivalry phenomenon. Our results suggest that, in the functional hierarchy of unconscious visual processing, the mechanism of metacontrast masking occurs after binocular rivalry.

2.1. Introduction

Metacontrast masking refers to the reduced visibility of a target stimulus in the presence of a spatially non-overlapping and temporally aftercoming mask stimulus (Breitmeyer, 1984). An appropriately chosen mask stimulus can completely suppress the conscious registration of an otherwise visible target stimulus. Thus, the mechanisms underlying unconscious and conscious registration of visual stimuli can be studied by using the metacontrast paradigm (Breitmeyer & Ogmen, 2000). Previous studies showed that metacontrast masking is observed even when the target and the mask are presented to separate eyes (dichoptic view) (Kolers, 1960; Schiller, 1965; Schiller & Smith, 1968). In binocular rivalry, produced when two dissimilar images are presented dichoptically, interocular competition between the images leads to only one of them reaching, whereas the other failing to reach, conscious registration (Blake & Logothetis, 2001). Physiological studies show that the loci of both metacontrast masking and binocular rivalry are beyond V1 area of the primary visual cortex, where the visual information coming from two eyes starts to interact (Leopold & Logothetis, 1996; Logothetis, 1998; Lumer et al., 1998). However, no study has yet addressed the question of finding locus of metacontrast masking relative to that of binocular rivalry. In this study, our aim was to combine metacontrast masking and binocular rivalry methods so as to assess where, relative to the functional locus of binocular rivalry, visual processes responsible for target suppression during metacontrast masking occur.

2.2. Experiment 1 – Relative Timing of the Mechanisms Underlying Metacontrast Masking and Binocular Rivalry

We used the binocular rivalry technique and metacontrast masking to suppress the visibility of a mask and a target stimulus, respectively. Dichoptic masking served as a control condition in which the visibility of the target stimulus is reduced. Our hypothesis is that the stages of processing before binocular rivalry are not responsible for metacontrast masking (hypothesis 1). According to our hypothesis, our prediction is that the target visibility is not reduced when the mask visibility is reduced. According to the null hypothesis, however, if metacontrast masking precedes binocular rivalry, then the target visibility has to be reduced. Illustrations of the predictions are shown in Fig. 2.1.

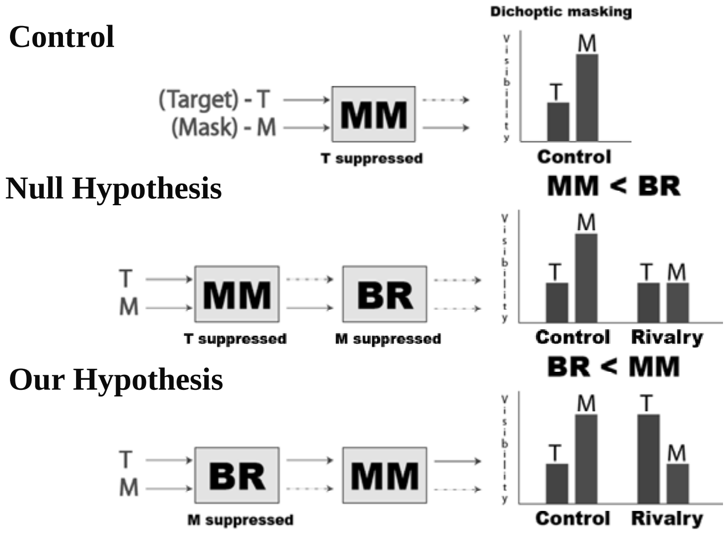


Fig. 2.1. Predictions of the visibility of the target and the mask stimuli are illustrated for the control condition and according to the null and our hypotheses, respectively.

2.2.1. Methods

2.2.1.1. Observers

A total of three observers one of whom naïve to the purpose of the experiment participated.

2.2.1.2. Apparatus

Visual stimuli were generated via the visual stimulus generator (VSG) card manufactured by Cambridge Systems (http://www.crsltd.com). This card was programmed by using its driver library and the stimuli were displayed on a 19’’ high-resolution color monitor with a 60 Hz frame rate. In a typical display, the stimuli were displayed on a uniform gray background. A head/chin rest was used to aid the observer to keep his/her head still while fixating his/her eyes on the fixation cross displayed at the center of the monitor. The distance between the monitor and the observer was set to 90 cm. Behavioral responses were recorded via a joystick connected to the computer, hosting the VSG card. A mirror setup was used to provide the left (right) eye to see only the left (right) side of the screen. Target and mask stimuli were presented in dichoptic view on the left or right side of the monitor.

2.2.1.3. Stimuli and Procedure

This experiment consisted of two conditions: rivalry and control (Fig. 2.2). The SOA between the target and mask was chosen to provide minimum visibility of the target and was kept the same in both conditions. The target and the mask were presented to the fovea in dichoptic view on white diamond fields in both conditions. Only in the rivalry condition, a vertical grating surrounded the target. In both rivalry and control conditions, the mask was surrounded by a horizontal grating. In addition to measuring the visibility of the target, we also measured the visibility of the mask in consecutive sessions to ensure that the mask is powerfully suppressed in the rivalry condition and its visibility is not impaired in the control condition.

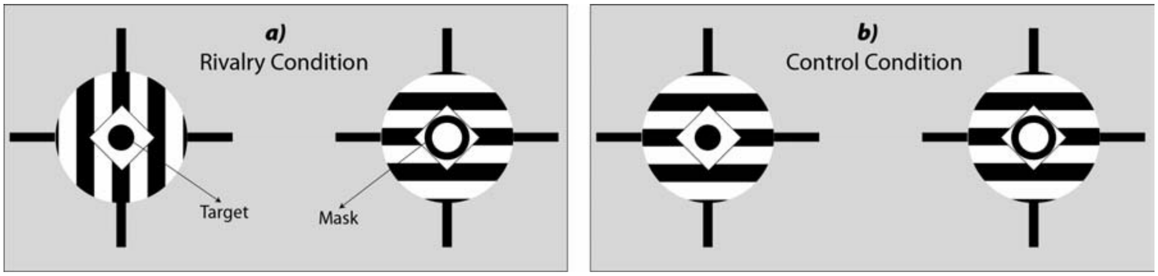


Fig. 2.2. Target and mask stimuli were presented dichoptically. a) In the rivalry condition, a trial starts when the vertical grating surrounding the target becomes dominant. b) In the control condition, the gratings surrounding the target and the mask are the same to avoid binocular rivalry and therefore to provide dichoptic masking. See text for details.

Since it has been demonstrated that dichoptic presentation of stimuli generates masking (e.g., Breitmeyer, 1984; Kolers, 1960; Schiller, 1965; Schiller & Smith, 1968), we expect to observe masking in the control condition. We compared the rivalry and control conditions in order to see how masking is affected by the suppression of the mask. Our hypothesis will hold if we observe substantial recovery of the target in the rivalry condition compared to the control condition.

Dissimilarity between the vertical and horizontal gratings (Blake & Logothetis, 2001) ensured rivalry of them so that one of the eyes was dominant. Fixation bars also accompanied gratings on both sides. Once the eye on the target side becomes dominant, the observer pressed the left button of the joystick to start a trial and immediately the target and the mask were presented. Since dominance of an eye remains several seconds as shown in previous studies (Blake, 2001; Blake & Logothetis, 2001) as well as in our pilot experiments, the visibility of the mask was effectively suppressed.

There were 9 combinations of paired target and mask stimuli. The target stimulus was a disk or a disk whose smaller portion is cut in the up or down part of it (Fig. 2.3). Similarly, the mask stimulus was an annulus or an annulus whose smaller portion was cut in the up or down part of it (Fig. 2.3). The number of trials in each block was balanced across combinations of paired stimuli. The observer pressed one of the three buttons of the joystick indicating the shape of the target or the mask. Accuracy of the observers was recorded to plot the visibility function. 72 trials were collected from each observer for each condition.

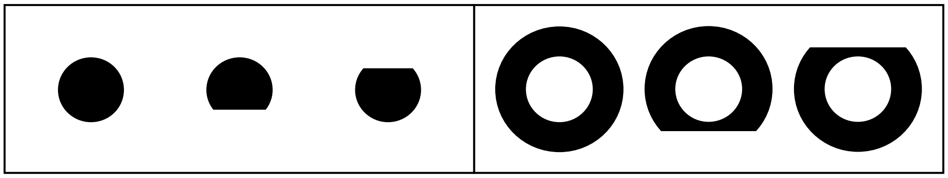


Fig. 2.3. Target (left panel) and mask (right panel) shapes for experiments 5.1 and 5.2.

Background luminance was 25 cdm^{-2}. The luminance of the target and the mask were 0 cdm^{-2} throughout the experiment. The inner and outer diameters of the mask were 0.25^o and 0.35^o, respectively. The target had a diameter of 0.25^o. The duration of the target and the mask was 20 ms. Gratings subtended a circular area having a diameter of 1.5^{o} and the spatial frequency of the grating was 6 cycles per degree. White and black areas in the grating were 50 cdm^{-2} and 0 cdm^{-2}, respectively.

2.2.2. Results

The percent of correct responses for identifying the target and mask stimuli obtained in the control and the rivalry conditions were compared (Fig. 2.4a). As expected, prominent masking on the target was observed in the control condition when the visibility of the mask was not suppressed. In this condition, the average accuracy of the observers for the visibility of the target and the mask was 41% and 84%, respectively The visibility of the target, however, improved substantially in the rivalry condition to 85% ($F_{1,2}$=42.082, p=0.023) when the visibility of the mask was significantly suppressed to 45% ($F_{1,2}$=29.251, p=0.033). Our findings are consistent with the hypothesis that the stages of visual processing before binocular rivalry are not responsible for metacontrast masking indicating that functionally the mechanism of metacontrast occurs after binocular rivalry. Therefore, binocular convergence is followed by binocular rivalry, which is in turn followed by metacontrast masking and finally conscious perception occurs as illustrated in Fig. 2.4b.

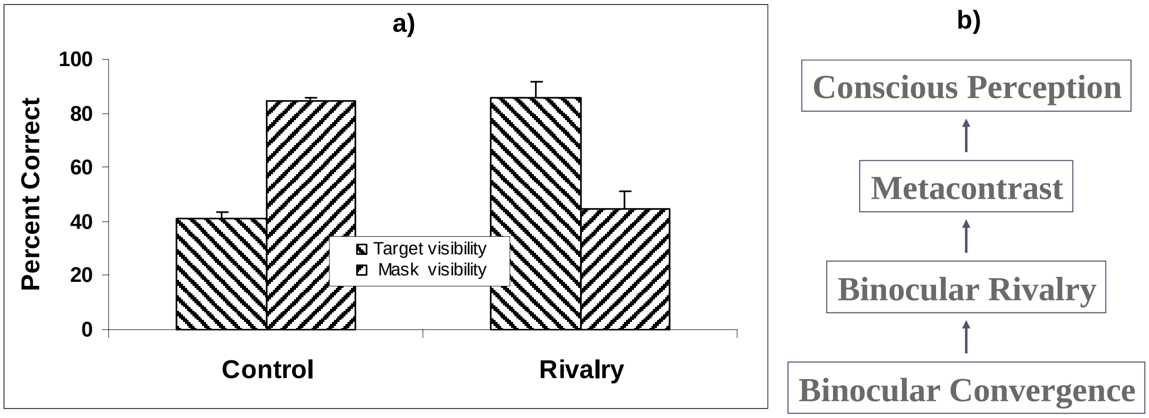


Fig. 2.4. a) The averaged percent correct of the target and the mask across observes in the control and rivalry conditions. The error bars correspond to 1 SEM. b) Functional hierarchy of unconscious metacontrast, binocular rivalry and binocular convergence processes in the brain before the conscious registration.

2.3. Experiment 2 – Target Recovery during Metacontrast Masking in Different Viewing Conditions

We can learn more about the underlying mechanisms of masking and its neural locus by changing the viewing conditions of the target and the mask stimuli. Previously, it was shown that a target stimulus presented to one eye can be masked by a mask stimulus to the other eye (dichoptic view) which suggests that metacontrast masking is a cortical process occurring after binocular convergence (Breitmeyer, 1984; Kolers, 1960; Schiller, 1965; Schiller & Smith, 1968). However, masking by light, which generates monotonic type-A masking functions, occurs in monoptic presentation (both stimuli presented to one eye only), therefore it was claimed that the most likely neural substrate for masking by light is sub-cortical or retinal (Breitmeyer, 1984; Schiller, 1965; Turvey

1973) and therefore the mechanisms and the locus during the metacontrast and type-A masking are different. It has been previously reported that not a significant target recovery is observed during type-A masking when M2 is presented dichoptically, i.e. when T and M1 are presented to one eye and M2 to the other eye (Robinson, 1968). This finding suggests that target recovery during type-A masking occurs because of the interaction of M2 with T-M1 sequence before binocular convergence at early levels. However since we already know that type-A masking itself occurs at early levels of processing, we can not discriminate whether type-A masking or target recovery in type-A masking occurs first. But the timing of the stimuli, i.e. the presentation of M2 followed by T-M1 sequence to obtain target recovery in type-A masking suggests that target recovery might be after type-A masking. To our knowledge, no study has yet tested target recovery during metacontrast masking in different viewing conditions. It was first reported by Breitmeyer et al. (1981) that the target recovery in metacontrast can be observed when M2 precedes M1 and strongly when it precedes both T-M1 sequence unlike the case that M2 follows T-M1 sequence to obtain recovery in type-A masking. This finding suggests that target recovery in metacontrast can occur before metacontrast masking even maybe before binocular convergence. Therefore it is reasonable to say that target recovery in metacontrast and type-A masking may occur because of different mechanisms as well as do metacontrast and type-A masking themselves. In chapter 1, we mentioned that target recovery in metacontrast can actually be called disinhibition as explained by the dual channel RECOD model because M2’s sustained response inhibits the transient response of M1 which in turn fails to suppress the sustained response of the target leading to a more visible target stimulus compared to the condition that it is masked by M1 alone. The aim of this experiment is to see whether we observe target recovery in metacontrast especially when M2 is presented to one eye and T-M1 to the other eye. As we discussed above, our prediction is that target recovery would occur if M2 is presented to the same eye with M1. We used the same three observers as in Experiment 1. A total of 72 trials were collected from each observer.

2.3.1. Observers, Apparatus, Stimuli and Procedure

We used the same stimuli and the apparatus as in Experiment 1. The exception was that no gratings or fixation bars were used since we do not use binocular rivalry paradigm. In this experiment, we changed the viewing of one stimulus while keeping the viewings of the other two stimuli fixed. We presented T-M1 to one eye to obtain monoptic masking as the control condition and presented M2 to the same eye (monoptic view) in the first condition and to the other eye (dichoptic view) in the second condition. In all cases, the stimulus onset asynchrony (SOA) between the target and the mask was set to an optimum value of 40 ms so as to provide minimum visibility of the target and the SOA between M1 and M2 was set to an optimum value of -80 ms so as to obtain maximum target recovery. The target shapes were identical as in Experiment 1 but we used a full ring stimulus for M1. M2, however, was like M1 used in Experiment 1. The inner and outer diameters of M2 were 0.35^o and 0.45^o, respectively.

2.3.2. Results

The percent of correct responses for identifying the target stimulus are shown in Fig. 2.5. As expected, prominent masking on the target was observed in the control condition when T and M1 were presented to one eye (monoptic view). The percentage correct during monoptic masking was 34%. The visibility of the target recovered significantly to 75% when M2 is presented to the same eye with T and M1 ($F_{1,2}$=63.879, p=0.015). However, when M2 to is presented to the other eye, target visibility was recovered only 6% from 34% which was not statistically significant ($F_{1,2}$=1.271, p=0.377). These results support the hypothesis that target recovery is caused because of the disinhibition of M1 response at early levels of information processing before binocular convergence.

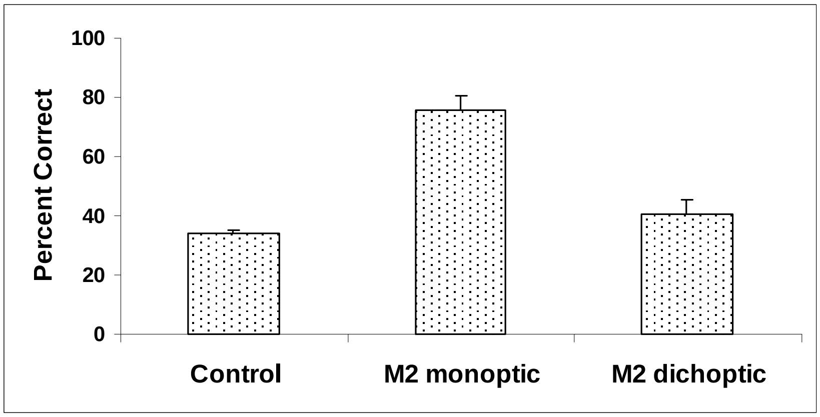


Fig. 2.5. The averaged percent correct of the target across observes in the control condition when T-M1 is presented to one eye (monoptic masking) and in the other conditions when an additional M2 is presented to the same eye with T-M1 sequence (M2 monoptic) and to the other eye (M2 dichoptic). The error bars correspond to 1 SEM.

2.4. Summary and Discussion

In this chapter, we used binocular rivalry paradigm along with metacontrast masking in order to further understand the underlying mechanisms of conscious registration. This is the first study, to our knowledge, that has shown that metacontrast masking occurs after binocular rivalry. Although many physiological studies have been carried out to locate the neural substrates of masking and binocular rivalry, there is no consensus yet about the mechanisms of masking or binocular rivalry and their neural loci. From this respect the results of this study could help the researchers to design experiments using both binocular rivalry and metacontrast in order find correlates of visual awareness in the brain. Our results may also suggest the view that metacontrast occurs at a very late stage of visual information processing in the higher visual areas of the brain in line with the studies that attention can modulate masking (e.g., Ramachandran & Cobb, 1995; Tata, 2002) since operation of attention on visual information processing takes place especially at higher visual areas. Like we did in this study, relationships between masking and phenomena of crowding or rapid serial visual presentation (RSVP) can be established and visual awareness can be studied considering many phenomena leading to awareness of stimuli (Kim & Blake, 2005). During “crowding” a stimulus can not be easily detected in presence of nearby stimuli, which otherwise clearly visible. This phenomenon, like masking, is observed especially in the periphery. During RSVP, a target stimulus can be identified easily but the two stimuli cannot be identified if they are presented in around a 300 ms window (Weichselgartner & Sperling, 1987). Competition between the nearby stimuli has been proposed to explain

RSVP and has been suggested that metacontrast could be due to a competition between the mask and the target at objection level of information processing (Keysers & Perret, 2002). In line with this view, since our results show that metacontrast is after binocular rivalry, it can be interpreted that masking occurs after the target and mask are identified as objects in the higher visual areas.

Our results here could also be explained by the dual channel RECOD model of masking. When the visibility of the mask is rendered invisible during binocular rivalry, not only the sustained response of the mask associated with its visibility but also its transient response could be reduced, both of which then cannot inhibit the sustained response of the target. Disinhibition studies in metacontrast, however, show a double dissociation between the visibility and the masking effectiveness of the mask (Ogmen et al., 2004). When the visibility of the mask is reduced, it can still mask the visibility of the target unlike the results that we found in this study by the binocular rivalry paradigm. Under the framework of the RECOD model, it can be suggested that binocular rivalry occurs as early as in V1 supported by the study of Tong and Engel (2001) where the transient and sustained responses of a stimulus can clearly be observed so that both of these responses are inhibited during binocular rivalry. Therefore, since dominantly the transient response of the mask is reduced during target recovery at an optimum SOA in metacontrast according to the RECOD model, our results from binocular rivalry experiment may support the view that disinhibition mechanisms occur before binocular rivalry. In fact, we have shown in the second experiment that target recovery occurs when the secondary mask (M2) is presented to the same eye with T-M1 but target recovery is not observed when it is presented to the other eye. This finding suggests the view that disinhibition in metacontrast occurs at early areas of the brain before binocular convergence. Therefore sustained-on-transient inhibitory mechanism that causes masking can be cortical and sustained-on-transient mechanism that causes disinhibition can occur at early areas. RECOD model, which implements inter-channel inhibitory mechanisms at the lumped post-retinal areas, can be improved to account our findings. Taken together, our results suggest the following order from bottom to top in the functional hierarchy of unconscious processes: disinhibition in metacontrast, binocular convergence, binocular rivalry, metacontrast, conscious registration.

A recent view of visual awareness suggests that the visibility of a stimulus occurs after its information is processed back and forth between lower and higher visual areas of the brain and that the feedback signal during processing of the mask inhibits or overtakes the target signal (Di Lollo et al., 2000; Lamme et al., 2002). Our results employing binocular rivalry paradigm may support this view such that during binocular rivalry early feedforward processing of the mask is interrupted and the mask information could not be processed by higher areas of the brain and therefore could not impair the visibility of the target by its feedback signals. However, it is very difficult to support this view based on the disinhibition results we have. Because disinhibition in metacontrast takes place before binocular rivalry and metacontrast masking, then target recovery cannot be due to interruption of feedback signals of M1 causing masking, as the interruption should occur at a late stage after binocular convergence according to this view. Findings about the disinhibition phenomena challenge the models of masking other than the dual channel RECOD model and can be further studied with other paradigms in order to understand better the conscious registration.

