January 2010

Orientation-specific Control of Attention

FENG DU
Washington University in St. Louis

WASHINGTON UNIVERSITY

Department of Psychology

Dissertation Examination Committee:

Richard A. Abrams, Chair
Todd Braver
Janet Duchek
Joel Myerson
Steven Petersen
Mark Rollins

Orientation-specific Control of Attention

By

Feng Du

A dissertation presented to the
Graduate School of Arts and Sciences of Washington University
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

December 2010

Saint Louis, Missouri

ABSTRACT OF THE DISSERTATION

Orientation-specific Control of Attention

By

Feng Du

Doctor of Philosophy in Psychology

Washington University in St. Louis, 2010

Professor Richard A. Abrams, Chairperson

Previous studies have shown that an irrelevant distractor matched to a sought-for color captures attention involuntarily, thus violating either temporal or spatial control of attention. However, whether an irrelevant distractor that matches a sought-for orientation can capture attention is still unknown. A task of rapid serial visual presentation (RSVP) was developed to examine whether an irrelevant distractor oriented in the same way as the target can capture attention. Participants were presented with a sequence of letters at fixation and were required to search for the target letter with a specific orientation. In all five experiments, six peripheral bars flanked the central letters either shortly before or after the appearance of the target letter. The present study found that six homogeneously oriented bars in the periphery (45˚ from the sought-for orientation) did not impair target performance compared to no peripheral bars at all. However, a peripheral orientation singleton that matched the target orientation captured attention and severely impaired central target identification. In addition, a peripheral orientation singleton that was orthogonal to the target orientation also captured attention and produced a similar impairment as the orientation-matched distractor. And the capture effect by the orthogonal singleton (90˚ from the sought-for orientation) was not due to the stimulus-

driven saliency of an orientation singleton because a horizontal singleton (45˚ from the sought-for orientation) did not capture attention in this task. In addition, an orientation singleton that was perpendicular to the target orientation still captured attention when two orthogonal letters that were perpendicular to the target orientation appeared in the central stream. Thus participants did not prioritize the orthogonal orientation (90˚ from the sought-for orientation) for its single occurrence in the central stream. The results indicate that a top-down control setting for a specific orientation does exist, but the orientation-based modulation of attention is not as perfectly tuned to target as color-based modulation. The unexpected capture by orthogonal distractors is likely due to the special characteristic of orientation tuning curves of visual neurons. Some studies showed that a proportion of V2 and V3 neurons in monkeys have bimodal orientation tuning curves with two peaks 90˚ apart (Anzai, Peng & Van Essen, 2007; Felleman & Van Essen, 1987). The present results are consistent with those single cell recording studies. Thus the present results indicate that feature preferences of visual neurons also play an important role in the feature-based attentional modulation. The allocation of feature-based attention is determined by a joint effect of three components including top-down guidance, stimulus saliency and feature preference of visual neurons.

Acknowledgements

The past five years of my study at Washington University has been an incredible journey for me. I am very grateful for having had so many great people mentoring, encouraging, and supporting me along the way. I would like to dedicate this dissertation to all of you.

First and foremost, I would like to express my gratitude to Richard Abrams for all the support and guidance over my years in graduate school. I really appreciate the countless time and amount of energy Richard had devoted to fostering my growth as a research scientist. I have learned many things from Richard, but the most valuable lesson that he taught me was to treat people with kindness and patience. He has been a mentor in the truest sense of the word.

Secondly, I would like to thank the members of my dissertation committee: Todd Braver, Janet Duchek, Joel Myerson, Steven Petersen, and Mark Rollins. Their feedbacks were very valuable for improving the quality of my dissertation work and clarifying the direction of future research. Also big thanks to faculties and staffs of our department who helped me along the process: Dave Balota, Jeff Zacks, Heather Rice, Jim Clancy and Meg McClelland.

Also, thanks to all the members of the Attention and Performance Lab for their support and advice. In particular, I enjoyed working with Chris Davoli and William Knapp on some wonderful research projects. And our undergraduate RAs: Molly Schlamb and David Hahn deserved recognition for collecting a portion of my dissertation data. There are many friends and fellow graduate students: Elaine Tamez, Alfred Yu, Lin Ma, Chi Zhang, and Yunfei Shi, and many more, to them I own big thanks, too.