Chapter 3

Electrophysiological Correlates of Visibility in Visual Masking

Visibility of a briefly presented stimulus (target) can be reduced in presence of a secondary stimulus (mask), a phenomenon known as visual masking. Electrophysiological correlates of visibility in masking are investigated by varying the onset asynchrony (SOA) between the target and the mask, both of which were presented to two visual fields of the observers. When a target in one visual field had a small gap at its center (CTR), its visibility was kept constant at around 100% at all SOAs. In the other condition the gap was at the lower or upper part of the target (DU) and its visibility was changed by varying the SOA. Visual evoked potential (VEP) responses were computed as a lateral difference between contralateral and ipsilateral VEPs with respect to the visual field that the gap stimulus was presented. Significant correlations were found between the perceived visibility of the stimulus and its VEP response in both CTR and DU conditions. Results suggest that visibility of a stimulus can be associated with the parietal EEG activity 200 ms after its presentation.

3.1. Introduction

Visual masking refers to the reduction in visibility of a stimulus, called the target, by another visual stimulus, called the mask (Breitmeyer, 1984). When the mask stimulus follows in time the target stimulus, it is called backward masking; and when the mask is followed by the target it is called forward masking. Stimulus configurations where the target and mask stimuli do not overlap spatially correspond to specific cases of backward and forward masking, called metacontrast and paracontrast masking, respectively. The plot of target visibility as a function of the stimulus onset asynchrony (SOA) between the target and the mask is called the masking function.

Both as a paradigm and as a research topic, masking has a long history of contributions to our understanding of spatio-temporal properties of visual perception (rev. Bachmann, 1994; Breitmeyer, 1984). However, neural correlates of masking remain largely unknown (rev. Breitmeyer & Ogmen, 2000). Metacontrast can be observed with dichoptic stimulus presentation, indicating that it involves cortical mechanisms (Kolers, 1960; Schiller, 1965; Schiller & Smith, 1968). The goal of our study was to investigate electrophysiological correlates of masking using cortically evoked visual potentials (VEPs).

Schiller and Chorover (1966) investigated whether the brightness reduction observed in metacontrast has correlates in VEPs. They used a disk and a non-overlapping ring as target and mask, respectively. In a first experiment, they presented the target in isolation and recorded VEPs for four different luminance values of the target. These recordings showed a decrease in the amplitude and an increase in the latency of VEPs, as the intensity of the target decreased. The VEP responses obtained when the target and mask were presented together at various SOAs, however, did not show analogous amplitude and latency changes to account for the reduced *perceived* brightness of the target under masking conditions. Consequently, they concluded that the amplitude and the latency of the VEP correlate with the physical stimulus intensity but not with its perceived brightness. Furthermore, they also pointed out that because of the nonlinearity of brain signals, a VEP in response to a paired-stimulus is not equal to the summation of VEPs in response to isolated presentations of target and mask.

However, in a subsequent study, Vaughan and Silverstein (1968) showed that the lack of correlation between perceived brightness and VEP in Schiller and Chorover’s (1966) study could be accounted for a stray-light artifact. Vaughan and Silverstein (1968) demonstrated a correlation between perceived brightness and the VEP under experimental conditions that eliminated this artifact. In particular, they found that the amplitude of the VEP component at a latency of 200 ms with respect to the target was reduced at SOA values where strong masking occurs. To quantify this effect, they computed the area under the VEP function for a time interval ranging from approximately 160 ms to 260 ms. The computed area was then superimposed on the masking functions of the two observers. Their results showed a high correlation between VEP recordings and the associated metacontrast masking functions. Other studies employing patterns as target and non-overlapping mask also found that backward masking causes a decrease in the amplitude and the area of late VEP components (Andreassi et al., 1976; Andreassi, 1984; Bridgeman, 1988).

One shortcoming of these studies is that the VEP measured during metacontrast represents the combined response to the target and the mask stimuli. As pointed out above, Schiller and Chorover showed that the knowledge of isolated target and mask responses is not sufficient to deduce the VEP response to the target under masking conditions. A similar conclusion was reached by Kaitz et al. (1985) in the case of paracontrast. In other words, because the VEP response generated by the target temporally overlaps with the VEP response generated by the mask, it becomes difficult to identify directly the VEP correlates of target visibility in metacontrast.

In order to overcome this problem, we adopted the “contralateral-ipsilateral” approach in EEG. As shown in Fig. 3.1a, the target-mask pair was presented simultaneously at the left and right visual fields. In each trial, one of the target disks, left or right, was randomly selected and a small gap was inserted in one of three positions inside the disk (to the top, the center, or the bottom of the disk). The target at the other visual field did not have any gap. The observers’ task was to identify at which visual field the gap was presented (2AFC: left, right). Thus, with the exception of this gap, the stimuli on the left and right visual fields were identical. The stimulus presented to the left visual field projects to the right hemisphere and vice versa. Consequently, the VEP signal recorded at the side contralateral to the target contains responses to the target, mask, and the neural signal that reflect the location of the gap. The VEP signal recorded at the side ipsilateral to the target contains responses to the target and the mask but not the gap information. Thus, the comparison of ipsilateral and contralateral VEPs reveals directly the task relevant information, i.e., visibility of the target’s figural details.

This contralateral-ipsilateral approach has been recently applied to masking studies (Jaskowski et al., 2002; Woodman and Luck, 2003). Jaskowski et al. (2002) studied the priming effect of the target on the mask and asked the observers to respond to the mask. Only two SOA values were used. Woodman and Luck (2003) used the common-onset paradigm (Enns & Di Lollo, 1997), where the onsets of the target and the mask are simultaneous (i.e., SOA=0ms), and the mask stimulus terminates either simultaneously (co-termination) or with an additional delay (delayed offset) with respect to the target. Woodman and Luck (2003) compared VEPs to behavioral performance for only two cases, co-termination and one value of delayed-offset. Two-point correlations do not provide a strong test, for they analyze the direction of change but not its pattern. Our goal in this study was to carry out a more extensive correlation study by using several SOA values. In addition, we have also included negative SOAs to investigate jointly paracontrast and metacontrast effects.

3.2. Experiment 1 – Electrophysiological Correlates of Visibility in Visual Masking

3.2.1. Methods

3.2.1.1. Observers

A total of four observers (three of whom were naïve to the purpose of the experiment) participated. All subjects had normal or corrected-to-normal vision.

3.2.1.2. Apparatus and Stimuli

Visual stimuli were generated via the visual stimulus generator (VSG) card manufactured by Cambridge Systems (http://www.crsltd.com). This card was programmed by using its driver library and the stimuli were displayed on a 24’’ high-resolution color monitor with a 160 Hz frame rate. In a typical display, the stimuli were displayed on a uniform gray background. A chin rest was used to aid the observer to keep his/her head still while fixating his/her eyes on the fixation cross displayed in the center of the monitor. The room was illuminated with a dim light. The distance between the monitor and the observer was set to 97 cm. Target and mask stimuli were presented at variable SOAs. Behavioral responses were recorded via a joystick connected to the computer, which drives the VSG card. An electroencephalography (EEG) machine manufactured by Biosemi was used (http://www.biosemi.com).

We presented targets simultaneously to both visual fields of the observers and as well as the masks but with an SOA (Fig. 3.1a). One of the targets had a gap localized either in the up, down or centre part of it (Fig. 3.1b). We expect to get almost no masking when the gap appears in the centre (CTR) for all SOA values but in the other condition (DU), we expect the visibility of the gap to change differentially at different SOA values. The rationale behind this expectation is because masking increases when the distance between the contours of the target and the mask become closer (Breitmeyer, 1984). The mask was designed to avoid feature inheritance (Herzog & Koch, 2001; Stewart & Purcell, 1970; Werner, 1935; Wilson & Johnson, 1985), i.e. to avoid observing the gap on the mask. The stimuli were presented at an eccentricity of 6 deg. Background luminance was 5 cdm^{-2}. The luminance of the target and the mask were 50 cdm^{-2} throughout the experiment. The inner and outer diameters of the mask were 1.7^o and 2.55^o, respectively. The target was spatially adjacent to the mask having a diameter of 1.5^o. The duration of the target and the mask stimuli were 12.5 and 25 ms, respectively. The gap was a 0.2^{o} by 0.2^{o} square.

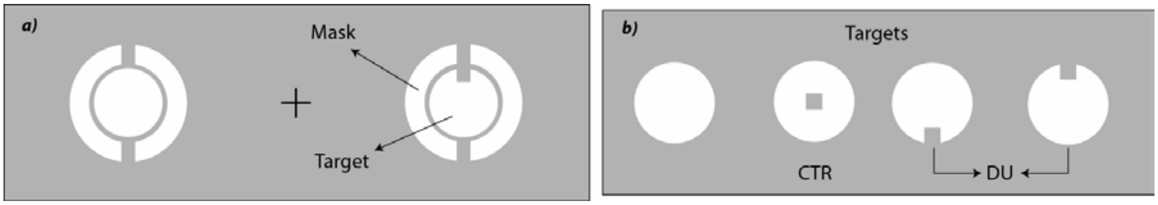


Fig. 3.1. a) Targets (disk stimuli) and masks (non-overlapping ring stimuli) appear on both sides at different SOAs. In this trial the gap appears on the upper part of one of the targets, therefore this trial represents DU condition. b) Shapes of target stimuli. While on one side the full disk appears as a target, on the other side the target has a gap either in the center part of it (CTR), or in the lower/upper part of it (DU).

3.2.1.3. Procedure

A block of trials started after an adaptation period in a dimly lit room. There were no audio signals throughout the recording. Observers were asked to reduce blinking their eyes and to maintain a stable posture as much as possible in a block of trials. The task of the observer was to press one of the two determined buttons of the joystick by their right hand thumb finger indicating the visual field that the gap was observed. This response requirement provided the observer to maintain his/her vigilant state and to avoid getting drowsy. The next trial started 1.5 sec after the response of the observer. There were 240 trials in a block of trials. The number of trials in each block was balanced across the conditions of gap location on the target (CTR vs. DU) and the side of the presentations of the gap. Seven SOAs ranging from -63 ms to 125 ms were used and they were randomly chosen for each block. The SOA value was fixed in a block. There were brief resting periods between blocks.

3.2.1.4. Data Recording and Analysis

EEG signals were recorded continuously with Ag/AgCI electrodes from 14 standard locations (Fp1, Fp2, F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, O1, Oz, O2) according to the international 10-20 electrode system and from two mastoids. Electrodes were mounted in a nylon cap and a conducting gel was applied to the surface of the skin where the electrodes were placed. Electrode impedances were kept less than 25 kΩ and they were monitored during the experiment for reliable recording. Brain signals were amplified by Biosemi Active-Two amplifiers and sampled at 512 Hz.

For processing the EEG data, a free MATLAB toolbox (EEGLAB) developed by the researchers at the Salk Institute was used (Delorme & Makeig, 2004). This toolbox provides an interactive GUI interface to load and process the EEG data. Custom scripts were written to visualize and process the EEG data by using the functions provided by the EEGLAB. Continuous EEG recordings were filtered by a high-pass filter having a cut-off frequency of 1Hz to remove linear trends. We used “eegfilt” function in EEGLAB for filtering signals to perform a zero phase digital filtering. After high-pass filtering, we divided the file into two by extracting the trials for the CTR and DU conditions. The baseline value computed from the 200 ms duration before the onset of the target was removed for each epoch. All channels were then subtracted by the reference channel average of mastoids. Independent component analysis (ICA) was then applied to these files. Artifact rejection was done by removing the eye blink artifact component because it is automatic, convenient and allows us to use all the single trials for averaging. In order to see differential effects between two hemispheres on EEG signals, recordings from P3/P4, O1/O2, C3/C4 and F3/F4 channels were used to plot contralateral and ipsilateral VEPs with respect to side of the presentation of the gap. (See Appendix-A for details in EEG data analysis).

3.2.2. Results

The percentage of correct values and response times were averaged across observers and plotted as a function of SOA for CTR and DU conditions (Fig. 3.2). As expected, performance was very close to 100% in the CTR condition at all SOAs which provides a baseline value. Averaged target-only performance was 96% in the DU condition and decreased down to 72% at SOA=25 ms. Thereafter performance increased and produced a U-shaped masking function. We also observed a small paracontrast masking effect at SOA=-63 ms. Although the main task of the observer was to respond as accurately as possible without any time constraint, we also recorded response times. As shown in Fig. 3.2, response times were higher in the DU condition especially during positive SOAs.

We applied repeated measures ANOVA test for statistical analysis. When the sphericity assumption was not met, the Huyn-Feldt correction was applied and the epsilon value is indicated in the results. In a 2 x 8 (condition x SOA) design, the main effect of the condition, CTR vs. DU, was found significant ($F_{1,3}$=12.302, p=0.039) indicating the difference in performance across different SOAs. The main effect of the SOA in the CTR condition was insignificant ($F_{7,21}$=0.701, p=0.533, ε=0.287) suggesting that change of

SOA did not change performance in this condition. Conversely, the main effect of SOA was significant in the DU condition ($F_{7,21}$=547.201, p=0.01, ε=0.498) and a quadratic contrast across SOAs was observed suggesting the U-shaped function when all seven SOAs and the target-only case were included ($F_{1,3}$=17.552, p=0.025). Although, by visual inspection response times are higher in the DU condition, the main effect of the condition (CTR vs. DU) ($F_{1,3}$=7.803, p=0.068) as well as main effect of SOA in both CTR and DU conditions was not found significant ($F_{7,21}$=0.625, p=0.726, ε=0.970; $F_{7,21}$=1.481, p=0.241, ε=0.845). However, significant negative correlation coefficients between averaged accuracy and averaged mean RT across observers were observed suggesting the inverse relationship between the response time and the difficulty of the task. The correlation coefficients in the CTR and DU conditions were -0.71 and -0.89, respectively (t=2.47, p=0.02; t=4.73, p=0.002; one-tail t-test, df=6) (See Appendix-A for statistical analysis).

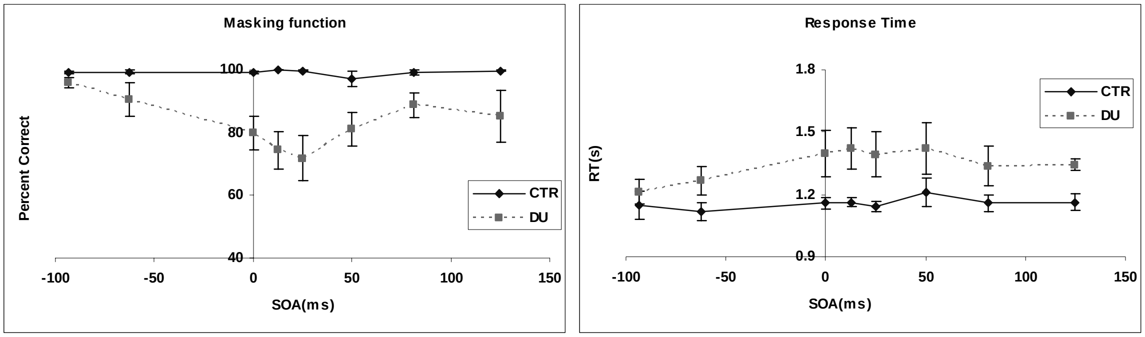


Fig. 3.2. The averaged masking functions (left panel) and response times (right panel) across observers for CTR and DU conditions. The error bars correspond to ±1 SEM. The shortest SOA (-94 ms) represents target-only presentation.

We analyzed contralateral and ipsilateral VEPs with respect to the side of the gap that was presented. An illustrative plot obtained from P3/P4 channels is shown in Fig. 3.3. The VEP plots from all SOAs and observers can be found in Appendix-A. According to our hypothesis, the differences between the contralateral and ipsilateral VEPs reflect the degree of the visibility of the gap stimulus. As shown in Fig. 3.3, performance during target-only presentation is 96% and the differences between contralateral and ipsilateral VEPs 200 ms after the onset of the target is greater than that of the case that when the performance is 74% at SOA=13 ms. In this study, we compute the mean value of the absolute differences between contralateral and ipsilateral VEPs from a time interval for each SOA and observer in order to correlate with the masking functions. Averaged VEP responses across observers from the [200-400] and [130-320] ms time range is shown in Fig. 3.4. As can be seen from this figure, VEP responses in the DU condition produced a U-shaped function similar to the averaged masking function. VEP responses in the CTR condition was higher almost at all SOAs and shows a more linear trend compared to the DU condition, which is similar to the visibility function obtained in the CTR condition. Especially the differences between the contralateral and ipsilateral VEPs are higher at parietal P3/P4 channels. However it is noteworthy that high correlations in the DU condition can be observed over the other areas which can be to some extent due to volume conduction.

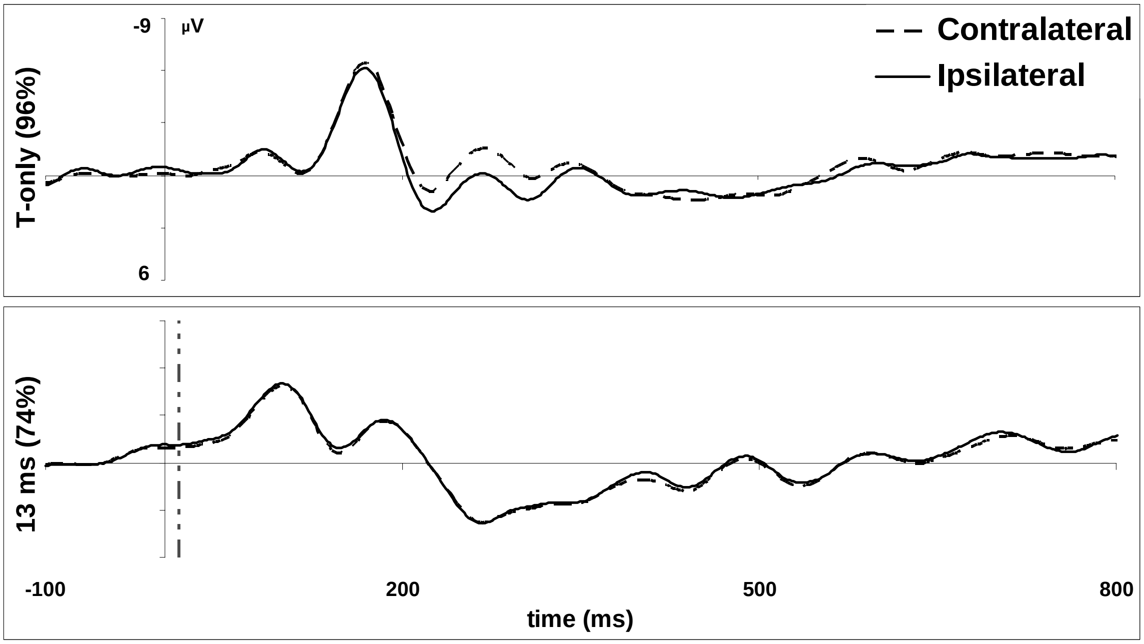
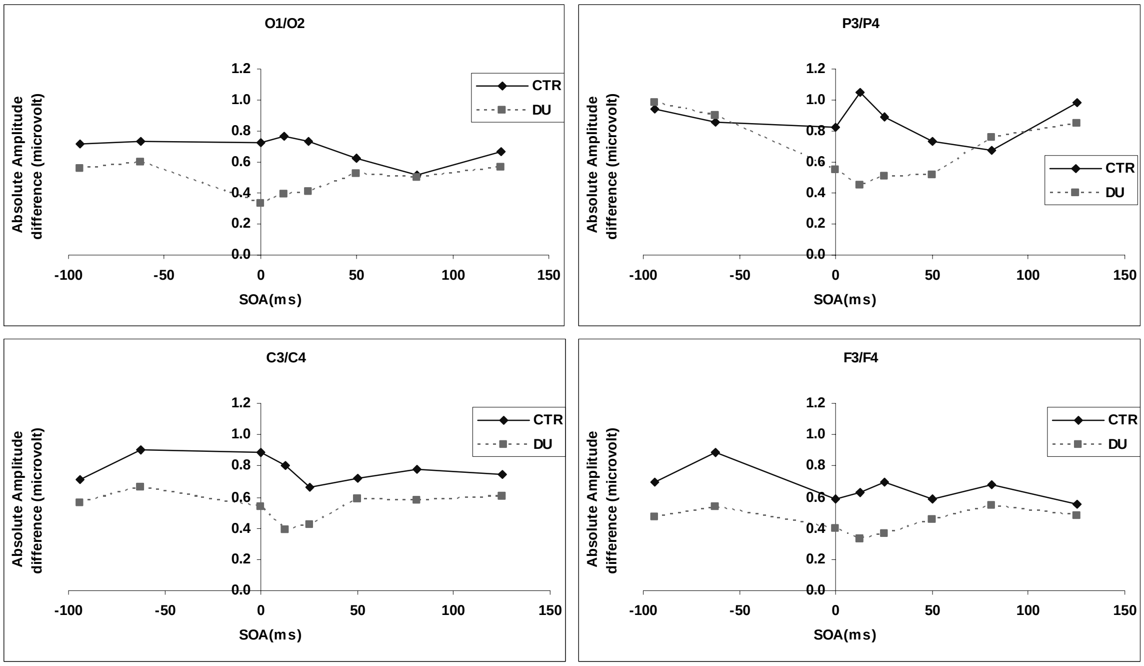


Fig. 3.3. Contralateral vs. ipsilateral VEPs averaged across observers to illustrate the effect of masking on VEPs. In each subplot, contralateral (dashed) and ipsilateral (continuous) VEPs obtained from either P3 or P4 channels are superimposed and plotted in the range [-100, 800] ms with respect to the onset of the target. Note the negativity is upward. The label in the y-axis indicates the stimulus configuration in that particular recording, for example, T-only indicates that only the target stimulus was used in the experiment. Similarly, the number outside the parenthesis in the y-axis indicates the SOA value in ms. The numbers in the parentheses show the percentage correct values averaged across observers. VEP waveforms were low-pass filtered by a Gaussian window function (SD=6 ms, 50% amplitude cutoff at 35 Hz).

VEP Response [200-400]ms



VEP Response [130-320]ms

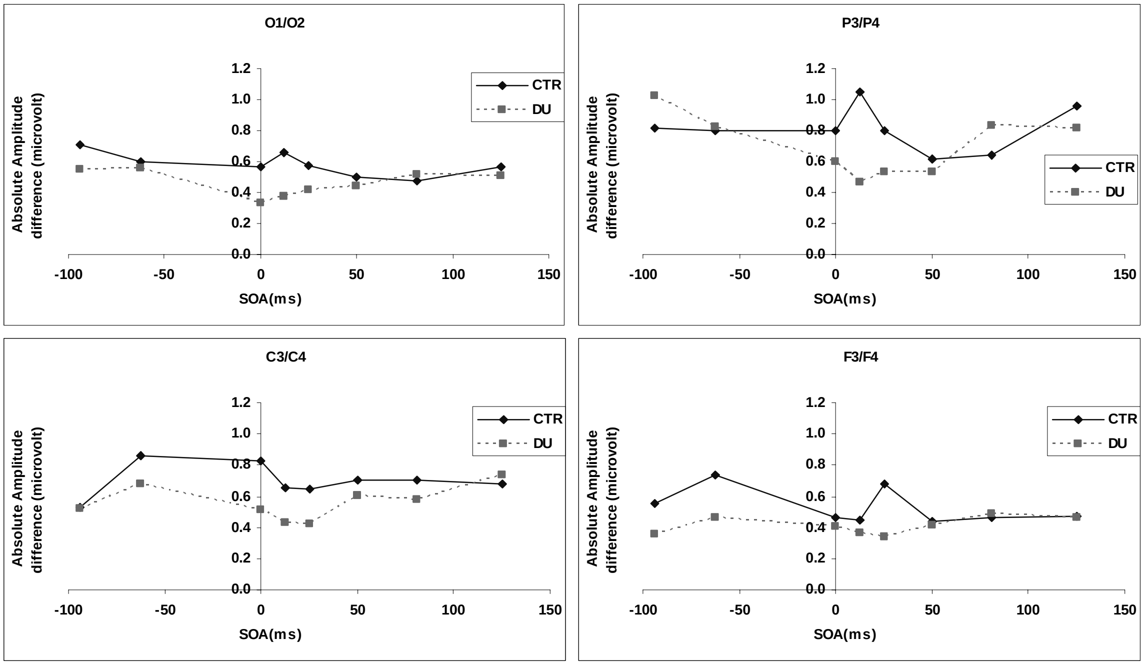


Fig. 3.4. Averaged VEP responses across observers obtained from four O1/O2, P3/P4, C3/C4, F3/F4 channel combinations and from two time intervals: [200-400] ms (upper panel), [130-320] ms (lower panel).

We statistically analyzed the VEP responses obtained from channels P3/P4 in the [200-400] ms time interval like we did for the psychophysical results above. The main effect of the condition, CTR vs. DU, was found significant ($F_{1,3}$=15.230, p=0.030) indicating the difference in performance across different SOAs between CTR and DU conditions. The main effect of the SOA in the CTR condition was insignificant ($F_{7,21}$=0.629, p=0.605, ε=0.398). Conversely, the main effect of SOA was significant in the DU condition ($F_{7,21}$=4.040, p=0.006) and a quadratic contrast across SOAs was observed ($F_{1,3}$=10.489, p=0.048). Statistical results between behavioral and VEP responses show a very close resemblance.

We also computed VEP responses in nine different time intervals up to 400 ms and computed correlation coefficients between the averaged VEP and averaged psychophysical results (accuracy). The time intervals were 150-200, 200-250, 250-300, 300-350, 350-400, 200-300, 300-400 and 200-400 in ms after the onset of the target. We also included 130-320 ms time interval, because it has been reported that visual awareness is associated with a posterior negative amplitude in this time range (Koivista, Revonsou, & Lehtonen, 2005). We found significant positive correlations in CTR and DU conditions across different channels. Overall, averaged correlation coefficients were high in the DU condition at different time intervals and channels. Significant correlations in the CTR condition were found especially over parietal areas. When we carefully look at Fig. 3.5, we see that the sum of correlation coefficients obtained from the CTR and DU conditions is highest in the [200-400] ms and [130-320] ms time range after the onset of the target over P3/P4 channels. In order to better see the correlation at these time intervals from P3/P4 channels, VEP and psychophysical results are superimposed and plotted in Fig. 3.6.

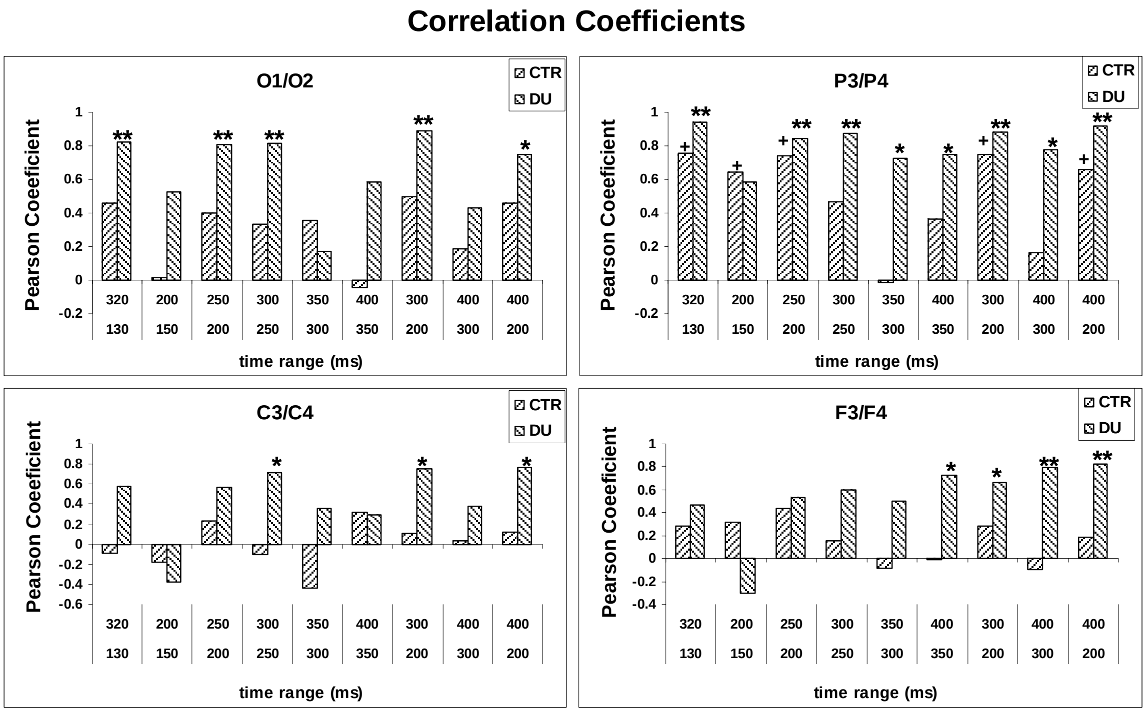


Fig. 3.5. Correlation coefficients between averaged accuracy and VEP responses across observers obtained from different time intervals and channel combinations for both CTR and DU conditions. The plus and asterisk signs indicate correlation coefficients significantly larger than zero for CTR and DU conditions, respectively: $^{+}p<0.05$, $^{*}p<0.05$, $^{**}p<0.01$ (one-tail t-test, df=6).

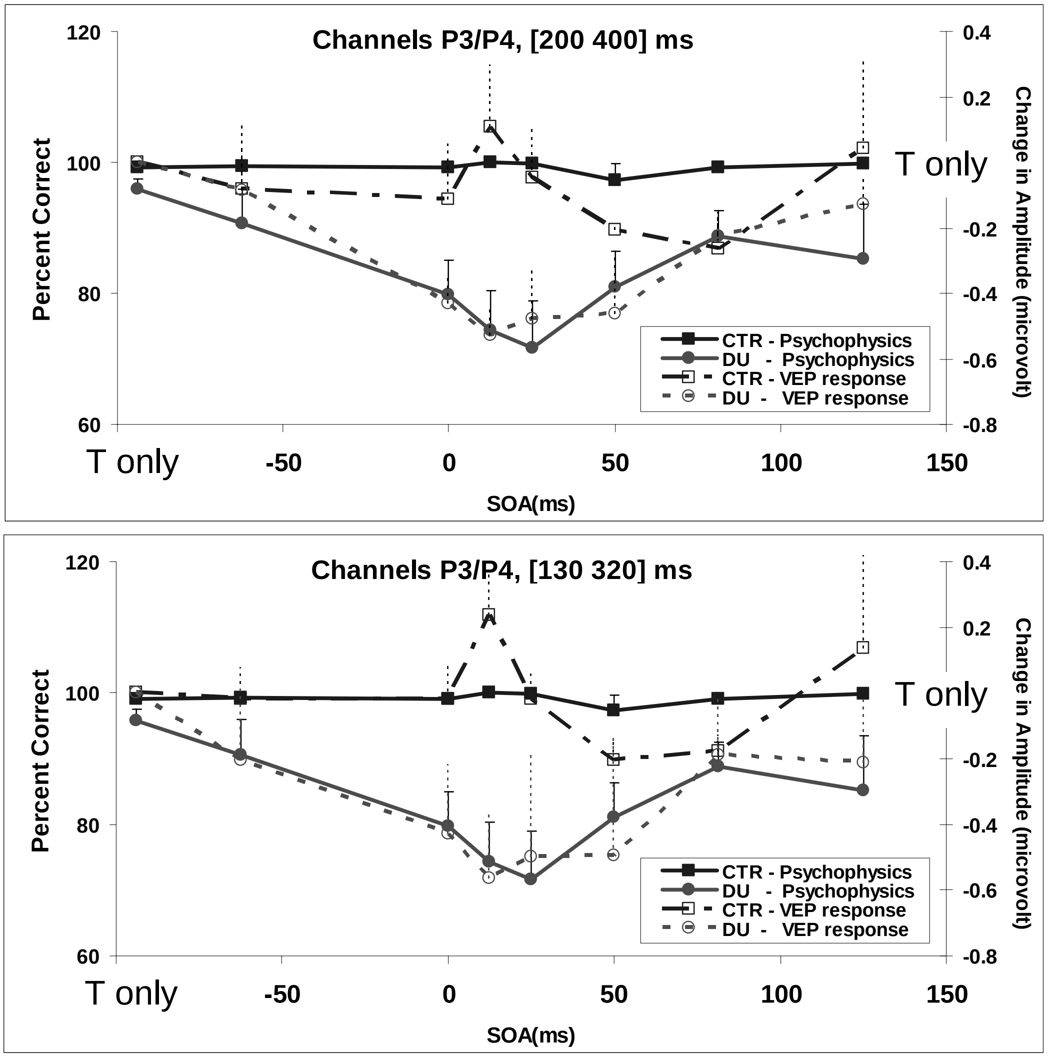


Fig. 3.6. Masking functions averaged across observers plotted as a function of SOA superimposed with VEP responses averaged across observers obtained from P3/P4 channels and in two time intervals: [200-400] ms (upper panel), [130-320] ms (lower panel). VEP responses in the CTR and DU conditions are subtracted from their target-only VEP response in order to make zero as the baseline corresponding to T-only presentations in both CTR (square) and DU (circle) conditions. Left y-axis shows percent correct for visibility functions (solid lines) and right y-axis shows the change in amplitude of VEP responses (dashed lines) from their respective baseline T-only values. The error bars correspond to +1 SEM.

3.3. Experiment 2 – Effectiveness of Sustained-on-Transient and Transient-on-Transient Inhibitory Mechanisms Assessed by a Reaction-Time Experiment Using Target Recovery Phenomenon in Metacontrast Masking

Paracontrast masking refers to the reduction in visibility of a stimulus, called the target, by another non-overlapping visual stimulus preceding the target, which is called the mask (M1). The dual-channel model of masking (Breitmeyer & Ganz, 1976; RECOD, Ogmen, 1993) proposes that interactions between transient and sustained responses generated by a paired stimulus cause increase of reaction times (RT) in response to the target during paracontrast mainly by suppressing the target's transient response (Ogmen et al., 2003). We investigated whether the suppression of the target's transient response is due to sustained or/and transient response of the mask. For this purpose, we used target recovery phenomenon (disinhibition), which refers to the recovery in visibility of the masked target in presence of a secondary mask stimulus (M2). By appropriately selecting the stimulus onset asyncrony (SOA) between M2 and M1, either the transient or the sustained response of M1 is suppressed.

Based on the results reported in Ogmen et al. (2003), sustained-on-transient (SonT) or transient-on-transient (TonT) or a combination of them might be effective in longer RTs during paracontrast. We can differentiate the contributions of the sustained and the transient channels on the transient response of the target (T) by using the disinhibition paradigm. The double dissociation between the masking effectiveness and the visibility of the primary masking stimulus (M1) suggests that masking effectiveness is a function of the transient response of M1 (assumption 2) and the visibility of M1 is a function of its sustained response (assumption 1) (Breitmeyer et al., 1981; Ogmen et al., 2004). Based on these assumptions, when the maximum target recovery is observed at SOA_Trecov as shown in Fig. 1.11, maximum inhibition on the transient response of M1 occurs (Fig. 3.7). Similarly, at SOA_M1msk, when the visibility of M1 is at its minimum, maximum inhibition on the sustained response of M1 occurs (Fig. 3.7).

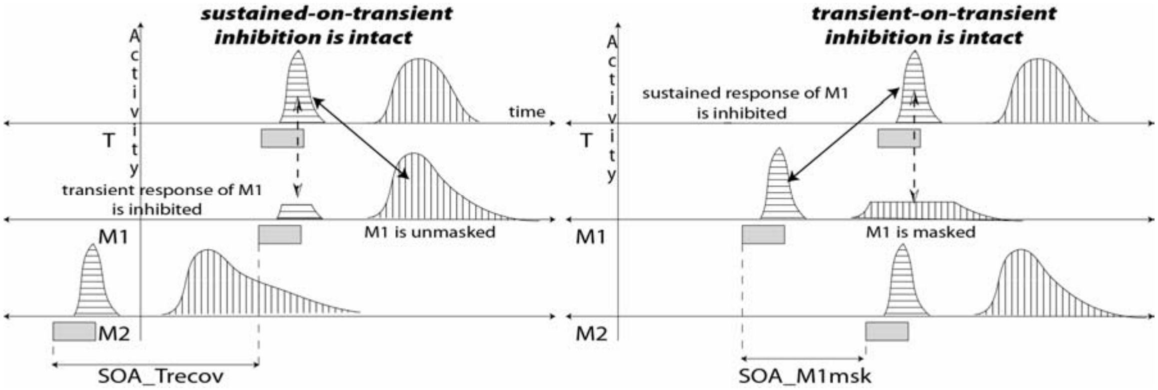


Fig. 3.7. At SOA_Trecov, transient response of M1 is inhibited but sustained-on-transient inhibition by M1 on T is intact (left panel). At SOA_M1msk, sustained response of M1 is inhibited but transient-on-transient inhibition is intact (right panel).

3.3.1. Methods

3.3.1.1. Observers

A total of six observers (four of whom were naïve to the purpose of the experiment) participated. All subjects had normal or corrected-to-normal vision.

3.3.1.2. Apparatus

The stimuli were displayed at a 75-Hz frame rate on a Sony Trinitron, 1024 x 768, color monitor. Stimulus presentation and response recording were controlled by a

Macintosch II-ci computer. RTs were recorded by a National Instruments NB-MIO-16 input/output board with an onboard AM9513 timer running at 1 kHz. At a viewing distance of 57 cm, the display screen was 35 deg x 27 deg. In a typical display, the stimuli were displayed on a uniform gray background. A head/chin rest was used to aid the observer to keep his/her head still while fixating his/her eyes on the fixation cross displayed in the center of the monitor. Behavioral responses were recorded via a keyboard connected to the computer, hosting the timer.

3.3.1.3. Stimuli

Reaction times were recorded using the methods in (Ogmen et al., 2003; Schiller & Smith, 1966). Target (T) could only appear on the left or right side of the fixation cross, but M1 and M2 appeared on both sides (Fig. 3.8). The task of the observer was to respond as fast and as accurately as possible by pressing either the left or right arrow key of the keyboard indicating the side where T appeared. By this task, we measure the localization performance of the observers. Stimuli configuration for this experiment is shown in Fig. 3.8. The stimuli were presented 1.6^{o} above fixation at an eccentricity of 2^{o}. Background luminance was 100 cdm^{-2}. The target was a 0.86^{o} disk. The target and the masks had contrasts of -100% (0 cdm^{-2}). Thickness of M1 and M2 were 0.8^{o}. Separations of T-M1 and M1-M2 were 2 min. The durations of the stimuli were 13.33 ms. SOA_Trecov and SOA_M1msk were -79 ms and 53 ms, respectively. SOAs between T and M1 ranged from -293 to -13 ms in multiples of 13.33 ms.

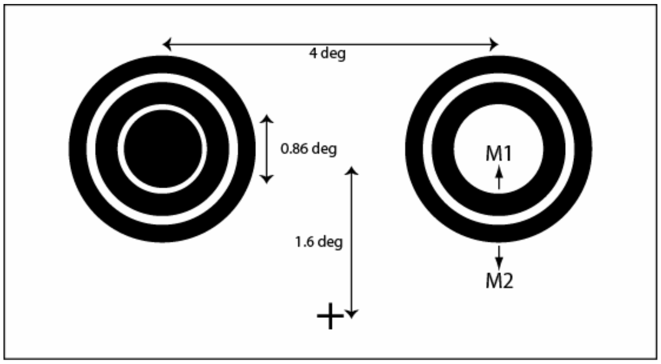


Fig. 3.8. Stimuli configuration for the RT experiment using disinhibition paradigm. Reaction times to the disk (target-T) were recorded.

3.3.1.4. Procedure

The SOA between the secondary mask (M2) and M1 was set to SOA_Trecov and SOA_M1msk in the first and second part of the experiment, respectively. The reaction time to T was recorded at negative SOA values between T and M1 starting from -240 ms to 0 ms. In the third part, we recorded RTs to the target but without presenting M2. By comparing the results from the first and the third part, we can test whether we can see a correlation between RT to the target and the visibility of M1 (Corollary 1). By comparing the results from the second and the third part, we can test whether we can see a correlation between RT to the target and the metacontrast masking of M1 (Corollary 2). The values of SOA_Trecov and SOA_M1msk were chosen based on the results reported in Ogmen et al. (2004).

In summary, this experiment consists of three parts. SOA_Trecov was chosen in the first part and SOA_M1msk in the second part. M2 was not presented in the third part and this part served as a control condition. Since both transient-on-transient (TonT) and sustained-on-transient (SonT) inhibitory mechanisms may be effective in the control part,

$RT_{control}$ can be expressed as the summation of each inhibitory mechanism's contribution to RTs as

$$RT_{control} = RT_{TonT} + RT_{SonT} + \text{constant}. \tag{3.1}$$

In the first part, by choosing the SOA between M2 and M1 as SOA_Trecov, we reduce TonT inhibition, thereby reducing RT_{TonT} to a small residual value $RT_{TonT}^{residual}$. Total reaction times in this condition can be expressed as

$$RT_{SOA\_Trecov} = RT_{TonT}^{residual} + RT_{SonT} + \text{constant}. \tag{3.2}$$

Similarly sustained response of M1 is inhibited by using SOA_M1msk in the second part, thereby reducing the RT_{SonT} to a small residual value $RT_{SonT}^{residual}$. Total reaction times in this condition can be expressed as

$$RT_{SOA\_M1msk} = RT_{TonT} + RT_{SonT}^{residual} + \text{constant}. \tag{3.3}$$

To test whether corollaries 1 or 2 hold, we compared ΔRTs obtained from the first and the control part and from the second and the control part, respectively. By roughly equating the residual RTs produced by SonT and TonT inhibitions to zero and assuming that the constant terms across conditions are equal, we can express ΔRTs in two conditions. In the first condition, ΔRTs that we calculate would estimate RTs due to TonT inhibition. Let

$$\Delta RT_1 = RT_{control} - RT_{SOA\_Trecov}. \tag{3.4}$$

From Equations (3.1) and (3.2),

$$\Delta RT_1 = RT_{TonT} - RT_{TonT}^{residual}. \tag{3.5}$$

With the assumption that

$$RT_{TonT}^{residual} \cong 0, \tag{3.6}$$

one obtains

$$\Delta \mathrm{RT}_1 \cong \mathrm{RT}_{\mathrm{TonT}}. \tag{3.7}$$

In the second condition, ΔRTs that we calculate would estimate RTs due to SonT inhibition. Similarly let

$$\Delta \mathrm{RT}_2 = \mathrm{RT}_{\mathrm{control}} - \mathrm{RT}_{\mathrm{SOA\_M1msk}}. \tag{3.8}$$

From Equations (3.1) and (3.3),

$$\Delta \mathrm{RT}_2 = \mathrm{RT}_{\mathrm{SonT}} - \mathrm{RT}_{\mathrm{SonT}}^{\mathrm{residual}}. \tag{3.9}$$

With the assumption that

$$\mathrm{RT}_{\mathrm{SonT}}^{\mathrm{residual}} \cong 0, \tag{3.10}$$

one obtains

$$\Delta \mathrm{RT}_2 \cong \mathrm{RT}_{\mathrm{SonT}}. \tag{3.11}$$

If both of the corollaries hold, we can say that both the transient and the sustained channels of M1 inhibit the transient response of T. We can understand which components contribute to the reaction time during paracontrast from this experiment by using the disinhibition paradigm.