Last but not least, I would like to convey my thankfulness to my beloved parents. I could not have accomplished any of this without their unconditional love and support. I am so grateful for everything you have done for me.

Table of Contents

List of Figures

Chapter1: Introduction

The visual scenes we are faced with in daily life are complex and constantly changing. These complex scenes present a challenge to our visual system in that multiple objects in the scene are competing with each other for a coherent neural representation. To solve this challenge, selective attention is used to efficiently filter information in the visual system by selecting behaviorally relevant information and keeping unwanted information out.

Over the past 50 years, psychologists and neurophysiologists have investigated the mechanisms of selective attention. Both behavioral and neurophysiological evidence has revealed the existence of some capacity limitations in information processing across the visual system. One of these limitations is in the consolidation of a perceptual representation into short term memory. Other possible limitations are in the processes of response selection and task switching. These capacity limitations make selective attention essential for avoiding overload of visual inputs from a dynamic world. Broadbent (1958) coined the limitation as an information bottleneck. Chapter 2 briefly reviews evidence supporting the existence of an information bottleneck.

The existence of information bottlenecks explains why we need selective attention. But an important question is how selective attention can be used to overcome those bottlenecks in the visual system. Chapter 2 reviews several theories of selective attention which were developed to address this question. For example, Broadbent (1958) developed the modern theory of attention by introducing bottleneck into psychological processing. The bottleneck allows only one stimulus to be processed at a time. Attention

acts as a gatekeeper and selects information to pass through the bottleneck for further processing. In contrast, Kahneman (1973) suggested that there is a capacity limited pool of unspecified cognitive processing resources and attention determines the allocation of limited amounts of resource to different stimuli or tasks. Information is processed in a parallel fashion. Stimuli or tasks with a higher priority receive a greater allocation of cognitive processing resources whereas irrelevant stimuli or tasks receive minimal allocation of attentional resources. More recent theoretical development leading to the biased competition theory (Desimone & Duncan, 1995) is also discussed in Chapter 2. According to the biased competition theory, multiple stimuli compete with each other for a coherent representation in consciousness. The competition between multiple stimuli is resolved by biasing neural representation toward a behaviorally relevant stimulus and inhibiting other behaviorally irrelevant stimuli.

The biased competition theory suggests that attentional bias can be guided by either physical salience or behavioral relevance of stimuli. This idea is consistent with a useful dichotomy of attentional control which was first introduced by Posner (1980). Two sources of attentional bias are exogenous, stimulus-driven bias and endogenous, goal-directed bias of attention. Stimulus-driven bias refers to attentional selection driven by bottom-up saliency of a stimulus which is purely decided by the intrinsic properties of the stimulus. Goal-directed bias of attention is driven by behavioral relevance of a stimulus which is influenced by people's prior knowledge and expectation. Although the two modes of attentional bias can work independently, recent studies reveal an interactive effect between stimulus-driven bias and goal-directed bias. Evidence for these two modes of bias and the simultaneous use of both modes will be reviewed in Chapter 2.

Chapter 3 focuses on feature-based modulation of attention. Recent studies showed that attentional selection is contingent upon sought-for features (features that discriminate a target from distractors) such as orientation, color and direction of motion. Studies have confirmed an important role for color in attention: During search for a target in a specific color, human subjects' attention will be involuntarily captured by an irrelevant distractor possessing the sought-for color (Folk, Remington & Johnston, 1992). And when monkeys perform a similar search, neural responses of V4 cells which prefer the sought-for color are selectively enhanced (Motter, 1994a). Just like color, orientation is another most basic visual feature. Visual analysis of orientation is critical for perceiving textures and segmenting surfaces to segregate figures from the background. However, our understanding of orientation-based capture of attention is relatively poor compared with our knowledge of color-based attention. The present study is designed to address a few key questions about orientation-based control of attention. First, is there a top-down attentional control setting maintaining a specific sought-for orientation? Although the question is a very simple and fundamental one, the answer is not presently known. Second, a recent study found that onset signals enhance attentional capture effects of a target-color-matched distractor (Du & Abrams, 2008, 2010). The results revealed an important synergistic interaction between stimulus-driven salience and goal-directed relevance. But the study only examined selection for color. Thus it is important to ask whether there are synergistic effects between the stimulus-driven salience of an orientation singleton and the goal-directed relevance of a sought-for orientation. Finally, two single cell recording studies showed that an orientation cue does modulate neural responses of cells in visual cortex (Haenny, Maunsell & Schiller, 1988; Maunsell, Sclar,