Choice RTs were run in separate experimental sessions, each consisting of six blocks of trials. The order of the three possible conditions were randomized across blocks and counterbalanced across observers. Each of the blocks consisted of 200 trials with 20 trials devoted to each of the ten SOAs. The orders of SOAs and target locations were randomized within a block. Order of session was counterbalanced across observers. At the beginning of the sessions, 20 choice RTs in which only target was presented were measured. These choice RTs provided baseline data.

3.3.2. Results

The RTs averaged across observers in all conditions are plotted in Fig. 3.9 as a function of T-M1 SOA. The accuracy of the observers was higher than 97% for all observers. The trend of the increase in RTs when the SOA approaches 0 ms is similar in all the three conditions whether M2 is used or not, which agrees with the findings of Ogmen et al. (2003). The increase near SOA=0 is likely to be due to the interference effect of the rapid presentation of M1 and T as discussed previously in Ogmen et al. (2003) as well as in chapter 1. We used repeated measures ANOVA for statistical analysis. When the sphericity assumption was not met, the Huyn-Feldt correction was applied and the epsilon value is indicated in the results. Statistical analysis of the data in a 3 x 10 (mask-type x SOA) design shows that the main effect of SOA is significant ($F_{9,45}$=44.940, p<0.001, ε=0.389) which suggest that the performance decrease in RTs from the baseline value of 250 ms across SOAs is due to the introduced M1 and/or M2. The main effect of the mask-type condition is found insignificant ($F_{2,10}$=2.364, p=0.146, ε=0.982) which suggest that the overall shape of the RTs obtained from all SOAs does not change. However, as we assume that the individual effects of presenting M2 at two different M2-M1 SOAs should yield different results at two different SOA ranges, we subtracted RTs from the two conditions when M2 was presented from RTs obtained in the control condition.

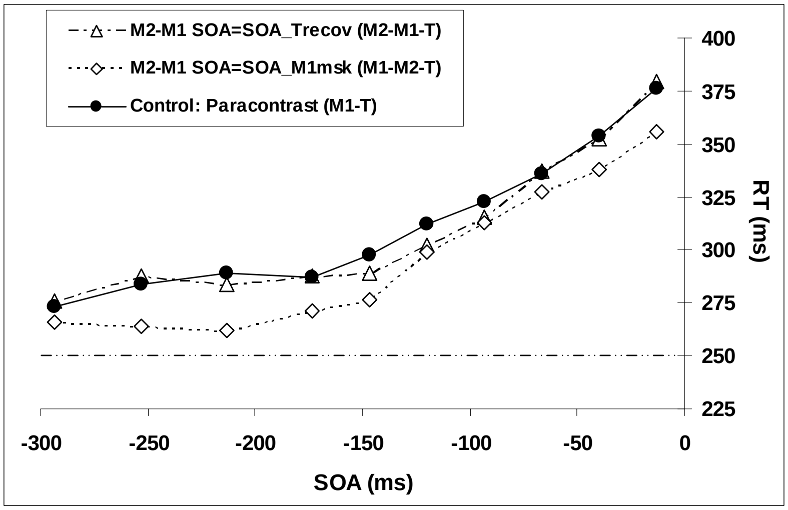


Fig. 3.9. Reaction-times (RTs) averaged across observers as a function of SOA between the primary mask (M1) and the target (T). Negative SOA represents that the target follows M1. Empty symbols correspond to the conditions when M2 precedes M1 by SOA_Trecov (triangle) and follows by SOA_M1msk (diamond). Filled circular symbols correspond to the control (paracontrast) condition where only the target and the primary mask are used. The horizontal dashed line shows the baseline RT obtained by presenting only the target.

The delta RTs averaged across observers are plotted in Fig. 3.10 as a function of T-M1 SOA. We see that ΔRT_1 reflecting TonT inhibition are noticeable in the range of SOA -150, -100 ms, while ΔRT_2 reflecting SonT inhibition has two peaks, one at SOAs around -213 ms and a second at SOAs around -40 ms. However, repeated measures ANOVA indicated that main effect of SOA was not significant for ΔRT_1 and ΔRT_2 ($F_{9,45}$=0.302, p=0.970; $F_{9,45}$=0.460, p=0.893). We tested whether the peak values are significantly greater than zero. For ΔRT_1, the peak value at SOA=-120 ms was not significant but the peak value in ΔRT_2 at SOA=-213 ms was found significant suggesting a sustained-on-transient inhibition at long SOAs as expected (p=0.233, p=0.026; one-tail t-test, df=5). Second peak at SOA -13 ms is also significant (p=0.003; one-tail t-test, df=5). However at SOAs -13 and -40 ms, only for ΔRT_2 condition where M1-M2 SOA=SOA_M1msk, M2 falls in between T and M1 temporally, which may produce an additional interference effect. When we look at the sum of ΔRT_1 and ΔRT_2, the overall shape agrees with the findings of Ogmen et al. (2003) by showing an increase of delta RTs during paracontrast masking.

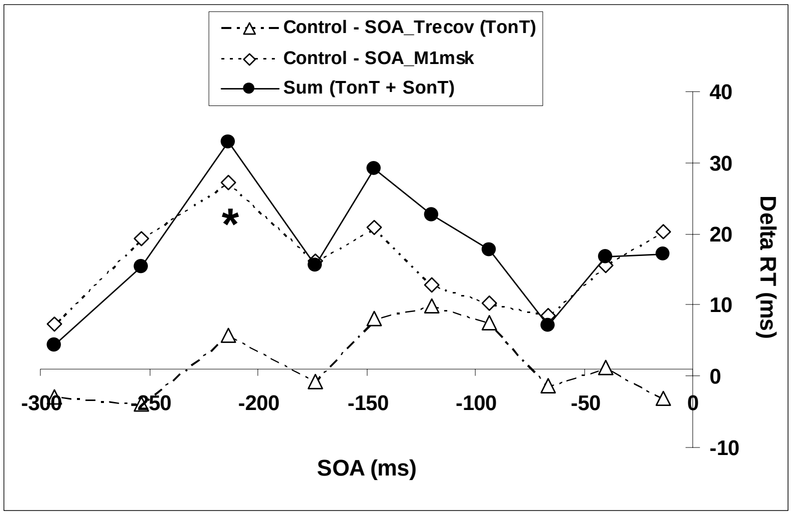


Fig. 3.10. Delta RTs computed from the data of Fig. 3.9, as a function of M1-T SOA. Empty symbols represent ΔRT_1 (triangle) and ΔRT_2 (diamond) reflecting transient-on-transient (TonT) and sustained-on-transient (SonT) inhibitory effect on RTs, respectively. For illustrative purposes, summation of ΔRT_1 and ΔRT_2 is shown as filled circular symbols which shows the inhibitory effect of both the sustained and transient response of M1 on RTs in response to the target. The asterisk sign indicates the peak value of ΔRT_2 being significantly larger than zero: *$p<0.05$ (one-tail t-test, df=5).

3.4. Summary and Discussion

In this study, we sought to determine electrophysiological correlates of visibility in masking. We presented target and mask stimuli to two sides of the visual field. We presented a small gap on one of the disk targets and we hypothesized that any difference between the contralateral and ipsilateral VEPs reflects the visibility of the gap stimulus. We used an objective two-alternative forced choice (2AFC) measurement of accuracy and collected behavioral responses during EEG recording. Besides using the target-only presentation, we used six positive SOAs for metacontrast masking and one negative SOA for paracontrast. Moreover, by changing the location of the gap on the disk target, we obtained two masking functions. In one of which (CTR condition), we did not observe any reduction in the visibility of the stimulus. In the other condition (DU), we obtained a masking function close to a U-shape.

We found significant correlations between the perceived visibility of a stimulus and its VEP response especially on parietal areas suggesting a possible neural substrate of masking. In fact a recent fMRI study showed that object recognition areas (late occipital cortex, LOC) are highly likely to be a neural substrate of masking (Green et al., 2005). We also found correlates of masking in the DU condition within the [200-400] ms time interval of the onset of the stimulus over occipital, central, and frontal channels. Response times in both CTR and DU conditions show a negative correlation with the accuracy. These results suggest that more brain areas are involved or modulated for a longer period of time when the visibility of the stimulus is reduced, which has also been supported by the previous studies (Haynes et al., 2005; Thompson & Schall, 1999; van Rullen & Koch, 2003).

The "contralateral-ipsilateral" approach that we employed in this study has been used especially in attention studies. It has been shown that EEG signals obtained from the contralateral side of the attended stimulus shows more negativity especially 200-250 ms after the onset of the stimulus on parietal areas compared to the ipsilateral EEG signals (Woodman & Luck, 1999). This relative negativity is called N2pc (N2-posterior-contralateral) component (Eimer, 1996; Luck & Hillyard, 1994).

Woodman and Luck (2003) investigated whether N2pc is observed during object-substitution masking (Enns & Di Lollo, 1997). They varied the offset asynchrony between the target and the four-dot mask. When they had common offsets (co-termination condition), visibility of the target was around 85% and as expected they observed N2pc. Even though visibility of the target was reduced to around 65% in the delayed-offset condition, the N2pc was not significantly different than the co-termination condition. When they used overlapping noise mask to obtain quantitatively the same target visibility as in the delayed-offset condition, they did not observe N2pc component. They also compared the VEPs obtained from the trials when the target is correctly identified or not in the delayed-offset condition. Although the contralateral-ipsilateral difference seems to be high in correct trials especially 400 ms onward of the target presentation as they also pointed out and attributed to a possible post-perceptual effect, the N2pc component did not differ statistically between correct and erroneous trials. Based on their findings, they concluded that attentional N2pc component can be evoked even when the visibility of the stimulus is reduced suggesting a degree of dissociation between awareness and attention.

However, Jaskowski et al. (2002) argued that N2pc can be a good correlate for visual awareness. They found that N2pc in response to the target was observed only when the visibility of the target was high with the longer SOA. Eimer and Mazza (2005) also suggested that N2pc can determine the visibility of a stimulus based on the results they found by employing change detection paradigm. In this study, we found that contralateral-ipsilateral differences in VEPs, which is similar to the N2pc component, can be a good correlate for the perceived visibility of a stimulus. Since the relation between attentional shift and N2pc component is well established in previous studies (Eimer, 1996; Luck & Hillyard, 1994), our findings may also be interpreted as showing a close relationship between awareness and attention.

A recent view about conscious perception is that conscious registration of a stimulus may occur by processing of visual information back and forth between the early retinotopic and higher brain areas with afferent and efferent connections (Rees, Kreiman & Koch, 2002). According to some of the models of metacontrast masking, processing of the target information is interrupted by the following mask (Breitmeyer & Ogmen, 2000) which is also supported by single cell studies on monkeys (e.g., Kovacs et al., 1995; Rolls et al., 1999). It remains unknown yet whether the target’s information is interrupted while it is processed in a feedforward or a feedback manner and also whether the processing of the mask’s information in a feedforward or feedback manner causes the inhibition. Lamme et al. (2002) showed that masking affects only late responses (after around 200 ms) of V1 cells when they become activated by the visual stimuli presented outside of their classical receptive fields (Lamme & Roelfsema, 2000). Thus they suggested that masking interrupts recurrent interactions between V1 and higher visual areas (Lamme et al., 2002). Our results agree with these cell studies such that we observe correlates of masking even over occipital areas within the 200 ms of the stimulus presentation. In contrast to Lamme et al. (2002), a recent fMRI study showed that visibility change during metacontrast masking correlates with the signals in the higher brain areas (such as fusiform gyrus [FS], posterior cingulated cortex [PCC], temporaparietal junction [TPJ], V5/MT) but not in the retinotopic areas (such as V1, V2, V3, V4) (Haynes, Driver, & Rees, 2005). However, they found that coupling between V1 and FG, i.e. the correlation coefficients between V1 and FG signals at different SOAs, correlate also with the U-shaped visibility function. They suggested that there is an effective connectivity between these two areas when the visibility of a stimulus increases. In line with the findings of aforementioned studies, we can suggest that conscious registration of a stimulus occurs at a late stage of information processing and modulates both lower and higher brain areas

Up to now, the following major findings in the masking literature can be explained quantitatively by the RECOD model: 1) Perceived visibility of a stimulus (i.e. U-shaped masking functions) during paracontrast and metacontrast (Ogmen et al., 2003), 2) RT in response to the target stimulus during paracontrast and metacontrast (Ogmen et al., 2003), 3) Target recovery in metacontrast (Ogmen et al., 2004). In this chapter, we further investigated the RT increase during paracontrast masking under the framework of the modified dual channel RECOD model. We used target recovery (disinhibition) phenomenon as a tool to investigate transient-on-transient and sustained-on-sustained inhibitory mechanisms on the RTs. Results suggest sustained-on-transient inhibition as the dominant mechanism in increase of RTs. This finding further supports the working hypothesis of the dual-channel model of masking (RECOD) as it has been reported that the model can explain the findings of masking and the target recovery (Ogmen et al., 2003, 2004).

Chapter 4

Temporal Dynamics of Peripheral Cueing Effects: Attention, Masking, and Priming

Visual cueing is a commonly used paradigm to study mechanisms and dynamics of attention. Peripheral cueing studies show that performance of observers rapidly improves as the duration between the cue and the search item (cue lead time, CLT) is increased. After reaching a peak value at around CLT=50 to100 ms, performance gradually decays to a lower plateau. This non-monotonic performance curve has been interpreted to support a two-component model for the deployment of attention: 1) An automatic, transient and 2) a voluntary, sustained component. In this study, we investigated the contributions of attention, masking, and priming in shaping the non-monotonic performance curve. We show that a specific combination of cue-type and post-stimulus mask is required to produce the non-monotonic performance curve. Furthermore, feature-based congruency between the cue and the search items can account for the transient enhancement of performance at CLTs of ca. 50-100 ms. Taken together, our results suggest that the deployment of attention is a monotonic process and that the transient enhancement of performance around CLTs of ca. 50-100 ms reflects a feature-based priming effect by the cue on the search item.

4.1. Introduction

Attention is a crucial mechanism that allows the visual system to deploy efficiently its processing resources according to ever-changing environmental needs. Cumulating evidence suggests that attention manifests itself in both spatial and temporal domains to produce a relative enhancement of targets of interest and/or suppression of distractor items (Carrasco et al., 2000; Dosher & Lu, 2000; Kastner & Ungerleider, 2000; Luck et al., 1997). Moreover, two broadly defined components of attention, exogenous and endogenous, have been identified (Jonides, 1981; Posner, 1980). The exogenous component is triggered automatically by external stimuli. For example, a brief salient flash can attract attention automatically to the region around its spatial location. The exogenous component is automatic/involuntary in the sense that it is highly resistant to mental (internal) control (Jonides, 1981). On the other hand, the endogenous component can be triggered directly by voluntary control, as well as indirectly through an interpretation of external stimuli. For example, the symbolic cue consisting of the word “left” presented at the center of the display can indicate the location of the target indirectly through a processing stage of semantic analysis. It has been suggested that the exogenous and endogenous components of attention also differ in their temporal dynamics. The time course of exogenous attention has been suggested to be transient, i.e. it is most effective within a brief temporal interval (ca. 50-100 ms) after its triggering (Müller & Findlay, 1988; Müller & Rabbitt, 1989a; Nakayama & Mackeben, 1989). On the other hand, endogenous attention has been associated with monotonic/sustained temporal characteristics, in that its efficiency increases gradually with time (Cheal & Lyon, 1991; Müller & Rabbitt, 1989b).

Cueing is a typical paradigm used to study the time course of attention. In a cueing experiment, a “cue” stimulus provides information about a “target stimulus”. Cues can be tailored to favor exogenous or endogenous components of attention. Cues that favor exogenous (endogenous) component are referred to as peripheral (central/symbolic) cues. In a typical experiment, a cue is turned on first, followed by target/distractor items, in turn followed by a “post-stimulus mask” which is used to curtail the visible persistence of target/distractor items. The temporal interval between the onset of the cue and the onset of the target item (cue lead time, CLT) is varied in order to study temporal course of attention triggered by the cue. The facilitation of accuracy produced by a symbolic valid cue increases monotonically as a function of CLT providing, evidence that the endogenous component has monotonic dynamics (e.g., Cheal & Lyon, 1989, 1991; Müller & Rabbitt, 1989b). An abrupt onset of a valid cue in the spatial neighborhood of the target item produces facilitation of accuracy at short CLTs but the facilitation tends to decrease at long CLTs (Cheal & Lyon, 1991; Müller & Findlay, 1988; Nakayama & Mackeben, 1989). As depicted in Fig. 4.1, this non-monotonic performance curve has been interpreted to reflect the cumulative effect of a fast transient exogenous attention along with a slower monotonic endogenous attention (Nakayama & Mackeben, 1989).

Because the non-monotonic profile of performance as a function of CLT is a critical piece of evidence supporting the existence of a transient component of attention, it is important to establish which factors contribute to its morphology. Interestingly, the decrease of performance at long CLTs was consistent but small in the studies by Müller and Findlay (1988) and, Cheal and Lyon (1991). A much stronger downturn in performance was reported by Nakayama and Mackeben (1989). One difference between these studies was the type of “post-stimulus mask”. Müller and Findlay (1988), and Cheal and Lyon (1991) used “local” post-stimulus masks, i.e. mask items appeared at the location of target and distractor items. Nakayama and Mackeben (1989) used “global” post-stimulus masks consisting of a high-energy noise pattern that covered the entire display. Given this difference, it is possible that the downturn of performance at long CLTs may reflect the operation of the post-stimulus mask rather then the temporal dynamics of attention mechanisms.

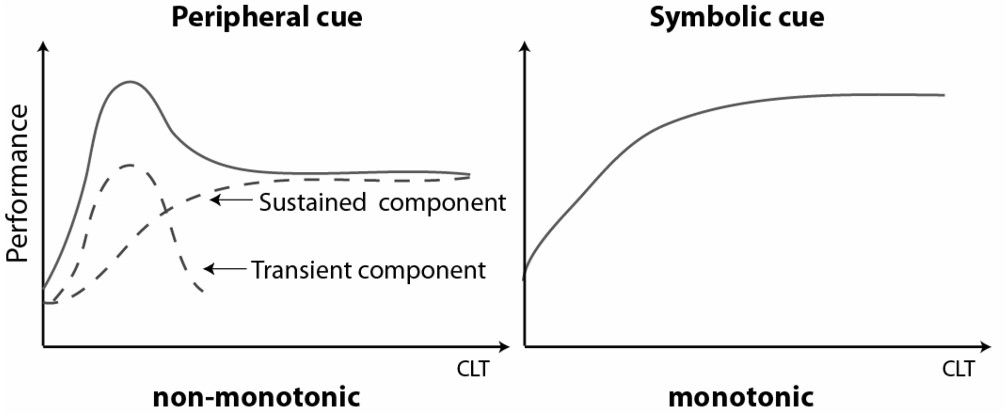


Fig. 4.1. Performance of observers as a function of cue lead time (CLT) shows non-monotonic (left panel) and monotonic (right panel) functions with a peripheral and symbolic cue, respectively (solid lines). It has been suggested that the non-monotonic function is composed of transient and sustained components (dashed lines) of attention while the monotonic function is produced exclusively by the sustained component.

Another difference between these studies was that Müller and Findlay (1988), and Cheal and Lyon (1991) used a cue of fixed duration, while Nakayama and Mackeben (1989) used a cue whose duration co-varied with CLT. Because the cue surrounded the search item, it could potentially act as a paracontrast mask. An increase in the duration of a paracontrast mask is known to increase its masking strength (Macknik & Livingstone, 1998). Hence an increase in CLT would produce an increase in the masking effectiveness of the cue on the search item. While early studies reported paracontrast effects when the mask preceded the target by 20-70 ms (Breitmeyer, 1984), more recent studies show that paracontrast effects can be observed when the mask precedes the target by about 400 ms, in particular when the mask has higher energy than the target (Breitmeyer et al., submitted). Taken together, these considerations suggest that masking effects by the post-stimulus mask as well as the cue may play an important role in shaping the non-monotonic performance function. This hypothesis was tested in Experiment 1.

4.2. Experiment 1 – Masking Effect of the Cue and the Post-Stimulus Mask

In this experiment, we examined to which extent the masking effect of the cue and the post-stimulus mask influenced the pattern of results. We investigated how, in a visual search experiment using the conjunctive search paradigm, the temporal course of focal visual attention drawn by an abrupt peripheral cue changes depending on the visual attributes of the cues. In a conjunctive search paradigm, the search item (target) is defined by a conjunction of two or more stimulus attributes, for example red *and* vertical. As mentioned above, Müller and Findlay (1988), and Cheal and Lyon (1991) reported that at long CLTs, there is a decay in performance compared to the peak performance around CLT=100 ms. However, the decay at long CLTs and the peak around CLT=100 ms were more prominent in the experimental results of Nakayama and Mackeben (1989). We hypothesized that the peripheral cues in Nakayama and Mackeben's studies may have forward masking effects on the search items. Their cue was a square surrounding the target stimulus and its duration was increasing linearly as CLT was increasing. In other words, the cue they used had a high contour contiguity with the target stimulus and its energy increased with CLT, both of which contribute to the masking strength (Breitmeyer, 1984). We varied the geometry of the cue stimulus to vary the effectiveness of its hypothesized masking effect. Furthermore, Cheal and Lyon (1991) used local post-stimulus masks and found a slight decay in performance at high CLTs. Nakayama and Mackeben (1989), however, used a powerful global noise post-stimulus mask covering the whole visual display and found prominent decay in performance at high CLTs. The aim of this experiment was to investigate the masking effect of the cue and the post-stimulus mask in the same experimental setup. To do so we used three types of cues and two types of post-stimulus masks (local and global).

4.2.1. Methods

4.2.1.1. Observers

A total of three observers (one of whom was naïve to the purpose of the experiment) participated. All observers had normal or corrected-to-normal vision.

4.2.1.2. Apparatus

Visual stimuli were generated via the visual stimulus generator (VSG) card manufactured by Cambridge Systems (http://www.crsltd.com). This card was programmed by using its driver library and the stimuli were displayed on a 24" high-resolution color monitor (Sony GDM-FW900) with a 160 Hz frame rate. The stimuli were displayed on a uniform gray background. A head/chin rest was used to aid the observer to keep his/her head still while fixating his/her eyes on the fixation cross displayed in the center of the monitor. The distance between the monitor and the observer was set to 97 cm. Behavioral responses were recorded via a joystick connected to the computer hosting the VSG card.

4.2.1.3. Stimuli and Procedure

We followed generally the methods used in Nakayama and Mackeben (1989). To study the masking effects of the cue on the search items, we used three types of cues whose contour contiguity and the separation with the search stimulus varied as follows: 1) a square box surrounding the search item (strong mask), 2) a cross surrounding the search item but with little contour contiguity (intermediate mask), 3) a non-surrounding cross, adjacent to the search item (weak mask) (Fig. 4.2). A post-stimulus mask stimulus was turned on immediately after the offset of the search items. The global post-stimulus mask stimulus consisted of randomly distributed white squares (0.6 x 0.6 deg) on a black background distributed over the entire area of the monitor (Fig. 4.3). The local post-stimulus masks were 30 x 30 min arc randomly chosen white or black squares. Local post-stimulus masks are expected to be less effective in masking because they have less energy compared to that of the global noise post-stimulus mask.

The stimuli appeared at 12 locations uniformly distributed on a circular array at an eccentricity of 2.5 deg with respect to a fixation cross (Fig. 4.3). The distractors were vertical black and horizontal white bars (30 x 15 min arc). A distractor was chosen randomly for each 11 locations other than the cued location. The stimulus at the cued location was either a distractor or one of two possible targets (Fig. 4.3). Targets were horizontal black and vertical white bars (30 x 15 min arc). There were eight CLTs ranging from 0 to 500 ms in each session and around 20 trials for each CLT value. The luminance of gray background was 10 cdm^{-2}. Black and white stimuli were at luminance values of 0 and 68 cdm^{-2}, respectively. In each trial, observers' task was to determine if a target was present and if so, to report its type (Fig. 4.3). Results were collected from each observer (N=3) in 5 sessions.

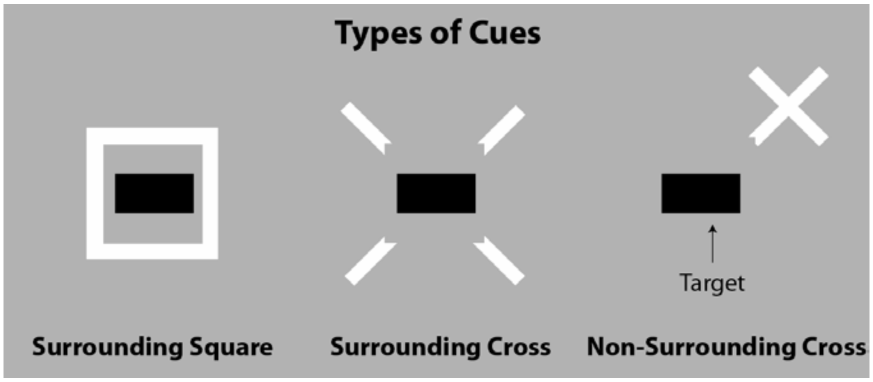


Fig. 4.2. Cues whose contour contiguity and the spatial separation with the search item are varied to modulate the strength of the hypothesized masking effect: A square box surrounding the search item (strong mask), a cross surrounding the search item but with little contour contiguity (intermediate mask), a non-surrounding cross, adjacent to the search item (weak mask).

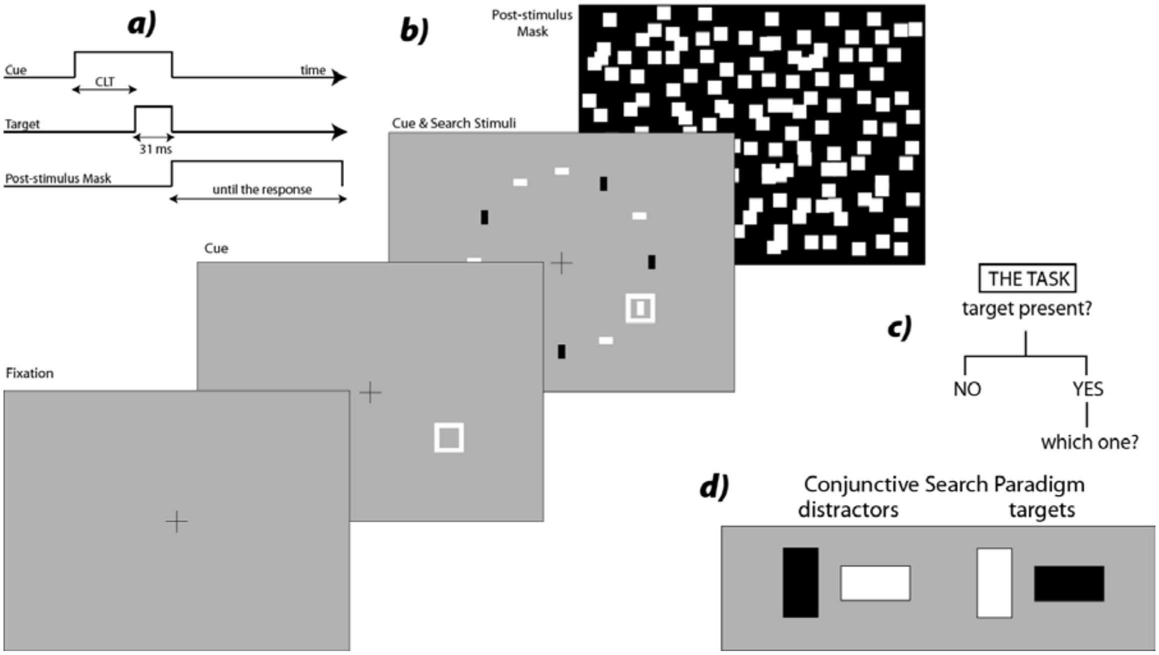


Fig. 4.3. a) Relative onset timings between the stimuli. b) Frames of stimuli used in a trial. c) The task of the observer. d) Shapes of odd targets and distractors.

4.2.2. Results and Discussion

The percentage of correct values were averaged across observers and plotted as a function of CLT for three types of cues and two types of post-stimulus masks (Fig. 4.4). When a *global* post-stimulus mask is used (Fig. 4.4a), the surrounding-square-cue produces a rapid facilitation of performance at short CLTs going from a near chance value (39%) at CLT=0 ms to a peak value of 80% at CLT=50 ms. As CLT is further increased, performance decays gradually to a lower plateau value of 60%. The overall shape of this function with its prominent downturn replicates the findings of Nakayama and Mackeben (1989). With the surrounding-cross cue, however, although performance increases rapidly at short CLTs, peak performance is limited at 68%. At CLT=156 ms, performance decreases to a value of 59% and then stays around the same value at higher CLTs. The non-surrounding cross cue yields a monotonic increase of performance reaching 59% at long CLTs. We used repeated measures ANOVA for statistical analysis. When the sphericity assumption was not met, the Huyn-Feldt correction was applied and the epsilon value is indicated in the results. The main effect of CLT was significant ($F_{7,14}$=13.398, p=0.018, ε=0.280). The main effect of cue-type was found insignificant ($F_{2,4}$=4.289, p=0.121, ε=0.832) but cue-type x CLT interaction was significant ($F_{14,28}$=3.207, p= 0.004). This result shows that the performance change due to the cue-type is not equal at all CLTs and hence the overall shape of time course of performance changes depending on the cue type.

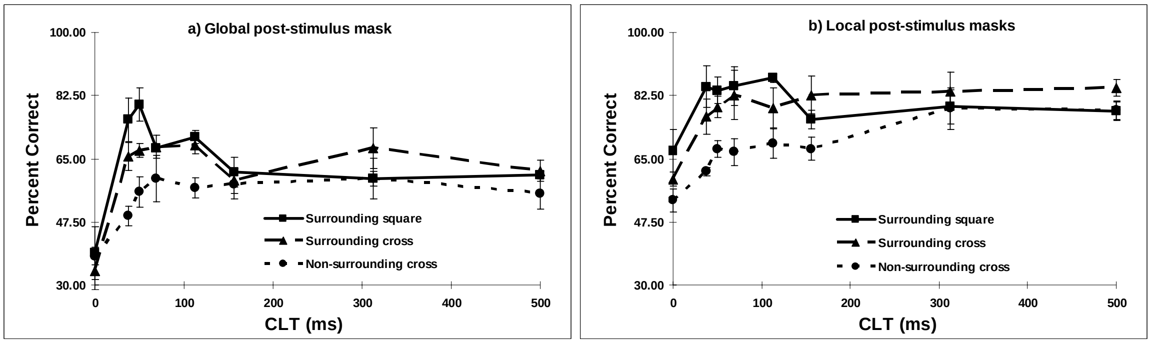


Fig. 4.4. Percent correct responses averaged across observers for the three types of cues using a) global, and b) local post-stimulus masks. The error bars correspond to ±1 SEM.

As we can see from Fig. 4.4, as the putative masking strength of the cue is increased, the performance at short CLTs does not decrease, but instead increases. Moreover, performance at long CLTs does not show a systematic effect of masking strength. As depicted in Fig. 4.5, paracontrast masking effect of the surrounding cue was expected to be strongest at long CLTs. However, our data do not support this prediction, suggesting that forward masking by the cue does not play a significant role in shaping the non-monotonic performance function.

When a *local* post-stimulus mask is used (Fig. 4.4b), the surrounding-square cue yields an increase of performance up to CLT=100 ms followed by a slight decay, as reported in a previous study (Cheal & Lyon, 1991). The other two conditions yield a more monotonic increase in performance. Statistical analysis of the data shows that the main effects of cue-type and CLT are significant ($F_{2,4}=7.615$, $p=0.043$; $F_{7,14}=14.435$, $p<0.001$). In contrast to the *global* post-stimulus mask condition, cue-type x CLT interaction was found insignificant ($F_{14,28}=2.101$, $p=0.180$) which suggests that time-course of performance does not change significantly with the type of the cue when a local post-stimulus mask is used.

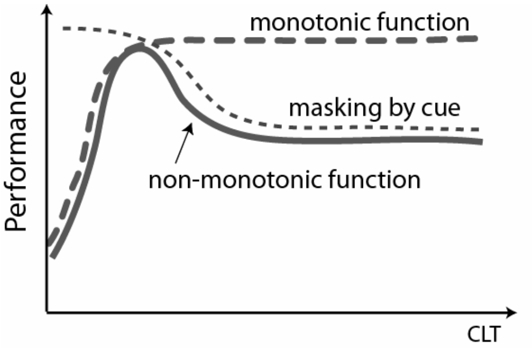


Fig. 4.5. Predicted outcome of the experiment according to the hypothesis that the cue exerts stronger forward masking effects at longer CLTs due to an increase in its energy as CLT is increased. Masking by a surrounding-square cue should be strongest generating a non-monotonic function. Masking by a non-surrounding cross should be very weak resulting in an approximately monotonic function.

Fig. 4.6 replots the results to visualize more directly the effect of the post-stimulus mask. The main effect of the post-stimulus mask is significant ($F_{1,2}$=47.112, p=0.021). Switching from local to global post-stimulus mask appears to reduce performance by approximately a constant amount for all CLTs with the exception of the CLT value where the surrounding-square cue produces a prominent peak in performance (Fig. 4.6, left panel, CLT=50ms). In fact, statistical analysis shows that the post-stimulus mask x CLT interaction is only significant ($F_{7,14}$=78.421, p=0.007) when the surrounding-square cue was used. This finding suggests that, with a surrounding-square cue, time-course of performance does not simply shift up or down when we vary the masking effectiveness of the post-stimulus mask. Therefore, a combination of a specific type of cue and a powerful global mask is necessary to observe a rapid facilitation followed by a prominent decay in performance. During the experiments, observers reported that it was easier to identify a target when its contrast polarity was congruent with that of the cue (i.e. both white). This observation led us to hypothesize that the specific type of cue required to produce a non-monotonic performance function may be one that exerts a “feature-based priming”, as found, for example, in “masked-priming” paradigms (e.g., Ansorge et al., 1998; Breitmeyer et al., 2004a; Klotz & Wolff, 1995; Neumann & Klotz, 1994). In masked-priming, a target whose visibility is suppressed by a temporally after-coming mask can nonetheless prime responses to the mask according to target-mask congruency. That the peak performance at CLT=50 ms shown in the left panel of Fig. 4.6 was immune to the effect of the post-stimulus mask supports this hypothesis. Furthermore, we would expect stronger priming by the surrounding-square cue compared to the other cues because the surrounding-square cue has stronger featural resemblance (edges of the square are composed of vertical and horizontal bars), as well as higher contour proximity and contiguity with the target items.

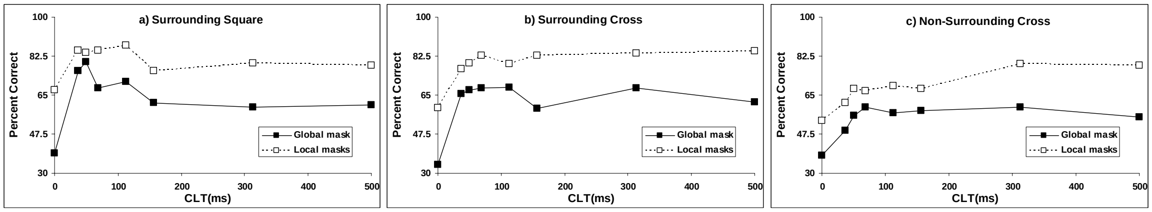


Fig. 4.6. Comparison of temporal course of peripheral cueing obtained with global (solid line, filled square) and local post-stimulus masks (dashed line, empty square) for three types of cues. Results are averaged across observers.

4.3. Experiment 2 – Priming Effect of the Cue

The conjunctive search paradigm that we employed in our experiments allows us to use congruent and incongruent contrast polarities between the cue and the search stimuli. By examining the performance obtained from trials having white and black search stimuli, we can measure the priming effect of the cue on performance. In experiment 1, only white cues were used. To carry out a more complete analysis of the congruency effect, we designed an additional experiment using black cues and analyzed the combined results in terms of cue-target congruency.

4.3.1. Observers, Apparatus, Stimuli and Procedure

Observers were same as in Experiment 1. The stimuli and procedures were identical to those of Experiment 1 with the only exception that the contrast polarity of the cue was black instead of white. We ran only the condition that produced the prominent non-monotonic performance curve, i.e. the surrounding-square cue with the global post-stimulus mask.

4.3.2. Results and Discussion

Results from Experiments 1 and 2 are combined into congruent and incongruent categories according to whether the cue and the targets had the same or different contrast polarities, respectively and plotted in Fig. 4.7. One can see that congruency affects the overall shape of the function relating performance to CLT; a non-monotonic function is observed when the cue and the target are congruent whereas a monotonic function is observed when they are incongruent. The effect of congruency x CLT interaction is significant ($F_{7,14}$=149.419, p=0.014) suggesting that the peak facilitation at short CLTs is mainly due the priming effect. These results suggest that cues that trigger spatial-based attention can, under appropriate conditions, also evoke feature-based priming.

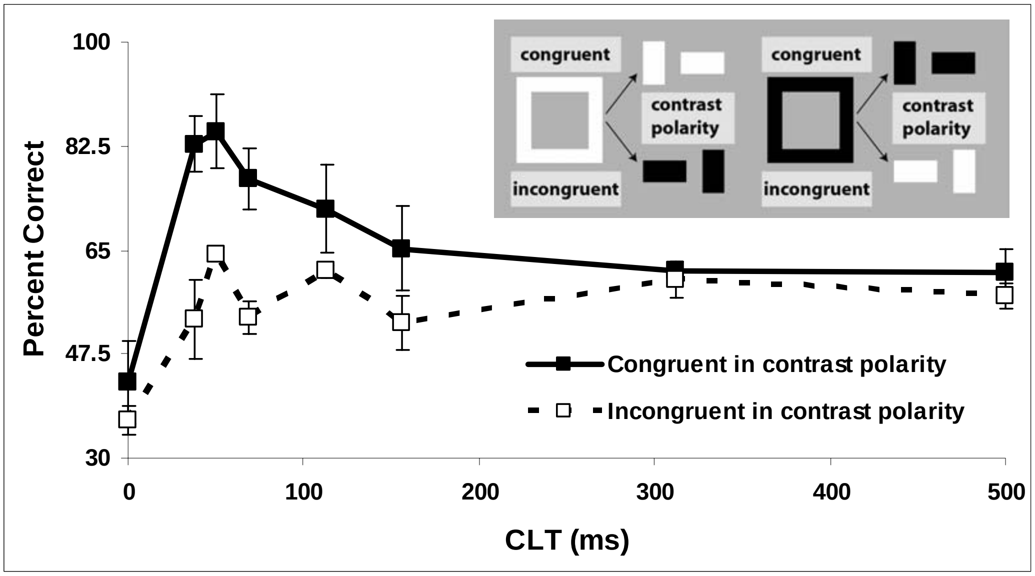


Fig. 4.7. Time course of performance when the target is congruent (solid line, filled squares) and incongruent (dashed line, empty squares) in contrast polarity with the cue. Results are combined from Experiment 1 and Experiment 2 with white and black cue respectively and averaged across observers. The error bars correspond to ±1 SEM.

4.4. Summary and Discussion

The first goal of this chapter was to test the hypothesis that the decrease of performance at long CLTs is due to a forward (paracontrast) masking effect of the preceding cue on the search item. As expected, decreasing the masking strength of the cue led to a more monotonic pattern in performance as a function of CLT. However, the transition from the non-monotonic function towards the monotonic function occurred due to a decrease in performance at short CLTs as opposed to an increase in performance at long CLTs, contrary to our prediction. Thus, the masking effect of the cue does not seem to play a major role in shaping the non-monotonic function. On the other hand, the masking effect of the post-stimulus mask plays a major role in producing the non-monotonic function when the surrounding-square cue is used. Based on this observation as well as on the phenomenal reports of the observers, we hypothesized that the cue may be exerting a feature-based priming effect on the search item, rather than a masking effect (Fig. 4.8). Results of the second experiment support this view.

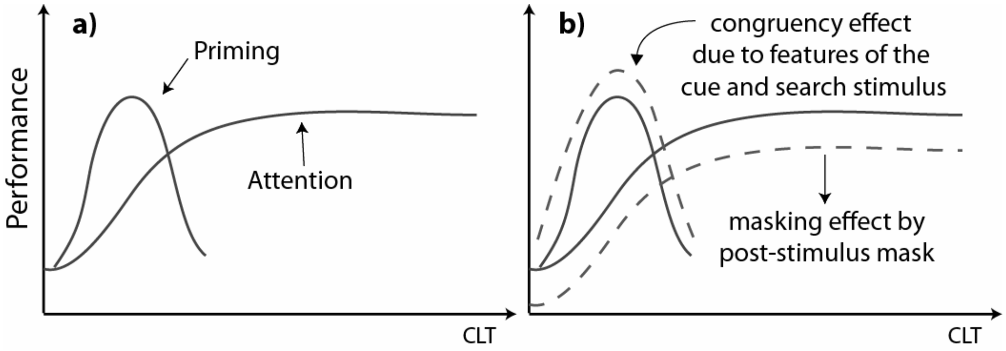


Fig. 4.8. a) Depiction of the model proposed to explain monotonic and non-monotonic effects of cueing. We suggest that the non-monotonic time course of performance in response to a peripheral cue results from a combination of two different effects that produce facilitation: a transient priming and a sustained attention. b) Attention shows a monotonic increase of performance. Priming effect of the cue may increase depending on the congruency between the features of the cue and those of the search stimulus. The masking effect of the post-stimulus mask reduces facilitation produced by attention. The priming effect is immune to masking, in agreement with masked-priming phenomenon.