Nealey & DePriest, 1991). However the patterns of attentional modulation in two studies were inconclusive because two studies showed different distributions of preferred combinations of cue orientation and stimulus orientation. Is there evidence for an orientation-specific control of attention among human subjects? Is there a synergistic effect between stimulus-driven saliency and top-down modulation? To answer these questions, I developed a new method based upon a research paradigm called the spatial blink (Folk, Leber & Egeth, 2002). Both the spatial blink paradigm and the general method of the present study are discussed in Chapter 3.

Five experiments are reported from Chapter 4 – 8. Among them, Experiments 1, 2 and 4 (Chapter 4, 5 and 7 respectively) were designed to examine whether an orientation-specific control of attention exist. Experiment 3 (Chapter 6) was designed to test whether there is a synergistic effect between stimulus-driven saliency and top-down modulation. Experiment 5 was designed to whether the orientation-specific control setting can be applied to either vertical or horizontal orientation. A meta-analysis of the effect size of attentional capture across five experiments was performed in Chapter 9. Chapter 10 is the general discussion which summarizes results from all five experiments. The theoretical contribution of the present dissertation was also discussed in Chapter 10.

Chapter 2: Visual Attention

We receive a continuous bombardment of visual information every day. However, our visual system has a limited capacity in multiple modules of visual processing. This limitation in the visual system, known as a bottleneck of information processing (Broadbent, 1958), enables selective attention to play a vital role in avoiding an overload of visual inputs. Depending on the temporary nature of the bottleneck, selective attention can either occur at an early stage (pre-perceptual stage) or a late stage (post-perceptual stage). Depending on the underlying mechanism of attention, there are two fundamentally different ways for selective attention to overcome information bottlenecks in the visual system. One way to avoid information overload is to restrict information processing in a small area of visual space. This type of attentional modulation is called location-based selection in that attentional process occurs at a particular spatial location. The alternative way to avoid information overload is to selectively process a subset of stimuli which possess sought-for features. This type of attentional modulation is a feature-based modulation that is strictly contingent upon a particular feature that subjects are looking for. The present chapter starts with evidence supporting existence of information bottlenecks, then a discussion about the locus of attentional selection, followed by a review of both location-based and feature-based attentional modulation.

In addition, the present chapter also reviews biased competition theory. A classical point of view usually treats selective attention as an excitatory mechanism which enhances visual processing at a selected location. In contrast, the biased competition theory emphasizes that a central role of attention is to bias competition for conscious representation in favor of a behaviorally relevant stimulus. Attentional bias can be a

5

location-based bias that is in favor of stimuli occupying a relevant spatial location. Alternatively attentional bias can be a feature-based bias in favor of stimuli possessing a behaviorally relevant feature such as a sought-for color or shape. And a feature-based bias is not necessarily limited to a specific location—it can extend throughout the visual field. Moreover, this biased competition theory suggests two sources of attentional bias. These modes of attentional biases, including both bottom-up influences (stimulus-driven saliency) and top-down feedback mechanisms (goal-directed relevancy), are also discussed in the chapter.

Bottlenecks of information processing

The capacities of information processing mechanisms, especially for some central processing modules, are limited (Broadbent, 1958; Chun & Potter, 1995; Desimone & Duncan, 1995; Kahneman, 1973). Many dichotic listening experiments clearly showed that listeners usually had very poor performance when they were presented with two questions simultaneously. And this origin of difficulty in dealing with two questions at the same time is probably perceptual in nature. For example, Broadbent (1958) presented subjects with a visual cue either before or after two auditory questions. The cue indicated which question subjects needed to answer. He found that subjects had much better performance in the pre-cue condition than the post-cue condition. In fact, subjects in the post-cue condition did not perform better than subjects who received no cue at all. More evidence along these lines comes from "shadowing" experiments. When listeners are required to "shadow" a message from the attended ear (repeat it out loud) and ignore a message from the other ear, most listeners cannot even identify whether the non-attended

message is in a male's or female's voice (Broadbent, 1958). But not everything from the non-attended message is missing: Listeners can report their own name embedded in a non-attended message (Moray, 1959).