Previous studies showed that performance in simple and conjunctive search tasks could be improved across trials when the information relevant to the search is kept consistent in consecutive trials. For example, Maljkovic and Nakayama (1994) asked observers to report the shape of a target defined by color or spatial frequency (e.g., target one color, distractors another color). This is a simple search paradigm where the target "pops-out". Performance was better when the trials were blocked according to the feature defining the target (e.g., target red, distractors green in a block) compared to the mixed design where the target and distractor colors changed unpredictably from trial to trial. This result has also been extended to the conjunctive search paradigm (Kristjánsson et al., 2002). Similarly, when a cue was used in conjunctive search, performance was better when a relationship between the cue and the search item (e.g., the relative position of the search item within the area covered by the cue) was kept consistent from trial to trial (Kristjánsson et al., 2001). Nakayama and colleagues attributed these temporal trial-to-trial modulations of performance to a priming effect resulting from rapid perceptual learning and short-term memory. Our experiments used a blocked design with respect to cue contrast polarity. Within each block, cue target congruency was randomized across trials. Therefore, we do not expect a major modulation by temporal trial-to-trial priming effects. On the other hand, we have shown that cue-target congruency within single trials affects performance strongly but only for short CLTs. Indeed, our results indicate that the relative enhancement of performance at short CLTs, hitherto attributed to a transient component of attention, can be accounted virtually in its entirety by a priming effect. According to this model, which is depicted in Fig. 4.8, exogenous and endogenous deployment of attention are monotonic processes and the non-monotonic performance function obtained by peripheral cues results from a transient priming effect. The priming effect that we observe can also be considered as an attentional activation from subcortical sites according to Bachman's (1994) masking model. We envisage a priming effect similar to that observed in masked-priming paradigms where a target whose visibility is suppressed by a temporally after-coming mask can nonetheless prime responses to the mask according to target-mask congruency (e.g., Ansorge et al., 1998; Breitmeyer et al., 2004a; Klotz & Wolff, 1995; Neumann & Klotz, 1994). Supporting this interpretation, our results show that the facilitation at short CLTs appears to be immune to the effect of the post-stimulus mask.. On the other hand, the monotonic processes appear to be affected by a constant amount across CLTs by the post-stimulus mask. This can be explained by the fact that the temporal relationship between the target and the post-stimulus mask remains fixed and thus is independent of CLT.

Chapter 5

Conclusions

This century could be one of the milestones for humankind as we have seen many important steps in building intelligent systems. From computer technology to neuroscience, many of the branches of science now seek to understand in a coordinated manner biological systems and their interactions with the environment. Like any organism that wants to produce something from its own, for example honey from bees, maybe the best fruit that this universe has produced is “life”, on earth. When we examine life forms, we see that self awareness with intelligence is one of the most powerful aspects of life providing enormous flexibility in adaptation. Nevertheless, although we are aware of ourselves and our environment, we do not even know how we achieve this awareness. Yet, our mind is capable of thinking and generating new ideas. One of the things that led science to advance so much in the preceding centuries is the understanding of the importance of experimentation. Whenever a problem is to be solved especially in natural sciences, one can come with a hypothesis and test that with an experiment.

Another important driving force in the technological progress is that we have learned to observe and copy or modify something that already exists. For example, if a plane can not approach the speed of sound look at the aerodynamics of birds; if one can not cure an illness plant some stem cells. In this dissertation, we used the human brain as a model, particularly the human visual system. Our broad, long term goal is to understand the mechanisms and dynamics underlying the conscious and unconscious registration of a visual stimulus. Particularly we have studied three aspects of conscious registration: 1) Temporal dynamics, 2) Neural Locus, and 3) Functional specificity. In order to address this question, we used three paradigms where the degree of conscious registration of a stimulus can be controlled systematically: 1) Binocular rivalry, 2) Visual masking, and 3) Visual attention (Fig. 5.1).

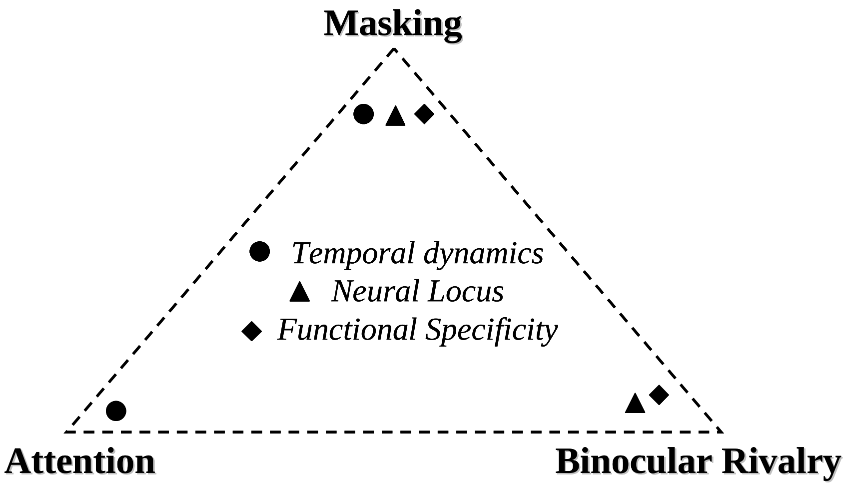


Fig. 5.1. Three aspects of conscious registration (temporal dynamics, neural locus, functional specificity) studied by three experimental paradigms (visual masking, visual attention, binocular rivalry).

In chapter 2 we combined binocular rivalry and masking paradigms. Studies of disinhibition in metacontrast suggest that there is a functional dissociation between a stimulus' masking effectiveness and its visibility (Ogmen et al., 2004). While two stimuli could be perceptually equally visible, they could affect differentially different areas of the brain, which can be called the priming effect of the stimulus caused by its unconscious processing. Since many of the phenomena and illusions in perception possibly occur at unconscious levels of information processing, their timing with respect to each other could help to build a functional hierarchy in visual information processing. Our results suggest that functionally the mechanisms of metacontrast are after binocular rivalry and the mechanisms of disinhibition in metacontrast before binocular convergence (Breitmeyer et al., 2005). Furthermore, masking is not observed when the visibility of the masking stimulus is reduced during binocular rivalry unlike disinhibition in metacontrast. These findings suggest the specificity of the underlying functionality of binocular rivalry and metacontrast masking paradigms.

In chapter 3 we investigated electrophysiological correlates of conscious registration in visual masking. We used a new methodology in order to overcome the difficulties that previous researchers experienced. Our results show a good correlation between the visual evoked potential (VEP) and behavioral responses when the stimulus is visible or reduced in a time interval of 200-400 ms after the onset of the stimulus. Computational models of masking should also take into account at which time the interruption or reduction of the stimulus' visual information starts in the brain leading to an impaired visibility. Our results also suggest that more brain areas are modulated when the visibility of a stimulus is reduced by masking. From our results we can say to some extent that the possible neural substrate of masking could be in parietal areas of the brain, which is in agreement with previous studies (Green et al., 2005). To study the underlying mechanisms of masking, we have adopted the dual channel RECOD model as a framework (Ogmen, 1993). Among the other models, this model is tested to account for the disinhibition results and is the only one that can explain the target recovery phenomenon in metacontrast. We further tested this model by using the target recovery phenomenon as an experimental tool in a reaction time (RT) study. Our results suggest that the transient activity of a stimulus is suppressed mainly by inter-channel inhibition.

In chapter 4 we investigated temporal dynamics of attention. Previous studies suggested that two concurrent, transient and sustained, components could shape the overall time course of attention when a peripheral cue is used (Nakayama & Mackeben, 1989). We tested whether these proposed components could be due to a mechanism other than attention, such as masking or priming. Our results put forward the importance of the masking effectiveness of the post-stimulus mask and the feature-based priming effect of the cue in observing a non-monotonic function of performance in peripheral cueing.

Taken together, our work contributes to the establishment of a functional hierarchy of brain processes in the following order: disinhibition in metacontrast, binocular convergence, binocular rivalry, metacontrast, conscious registration. Dynamics in parts of the hierarchy shed light on the temporally complex interactions, while inhibitory mechanisms are effective in masking; facilitatory interactions take place in attention. Work can be extended further by combining other paradigms that control conscious registration, (e.g., Troxler fading effect; Troxler, 1804) with the ones we studied to incorporate a broad range of mechanisms into the hierarchy. In Troxler fading effect, while observers maintain fixation in central vision, a stationary point in the periphery fades from awareness in a few seconds. It was shown that fading can be initiated and prolonged by transient masking stimuli (Breitmeyer & Rudd, 1981). While we show a functional hierarchy of processes by using psychophysical experiments and find electrophysiological (EEG) correlates of visibility, anatomical loci of these processes can be investigated by using tools having better spatial resolution (e.g., fMRI). Besides masking interaction, which is via stimulus pathways, the visibility of a stimulus can also be reduced directly by applying TMS on visual areas (Corthout et al., 1999). Moreover, TMS can act as a secondary stimulus and cause target recovery (Ro et al., 2003). As Breitmeyer et al. (2004b) shows differences between interactions of masking and TMS, a comparison of these interactions in the functional hierarchy of unconscious processes would provide additional insight into the nature of the interference through different means. The approach whereby we vary stimulus parameters to elucidate dynamics can reveal more about temporal aspects of information processing. Future studies can test the priming effect on attentional performance by using various features to define search stimuli. Correlates of visibility and its neural locus can be investigated in disinhibition and binocular rivalry paradigms by combining EEG and fMRI tools to obtain better spatial and temporal resolution.

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APPENDIX – A

Methods for Data Analysis

A.1. Processing of EEG Data

We followed the guidelines explained in detail by Picton et al. (1995, 2000) and van Boxtel (1998) while using ERPs in our EEG studies. For processing the EEG data, a free MATLAB toolbox (EEGLAB) developed by the researchers at the Salk Institute was used (Delorme & Makeig, 2004). This toolbox provides an interactive GUI interface to load and process the EEG data. Custom scripts were written to visualize and process the EEG data by using the functions provided by the EEGLAB. Developers of this toolbox suggest that in order to fully understand the event related brain dynamics advanced methods have to be developed (Delorme et al., 2002; Makeig, 2002; Makeig et al., 2002, 2004). It is well known that the EEG signals are nonlinear and therefore applying the linear (and time-invariant) algorithms to EEG signals developed in studies of classical signal processing may not be appropriate and thus the dynamics of the EEG signals may not be fully understood (Jansen, 1996). For this reason nonlinear processing techniques are being developed for analysis of EEG signals (e.g., Basar, 1998; Gauatama et al., 2003; Natarajan et al., 2004; Nunez, 2000) and moreover it has been found that the prestimulus or the ongoing EEG activity affects the evoked potentials (Jansen & Brandt, 1991). Since an ensemble averaged event-related potential (ERP) only leaves the phase-locked signals to the time-locked events, Makeig et al. (2004) suggest visualizing the whole single trial responses in a two-dimensional (2-D) trial-by-latency image which they call the ERP image (Jung et al., 2001b) (top panel in Fig. A.1). These single trials can be sorted according to any criteria, such as their phase or RT latency. The developers of the EEGLAB package suggest the use of inter-trial phase coherence (ITPC) and event-related spectral perturbation (ERSP). ITPC shows the phase locking of EEG signals to time-locking events across trials (Lachaux, et al., 1999; Tallon-Baudry et al., 1996). ERSP measures the change in spectral power from baseline (Makeig, 1993). All these features are available in the EEGLAB package and they were used when needed in processing our data. Fig. A.1 is produced from our EEG studies to illustrate ERP image, ITC and ERSP.

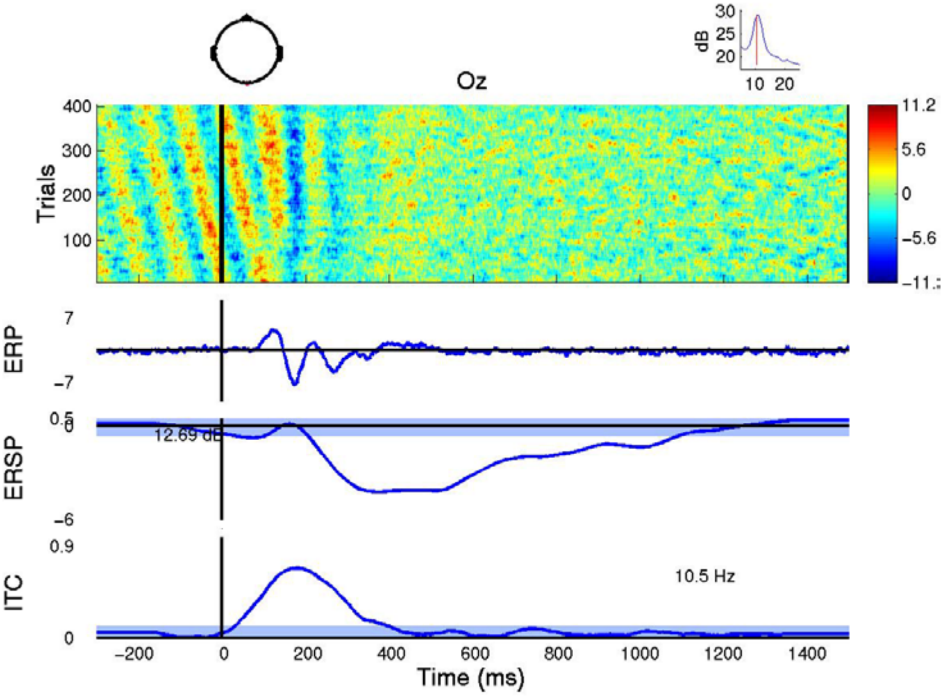


Fig. A.1. Recordings from channel Oz obtained in 400 trials. The small circle on the head shape represents the channel’s location. The small plot on the top-right shows the channel’s power spectrum up to 25 Hz, and the vertical line in the plot indicates the frequency at which the highest power is observed. The top plot in the middle shows ERP image of the individual trials sorted at 10.5 Hz. The magnitude of the contrast in the plot shows relative differences in activities as shown by the color bar on the right. The higher the contrast the bigger the difference is. The second plot from the top shows the ensemble averaged ERP. The two plots from the bottom show ITC and ERSP of single trials at frequency 10.5 Hz, respectively. The gray short-width bar covering the whole time range in these plots shows the significance level obtained by surrogate data of the single trials.

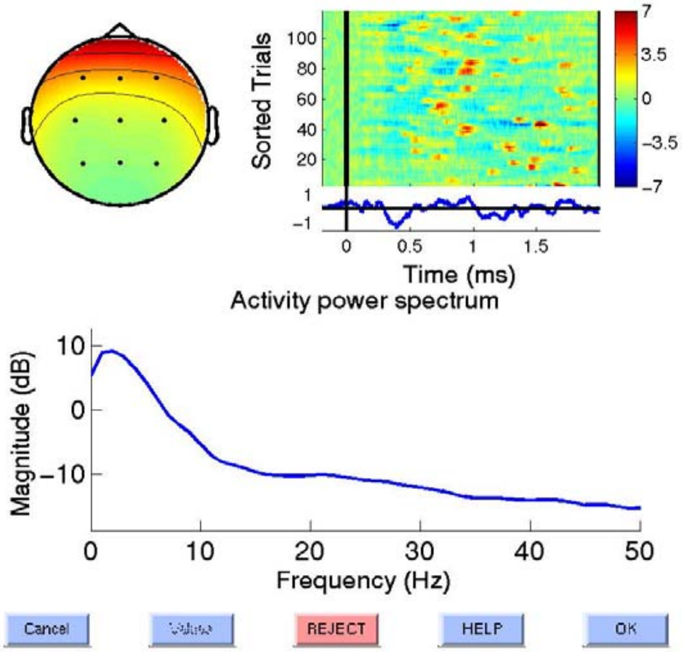


Fig. A.2. An eye blink component can be identified because of the following reasons. After applying ICA, a component's activations can be projected back to each channel and can be plotted on a scalp map in order to investigate how much an electrode recording contributed in forming a component. Top-left panel shows this component's scalp map projection. Voltage changes in recordings caused by eye blinks depend on the distance between the eyes and the recording electrodes. Also since mostly both eyes blink at the same time, frontal recordings are affected almost equally and much stronger than other recordings. The magnitude of the contrast in the plot shows relative differences in activities. The higher the contrast the bigger the difference is. Small circular points designate the locations of the channels. Top-right panel shows the activations of this component for all single trials plotted in a 2-D ERP image. Below the ERP image, the averaged ERP of the component is shown. The magnitude of the contrast in the plot shows relative differences in activities. Eye blinks generate relatively high amplitude changes which occur randomly and fade fast as shown in the ERP image. The bottom panel shows the activity power spectrum of this component. It smoothly decreases and does not have a peak especially around 10 Hz both of which are not characteristics of brain signals. Using the same rationale, similar eye blink components have been extracted by several studies (e.g., Jung et al., 2000a, 2000b; Makeig et al., 2002).

Various algorithms implementing independent component analysis (ICA) are also provided by EEGLAB (Bell & Sejnowski, 1995; Cardoso & Souloumiac, 1995; Hyvarinen & Oja, 2000). By applying ICA to concatenated single trials, maximally temporally independent but spatially fixed linear components are achieved. Although the assumption of spatially fixed brain sources having temporally independent time course responses cannot fully hold for the highly nonlinear brain signals, ICA might be informative about the brain dynamics (Jung et al., 2001a; Makeig et al., 2002). ICA has been found to be useful especially removing EEG artifacts such as eye blinks, muscle or eye movements (Jung et al., 2000a, 2000b). Since eye blinks independently occur in a short window of time across trials, an independent component can fully account for all the eye blinks. We can reconstruct artifact free recordings by removing this eye blink component and projecting back other components' contributions to each channel. A typical eye blink component obtained from our pilot studies is shown in Fig. A.2. EEGLAB also provides dipole fit (DIPFIT) plug-in to localize brain sources as a dipole similar to the brain electrical source analysis (BESA) software (Miltner et al., 1994).

Recordings saved in "BDF" extension files were loaded by EEGLAB. Trigger timings were read from the file, which is saved in an extra channel. EEGLAB keeps track of single trials by "event" structures. Each event can have many fields. Each field represents a property of the single trial. For example in our EEG experiments, a target stimulus having a gap can randomly appear either on the left or on the right. This was indicated in a field of the event structure of the related single trial. Similarly whether the trial is for CTR or DU condition was saved off-line. After defining every event we filtered the continuous EEG recording by a high-pass filter having a cut-off frequency of 1Hz to remove linear trends. We used "eegfilt" function in EEGLAB for filtering signals. This function uses built-in MATLAB functions to construct a two-way least-squares finite impulse response (FIR) filter. The constructed filter is used by the "filtfilt" function of MATLAB to perform a zero phase digital filtering. After high-pass filtering, we split the file into two by extracting the trials for the CTR and DU conditions. The baseline value computed from the 200 ms duration before the onset of the stimulus was removed for each epoch. All channels were then subtracted by the reference channel average of mastoids. ICA was applied to these files. Mostly eye blink components were removed by artifact rejection because it is automatic, convenient and allows us to use all the single trials for averaging. Note that these preprocessing stages were carried out for every file. If we have for example 8 SOAs, then there were 16 files for CTR and DU conditions. We plot the recordings from central channels such as Oz, Pz or Cz for both conditions and compare them. In order to see possible differential effects between the two hemispheres on EEG signals, recordings from P3/P4, O1/O2, C3/C4 and F3/F4 channels were also be examined. For example, if the target having the gap appears on the left side of the observer then O1 recording was used as ipsilateral channel and O2 as contralateral because O1/O2 electrode is recording from the left/right hemisphere.

In our EEG analysis, we computed the VEP response as follows. First, we found the ensemble average of the contralateral and the ipsilateral VEPs by using all trials obtained from an observer for both CTR and DU conditions. Then, we computed the absolute differences between contralateral and ipsilateral VEPs at every measured point in a time interval and took the average of this difference with the number of points in that time interval, which allows us to compare VEP responses computed from different time intervals. VEP response can be expressed as

$$Vep\_response = mean\left(\left|acon(t_1;t_2) - aips(t_1;t_2)\right|\right), \tag{A.1}$$

where acon and aips stand for the averaged contralateral and ipsilateral VEPs across all trials, respectively. The time interval is determined by an array $[t_1;t_2]$ in ms, and after taking the absolute value of the differences between acon and aips at each point in this time interval, we simply find the mean value of this vector to find the VEP response.

A.2. Statistical Data Analysis

We used SPSS program (http://www.spss.com) or statistics toolbox of MATLAB (http://www.mathworks.com) or Microsoft Excel in our significance tests. Within-subject (repeated measures) designs were analyzed in SPSS program. A row entry in the program represents an experimental unit (independent observation), i.e. a score obtained from an observer. A column represents the score (variable) that we obtain from an observer under a condition or treatment. For example, in our EEG study we have two conditions (CTR and DU) for our behavioral as well as VEP results. After entering the data for both conditions, we apply “General Linear Model” test to perform repeated measures ANOVA. By appropriately entering the data, we can test the effect of the condition (CTR vs. DU), or for example the effect of SOA in each condition on the performance of the observers. We applied this test whenever applicable in our results.

In our EEG study, we also found the Pearson correlation coefficient between the results that we obtain under two conditions especially to investigate the correlates of masking on VEP signals. A correlation coefficient (r) can be expressed as

$$r = \frac{\sum (X - \mu_x)(Y - \mu_y)}{N\sigma_x\sigma_y}, \tag{A.2}$$

where X and Y stand for samples (scores) obtained from two populations, respectively. Summation of the multiplication of the deviations of X and Y with their respective mean values (μ_x and μ_y) is averaged with the number of sample points (N) to find their covariance. When the covariance is divided by the product of their standard deviations (σ_x and σ_y), we obtain the correlation coefficient (r) in between -1 and +1. The +1 (-1) value represents a perfect positive (negative) correlation between these two measures. Correlation coefficient gives an idea of how these two measures affect or depend on each other. However, it does not necessitate a cause-effect relationship between these two measures because another dependent variable may exist such that it affects both of them in a way that those two correlate. Significance of a correlation coefficient, whether it is statistically significantly greater than zero or not, can be tested by converting the correlation coefficient to a t-value (Bobko, 2001). T-value can be expressed as

$$t = \frac{r \times \sqrt{df}}{\sqrt{1 - r^2}}, \tag{A.3}$$

where r stands for the correlation coefficient and df stands for the degrees of freedom, which is equal to the number of samples (n) to be correlated minus two, i.e. df=n-2. In our EEG analysis, we had 7 Soas and one T-only presentation in an experiment, and therefore n was 8 and df was 6. From this t-value we obtain its probability and therefore its significance compared to an alpha value, for example in Microsoft EXCEL this probability (p) can be found as

$$p = tdist(r, df, tails), \tag{A.4}$$

where tdist stands for t-distribution, r is correlation coefficient, df is degrees of freedom and tails stands for whether the test will be one-tail or two-tail. We chose one-tail t-test because we tested for positive correlations between VEP responses and behavioral results. If we have many correlation coefficients for example under a condition from many observers, then by using “Fischer-transform” a correlation coefficient (r) can be converted to a z-score as

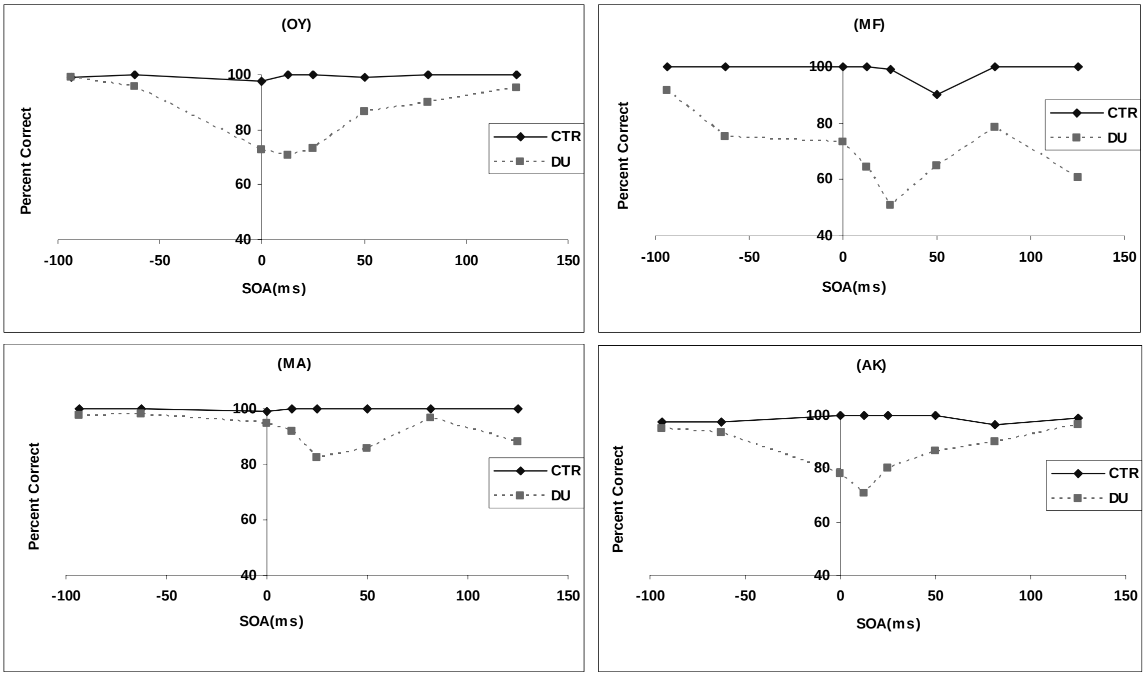
$$z\_score = \frac{1}{2} \times \ln\left(\frac{r+1}{r-1}\right). \tag{A.5}$$

This transform reduces the skew and makes the sampling distribution more normal. Those z-scores then can be entered to a one-sample t-test to find whether they produce a significantly different than zero correlation.

A.3. Additional VEP Figures and Results

In this section we have figures obtained from the EEG results for each observer. Masking functions and response times for each observer are plotted in Fig. A.3. The VEP responses for each observer from two time intervals ([200-400]ms and [130-320]) are plotted in Fig. A.4. Individual correlation coefficients can be found in Fig. A.5. VEPs (P3/P4) for observers are plotted in Fig. A.6, Fig. A.7, Fig. A.8 and Fig. A.9, respectively. In each of those figures, contralateral vs. ipsilateral VEPs for CTR and DU conditions are plotted. In each subplot of a figure, contralateral (dashed) and ipsilateral (continuous) VEPs obtained from either P3 or P4 channels are superimposed and plotted in the time interval [-80,400] ms with respect to the onset of the target. In each plot, the negativity is upward. Reference channel is the average of mastoid channels. The label in the y-axis of a subplot indicates the stimulus configuration in that particular recording, for example, T-only indicates that only the target stimulus was used in the experiment. Similarly, the numbers outside the parenthesis in the y-axis indicate the SOA value in ms. The numbers in the parentheses show the percentage correct values of the observer. The plots on the left column are for the CTR condition, and on the right column are for the DU condition. By comparing the VEPs on the left and the right column, we can determine the range at which masking of the target is effective.

Masking Functions



Response Time

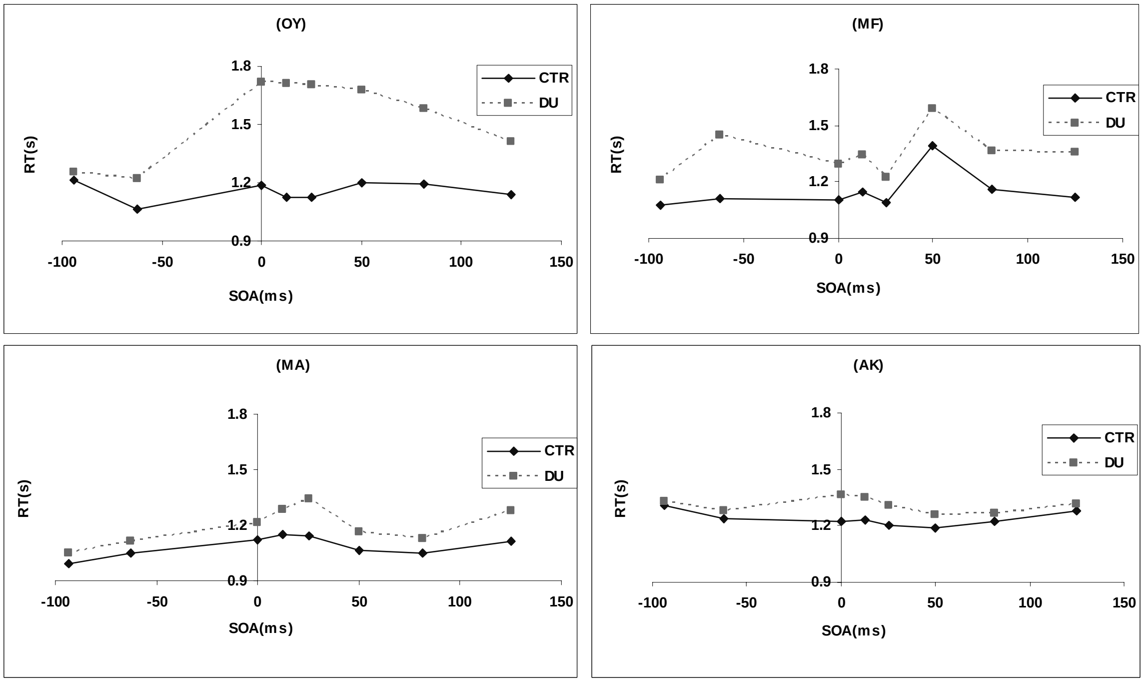
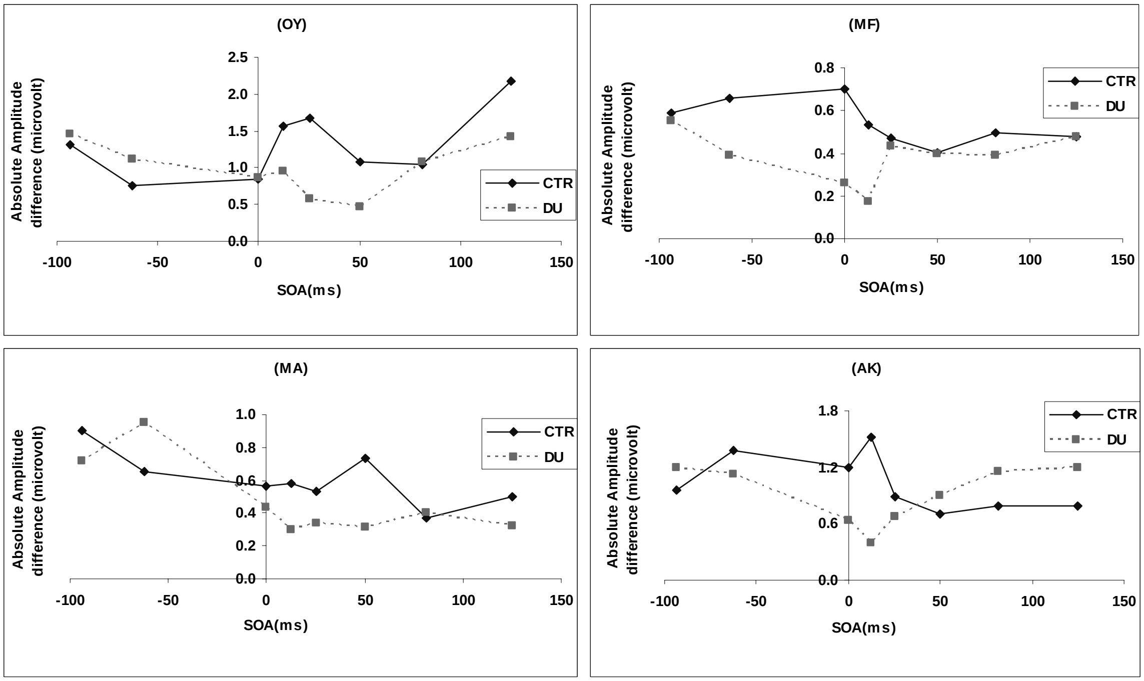


Fig. A.3. Masking functions and response times for each observer obtained in the CTR and DU conditions.

VEP Response (P3/P4) [200-400]ms



VEP Response (P3/P4) [130-320]ms

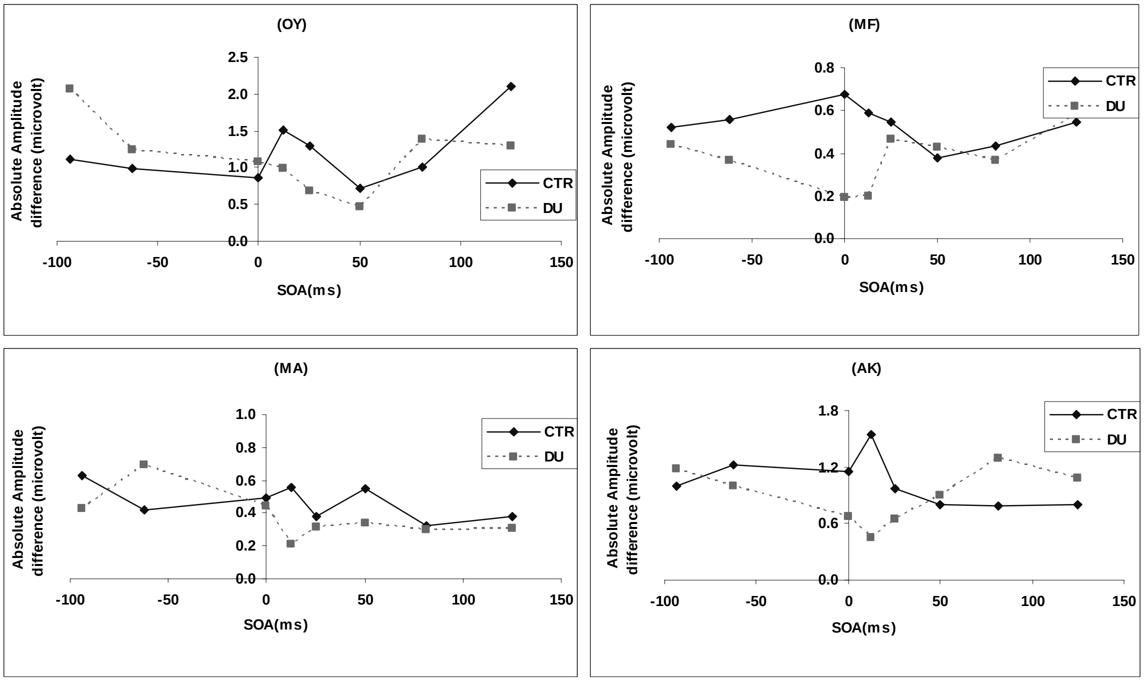


Fig. A.4. VEP responses obtained for all of the observers from channels P3/P4 in two time intervals: [200-400] ms (upper panel), [130-320] ms (lower panel).

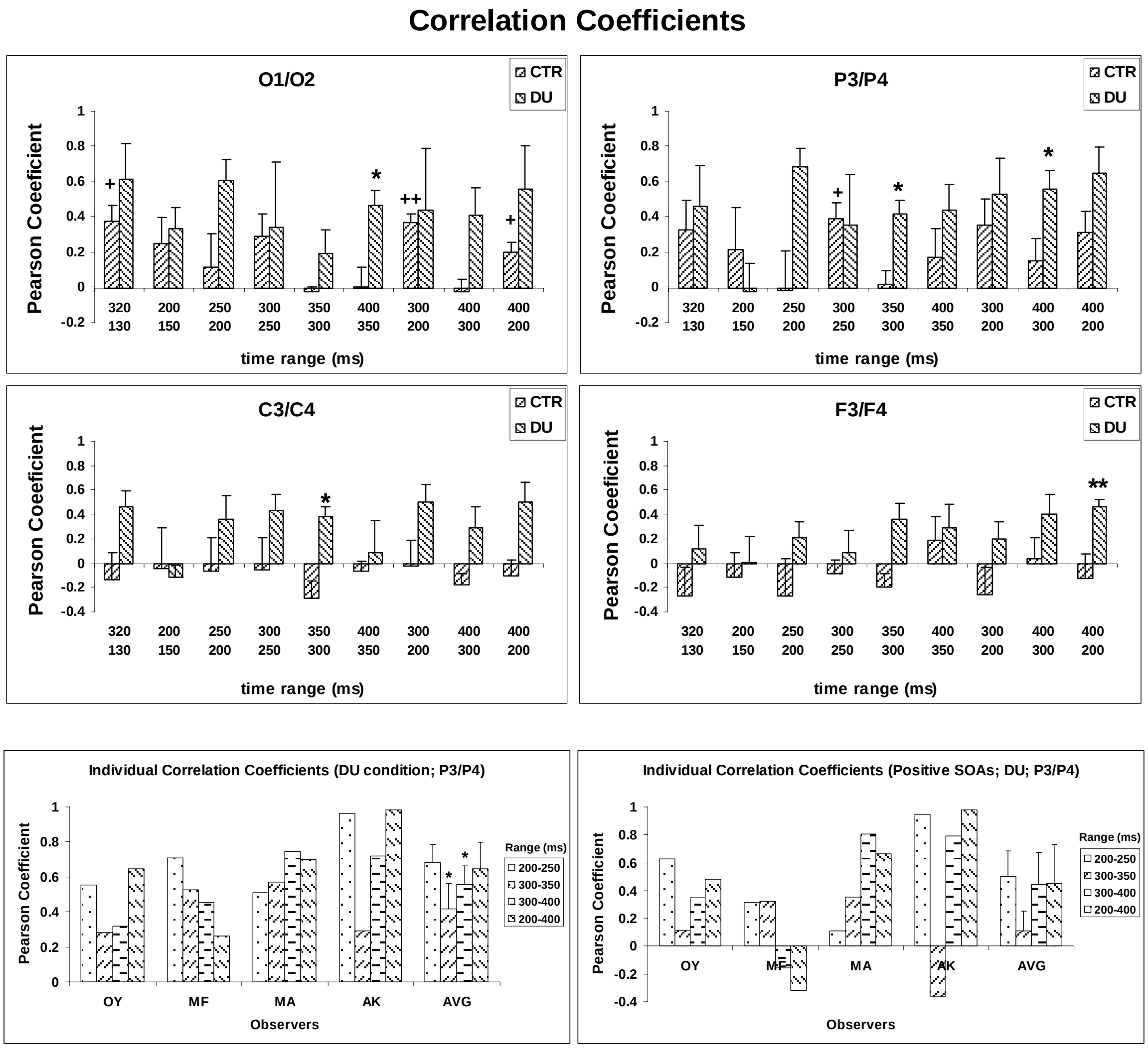


Fig. A.5. Averaged correlation coefficients across observers between behavioral and VEP responses obtained from different time intervals and channel combinations for both CTR and DU conditions (top panel). Individual correlation coefficients for different time intervals in the DU condition obtained from all SOAs (left bottom panel) and positive SOAs (right bottom panel). Error bars represent 1 SEM. The plus and asterisk signs indicate correlation coefficients significantly larger than zero for CTR and DU conditions, respectively: $^{+}p<0.05$, $^{++}p<0.01$, $*p<0.05$, $**p<0.01$ (Individual correlation coefficients are converted to z-scores; one-tail t-test, df=3).

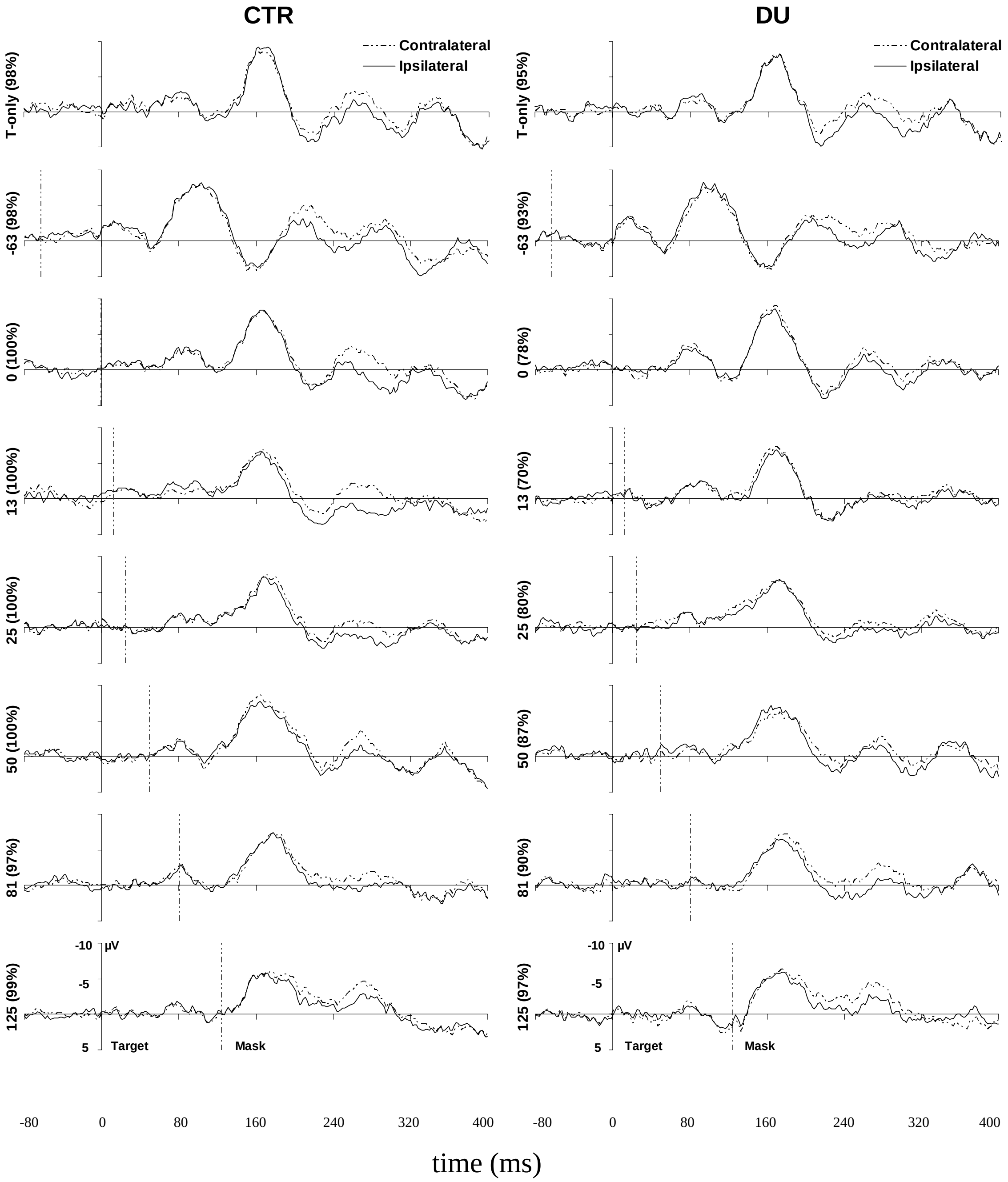


Fig. A.6. VEPs from observer AK.