The aforementioned evidence implicates a gate with an extremely limited processing capacity. This gate was initially termed as **bottleneck**, allowing only one message from one channel to be attended at a time (Broadbent, 1958). In the filter model, Broadbent (1958) proposed that a bottleneck occurs before pattern recognition, and that attention determines what information reaches the pattern recognition stage. This model asserts that a selective filter (selective attention) allows information to come in from only one channel at a time, to be processed for pattern recognition. But Broadbent's filter model was soon challenged by his followers. For example, Treisman (1960) found that semantic information of context can cause listeners to report relevant information from the unattended ear. This contextual "intrusion" effect from the unattended ear and the cocktail party effect (people can pick up a whisper of their own names even in a noisy crowd) called for a new bottleneck theory. Thus Treisman proposed in her attenuation theory that a selective filter (selective attention) does not completely filter out unattended messages. Instead, it causes a decrease in the perceived intensity of an unattended message. As a result, this unattended message is usually not strong enough to reach its threshold unless it has a very low threshold to begin with (e.g. a person's name or other emotionally evoking stimuli).

The locus of attentional selection

In general, bottleneck theories take selective attention as a filter of information. These theories initially suggested that attentional selection occurs at an early stage of information processing, and more specifically, before perceptual recognition. This proposition invoked a hot debate about the locus of attentional selection. Therefore, bottleneck theories were divided into two groups: Early selection theories and late selection theories. Early selection theories posited that selective attention occurs at an early stage in order to protect perceptual processes from being overloaded (Broadbent, 1958; Treisman, 1960). On the contrary, late selection theories suggest that selective attention operates at a later stage after perception. Selective attention works in that way to protect some central processes (such as consolidation into short term memory) from being overloaded (Norman, 1968). The cocktail party effect (Moray, 1959) and contextual "intrusion" (Treisman, 1960) were initially cited as evidence against early selection theories because some semantic information from an unattended source remains accessible after perception and eventually influences subjects' response. However, these two findings were insufficient for rejecting early selection theories because early selection theories can accommodate the two findings by assuming a relatively low detection threshold for familiar stimuli such as one's name. Nevertheless, more and more studies provided convincing evidence in favor of late selection theories. For example, Sperling (1960) showed that a spatial cue shortly after visual presentation enhanced the memory performance of the cued stimulus. Since cues were presented after the stimuli, it is simply impossible for the cues to have improved perceptual processing. Instead, location-based attentional selection occurs at a post-perceptual stage in working memory.

Studies of the Psychological Refractory Period (PRP) also support late selection theories of attention. In a typical experiment of PRP paradigm, participants are asked to perform two separate speeded tasks (T1 and T2) in rapid succession. Psychological Refractory Period refers to the slack time in response to the second task (T2) when it is present at short T1-T2 stimulus onset asynchrony (SOA). But late selection theories and early selection theories offer different explanations of the origin of PRP. For example, a typical late selection theory assumes that perceptual processes for both T1 and T2 can operate simultaneously. However, there are bottlenecks in central processes after perception that can process only one task at a time. When those central processing mechanisms are engaged by T1, the central processes of T2 are delayed. Thus a late selection theory predicts that factors influencing speed of T2 perception, such as a reduction in contrast of T2, would increase RT of T2 at long SOAs much more than that at short SOAs, whereas factors that slow central processes of T2 (e.g. response selection) would increase RT of T2 to an equivalent extent irrespective of SOA. In contrast, an early selection theory predicts that a reduction in contrast or response selection would increase RT of T2 to the same extent for different SOAs (Luck & Vecera, 2002).

The prediction based on late selection theory has received support from many studies. For example, Pashler (1984) used a search task either as a single task or as a T2 task in a PRP paradigm. He manipulated both the contrast of the stimuli in the search display and the absence/presence of a target. He found that lowering contrast slowed down visual search to a greater extent when search was performed alone than when it was performed shortly after T1. But absence/presence of target had essentially the same effect on search under single-task and PRP dual task conditions. Thus Pashler (1994) argued that response

selection of T2 rather than perception of T2 is postponed in the PRP paradigm. The results also indicated that attentional selection occurs at some post-perceptual stages. This conclusion has also been confirmed by event-related-potential (ERP) studies. A study showed that the P3 wave (an index of perception and categorization) is not delayed when the T1-T2 interval is short in a PRP paradigm (Luck, 1998), whereas components that follow response selection are delayed (Osman & Moore, 1993).