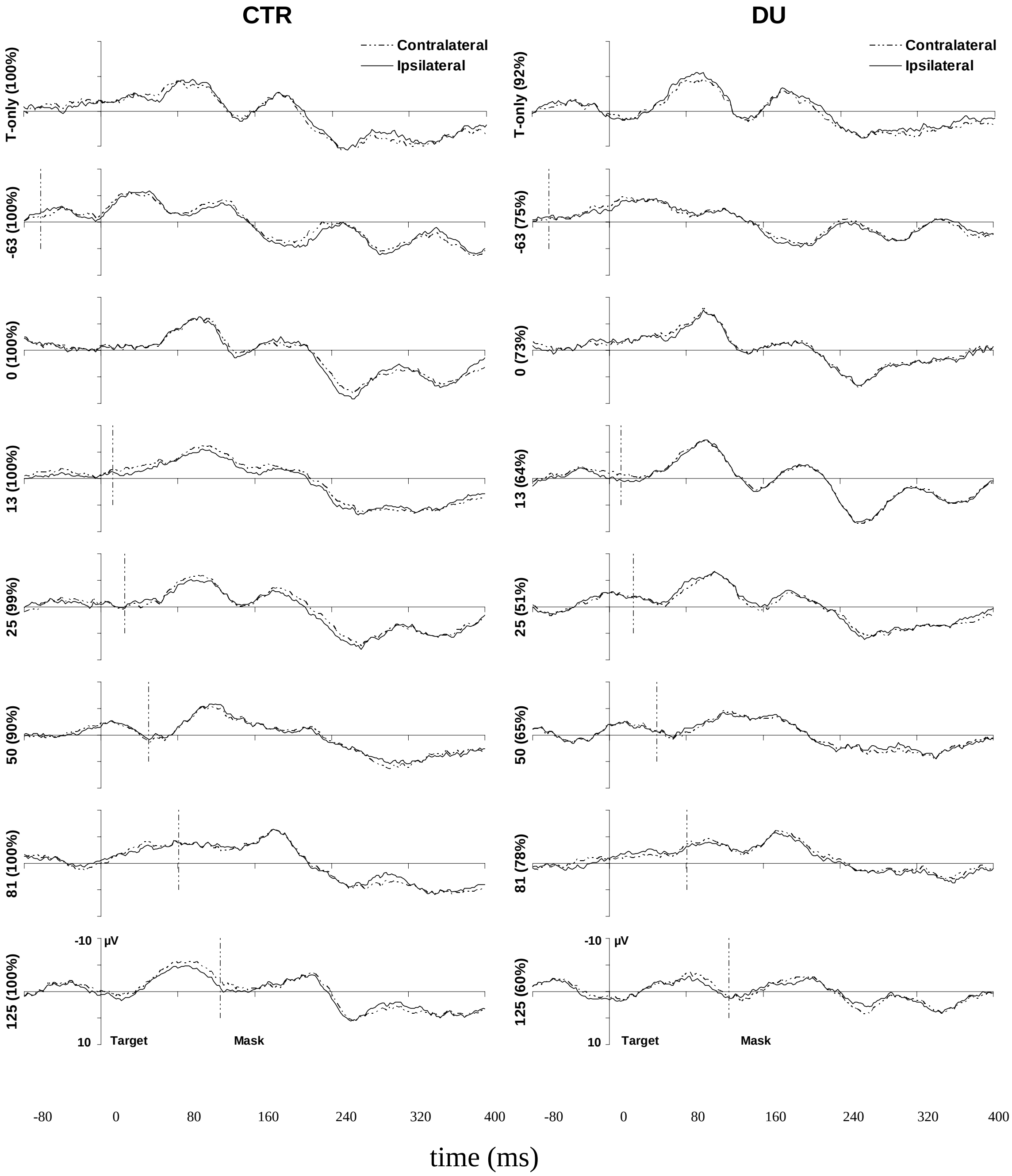


Fig. A.7. VEPs from observer MF.

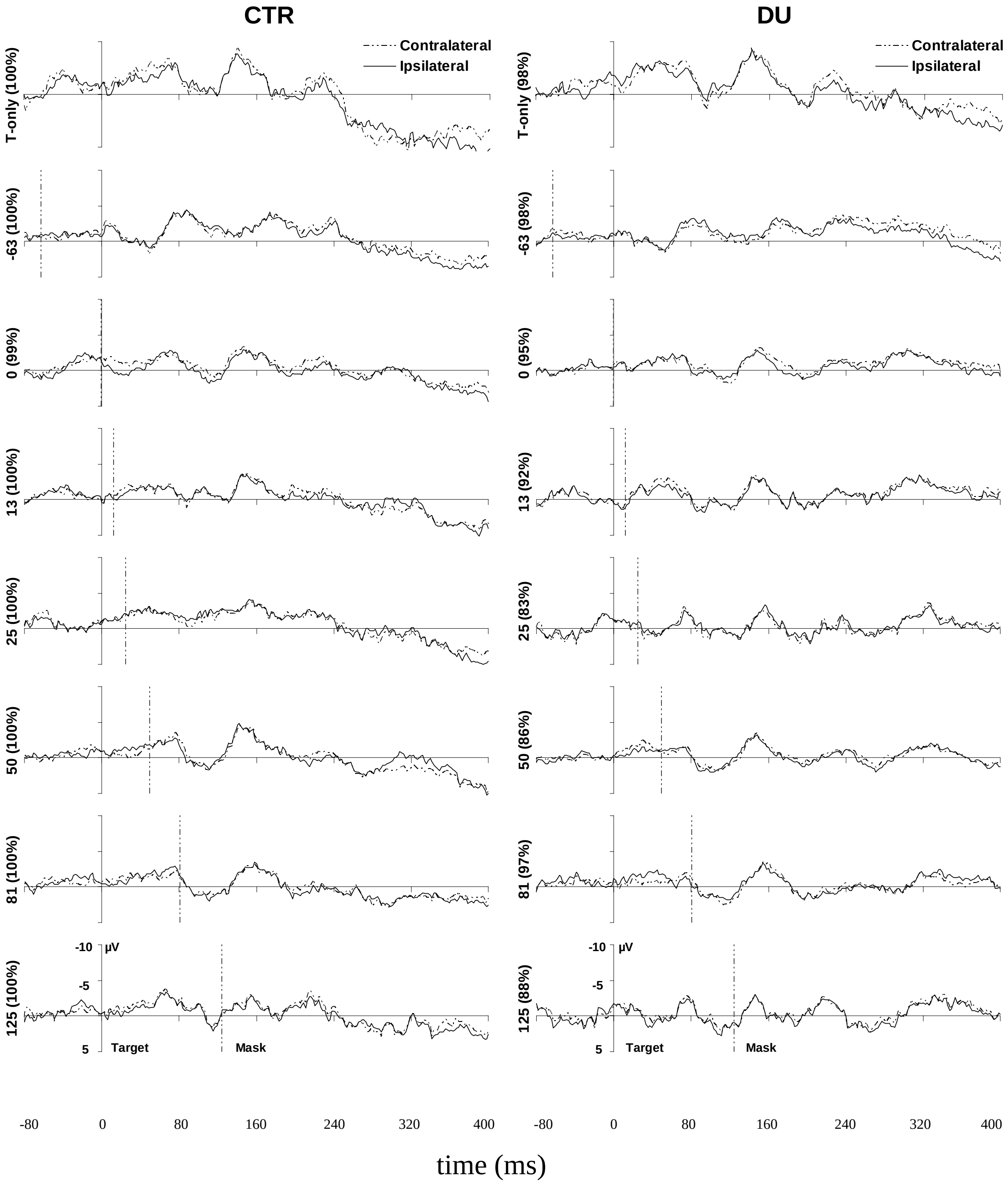


Fig. A.8. VEPs from observer MA.

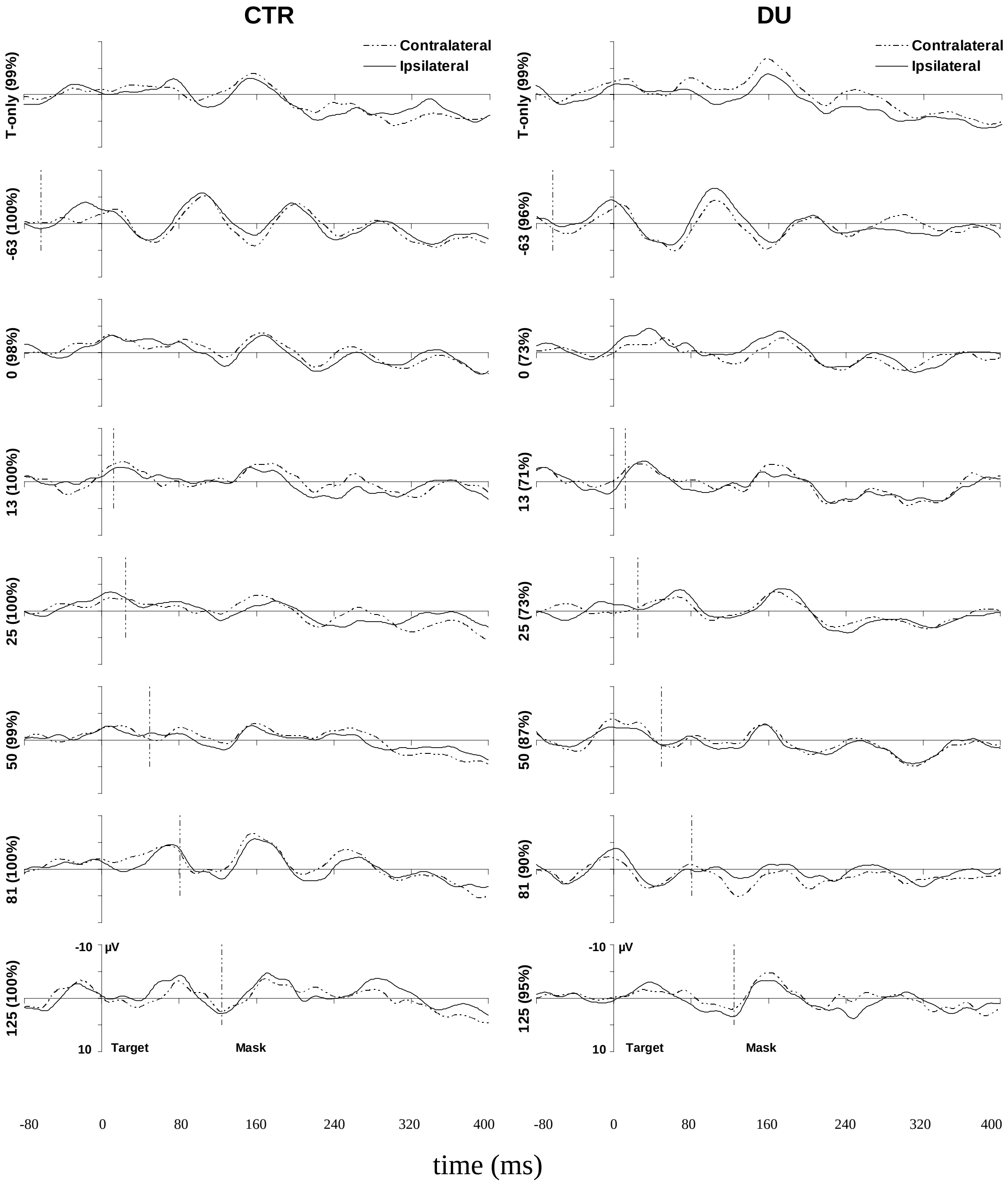


Fig. A.9. VEPs from observer OY.

We also analyzed the results obtained from the first, middle and last 40 trials (Fig. A.10). The optimum SOA in the DU condition is 25 ms in the first and middle 40 trials. The highest masking strength decreases in time and the optimum SOA shifts to 12.5 ms in the last 40 trials. This also agrees with the finding that masking reduces after a perceptual learning period (Breitmeyer, 1984). Response times and VEP responses show similar results as in Fig. 3.2 and Fig. 3.4.

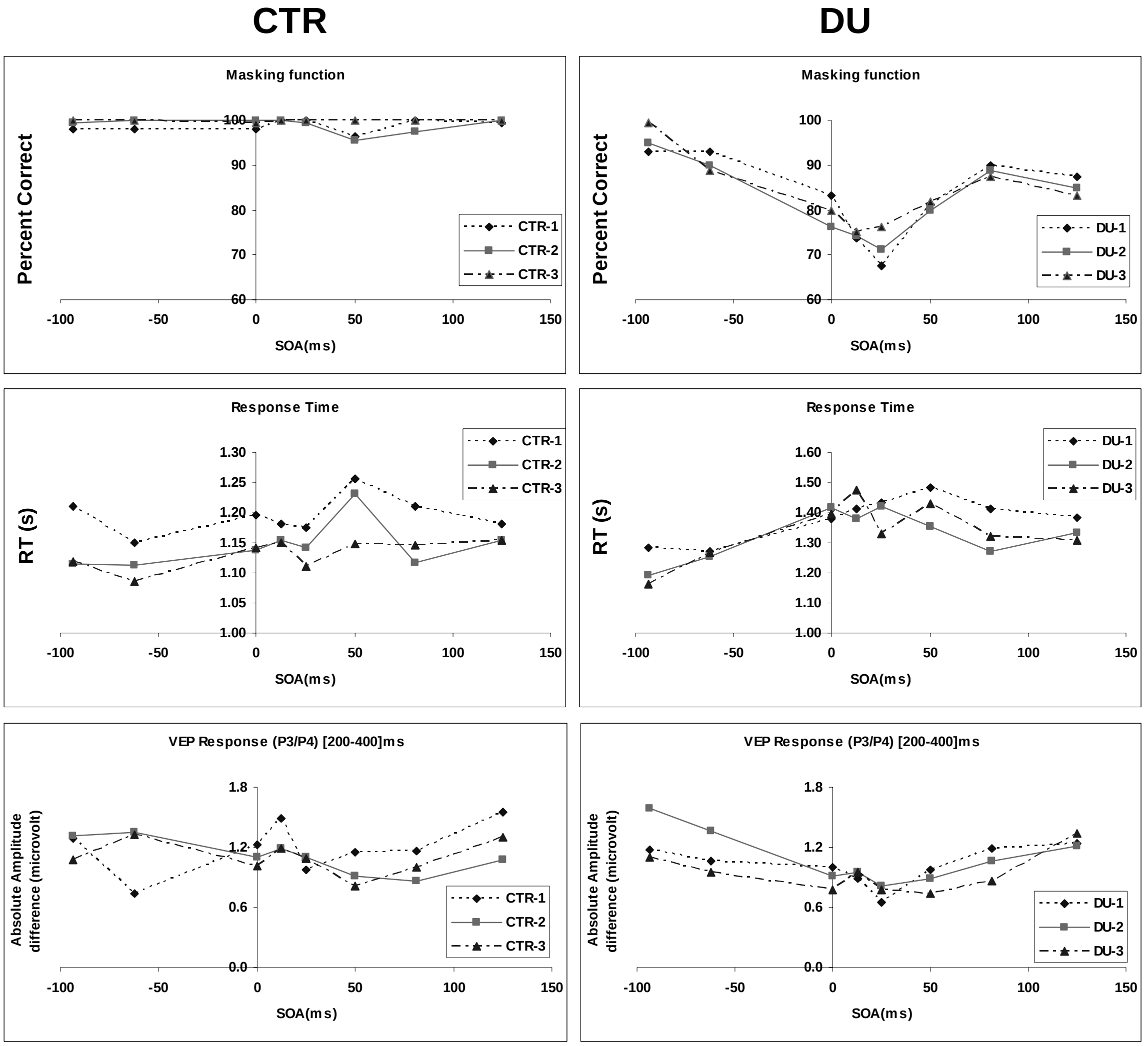


Fig. A.10. Averaged visibility functions, response times and VEP responses across observers from the first 1/3 (dotted-diamond), middle 1/3 (solid-square) and last 1/3 (dashed-triangle) trials for both CTR (left column) and DU (right column) conditions.

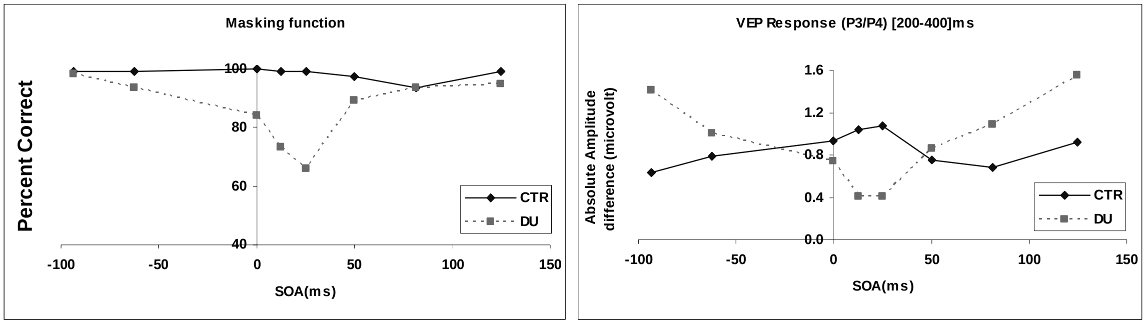


Fig. A.11. Visibility functions and VEP responses obtained from one observer (AK) for both CTR and DU conditions when the stimulus-response is compatible. The shortest SOA (-94 ms) represents target-only presentation.

We also analyzed stimulus-response compatibility in our study and whether the differences between the contralateral and ipsilateral VEPs are contaminated by movement related potentials. In one experiment, we wanted to see whether we obtain similar results as shown above when the stimulus-response (S-R) is compatible. Results obtained from one observer are shown in Fig. A.11. As can be seen, we obtain highly correlated VEP responses with the psychophysical results. It can be considered that in a correct trial since the same hemisphere is used for the response and the stimulus visibility, the S-R compatibility would produce a positive effect in seeing the VEP differences between the contralateral and ipsilateral VEPs. Similarly the less difference would also be attributed to the negative effect of incompatibility between stimulus and response in wrong trials. In order to test whether the S-R compatibility is effective, we collected from one observer when S-R is compatible and incompatible at four SOAs and also in passive view of stimuli from two SOAs in one session. Results are shown in Fig. A.12. As can be seen in this figure, the VEP responses decrease while visibility decreases even when S-R is incompatible or in passive view. This shows that the effect we observe, i.e. the difference between the contralateral and ipsilateral VEPs, almost fully depends on a perceptual factor, i.e. the perceived visibility, occurring in the brain although the activity leading movements can modulate this response since a main attribute of awareness depends on reporting the visibility of a stimulus. Nevertheless, in order to rule out movement related activity in our study, we collected our data as described above from observers by asking them to use their one-hand (right hand thumb finger) in responses. This approach of using one hand was previously used in similar EEG and fMRI studies (e.g., Haynes et al., 2005; Woodman & Luck, 2003).

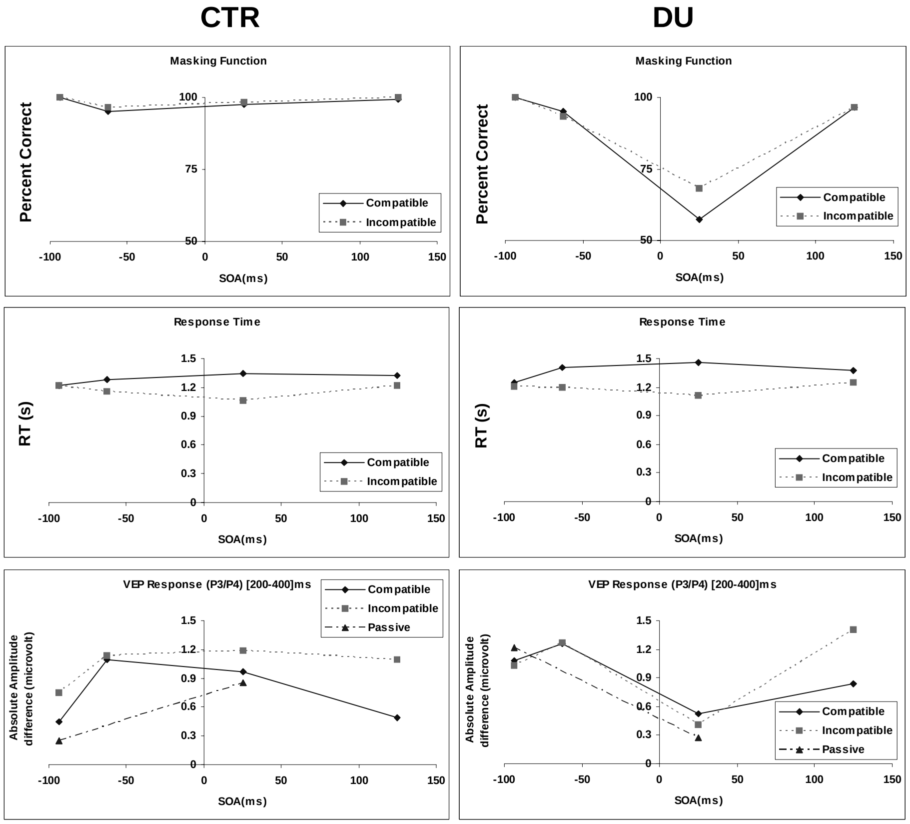


Fig. A.12. Visibility functions, response times and VEP responses obtained from one observer during the conditions that S-R is compatible (dotted-circle), incompatible (solid-square) and stimuli are passively viewed (dashed-triangle) for both CTR (left column) and DU (right column) conditions.