More evidence came from recent studies on a rapid serial visual presentation task (RSVP) called attentional blink. In an attentional blink (AB) task, subjects are presented with a stream of visual stimuli at a rapid speed of 10 items per second and required to report two targets embedded in that RSVP stream. If they correctly report the first target (T1), they are most likely to miss the second target (T2) if it follows within about 500 ms of T1 in the same location (Raymond, Shapiro, & Arnell, 1992). The impairment of T2 performance, or "blink", lasts for a few hundred milliseconds. Studies on AB suggested that attentional selection may be driven by bottlenecks at post-perceptual processing stages such as short-term consolidation into working memory and response selection (Chun & Potter, 1995; Jolicoeur, 1999; Jolicoeur & Dell'Acqua, 1998; Vogel, Luck & Shapiro, 1998). For example, Shapiro and colleagues found the visual cocktail party effect during the "blink" period of AB. The results indicated that some information such as participants' own name can survive AB (Shapiro, Caldwell & Sorensen, 1997). In addition, stimuli presented during the "blink" period still produce a priming effect though they cannot be correctly reported by subjects (Shapiro, 1997). More electrophysiological data also implicate a post-perceptual origin of AB impairment. For example, a study showed that missed words, which participants failed to report in AB task, are able to

induce the same amplitude of N400 wave (an index of semantic processing) as the correctly reported words (Luck, Vogel & Shapiro, 1996). Thus some semantic information of words is accessible even when those words are seemingly filtered out by selective attention. In conclusion, many studies provide converging evidence that the delayed working memory consolidation of T2 is the origin of AB impairment (Chun & Potter, 1995; Vogel & Luck, 2002; Vogel, Luck & Shapiro, 1998).

Even though early selection theories cannot accommodate many of the findings from dual-tasks studies, it does not mean that selective attention always occurs at post-perceptual stages. On the contrary, electrophysiological data convincingly showed that attention can also occur before perceptual categorization. For example, it has been confirmed that early components of ERP responses, such as N1 and P1 waves, start to differentiate stimuli at attended locations from those at unattended locations at about 100 msec of stimulus onset (Heinze, Luck, Mangun & Hillyard, 1990; Magun, 1995; Mangun & Buck, 1998). Single cell recording from monkeys also indicates that attention can modulate sensory process at intermediate visual area V4 (Luck, Chelazzi, Hillyard & Desimone, 1997). Stimuli at attended locations, compared to stimuli at unattended locations, elicit higher firing rates in V4 neurons as early as 60 ms after stimulus onset. Therefore, attention also modulates the early sensory processing at the extrastriate area of visual cortex, at least under some conditions (Luck & Vecera, 2002).

Spatial attention and "spotlight" metaphor

Visual inputs from a complex scene at a given moment would have certainly overloaded our visual system if it had not been modulated by selective attention. An

obvious solution is to process stimuli from a restricted area of the visual field. As a result,

spatial attention has been one of hottest areas of attention research for more than 50 years.

One classic research paradigm for studying spatial attention is the cuing paradigm.

Numerous studies showed that once a location is selected by covert attention (without eye

movement to that location) in advance, the information processing is largely enhanced at

that location. For example, many cuing studies showed that detection or discrimination of

targets at an attended location is usually faster and more accurate than that at an

unattended location (Henderson, 1991; Posner, 1980; Posner, Snyder & Davidson, 1980;

Vierck & Miller, 2008). Therefore, visual spatial attention is often thought to be an

excitatory mechanism. The main analogy of spatial attention is that of a spotlight moving

across an internal representation of space like a flashlight moving at night. Only objects

within the beam of the attentional "spotlight" can be selected and receive further

processing (Eriksen & Eriksen, 1974), whereas objects out of the spotlight are filtered. As

a refinement of the spotlight model, the zoom lens model suggested that the size of the

attentional "spotlight" changes adaptively according to task demands. The zoom lens

model is consistent with a lot of behavioral studies which showed that the spatial filter of

attention does change size (Turatto, Benso, Facoetti, Galfano, Mascetti & Umilta, 2000;

Yeshurun & Carrasco, 1998)

The spotlight metaphor of attention not only accords with behavioral data but also

receives supports from single cell recording studies on monkeys. Many studies reported a

location-based facilitatory effect of attention when there is only one stimulus in the

receptive field (McAdams & Maunsell, 1999, 2000; Spitzer, Desimone & Moran, 1988).

They showed that neural responses of an attended stimulus are much stronger than that of

an unattended otherwise identical stimulus when there is no competing stimulus in the receptive field (Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Luck et al. 1997; McAdams & Maunsell, 1999).

In addition, spatial attention has been demonstrated to dramatically increase the baseline firing rate of neurons (up to 30-40%) in visual cortex even when there was no visual stimulus in the RF (Luck et al. 1997). In accordance with this baseline firing rate increase, Kastner and his colleagues found, using FMRI, that spatial attention enhances neural activity in visual cortex in the absence of visual stimulation (Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999). Converging evidence from ERP studies showed that spatial attention can selectively enhance sensory processing in extrastriate cortex but not within striate cortex when a target location is selected in advance (Mangun, 1995; Mangun & Buck, 1998). Moreover, an ERP study confirmed that post-perceptual cognitive processes are also enhanced by spatial attention (Mangun & Buck, 1998).

Inhibitory effect of attention

The spotlight metaphor implies an excitatory effect rather than an inhibitory effect of attention. The intuition that selective attention is the same as facilitation at an attended location is inaccurate or at least incomplete. Many psychological studies clearly showed that selective attention also filters out unwanted information by inhibiting recently visited locations or irrelevant stimuli.

The first line of evidence for an inhibitory effect of attention is studies of inhibition of return (IOR). Posner and his colleagues first discovered inhibition of return by using a classical cuing paradigm (Posner & Cohen, 1984; Posner, Rafal, Choate & Vaughan,

1985). When the stimulus onset asynchrony (SOA) between exogenous cues and subsequent targets is less than 300ms, an exogenous cue (e.g. an uninformative peripheral flash) can orient attention reflexively toward the cued location and produce facilitation at that location (a relatively faster RT at a cued location compared with that at an uncued location). But when the SOA is longer than 300ms, facilitation changes to inhibition (a slower RT to targets at a cued location than that at an uncued location). IOR was initially found to be associated with cued locations (Posner & Cohen, 1984). More recent studies also indicated that IOR can be tagged to objects (Tipper, Driver, & Weaver, 1991).Thus Klein (2000) proposed that IOR is important for survival because it encourages orienting towards novel locations or objects, and hence might facilitate foraging and other search behaviors

By naming the poorer performance at previously attended locations 'inhibition of return', Posner et al. implied both a cause and an effect. The cause of IOR was attributed to orienting of attention towards a location and subsequent removal of attention from that location. The effect was to discourage attention from re-orienting back to an originally attended location. Since a shift of attention towards and then away from a cued location seemed strongly implicated, IOR usually does not follow a shift of attention that was directed endogenously (voluntarily) by an arrow presented at fixation (Posner & Cohen, 1984; Rafal et al., 1989). But a recent study indicated that IOR might be masked by a sustained facilitation of endogenous attention (Weger, Abrams, Law & Pratt, 2008). And Weger et al. found that IOR can be observed even when orienting is guided by a voluntary control setting of attention.

It also has been demonstrated that oculomotor programming plays an important role in creating IOR (Rafal et al., 1989). In the Rafal et al. study (1989), they presented arrows at fixation or luminance changes in the periphery to signal the observer to execute or prepare an eye movement (saccade) or to shift visual attention without shifting gaze. A delayed response to a target was found if the target was presented at a location that subjects had planned to fixate or actually had just fixated, irrespective of central or peripheral cue. By contrast, when subjects were instructed to keep their eyes fixed and to make covert orienting of attention, the IOR effect was observed only following peripheral cues but not observed following central cues. This result indicates that the machinery responsible for eye movements may be critical for IOR.

The second line of evidence for inhibitory effects of attention comes from negative priming studies (Christie & Klein, 2008; Fox, 1995; Fox & De Fockert, 1998; Milliken, Joordens, Merikle & Seiffert, 1998; Tipper, 2001). Negative priming usually refers to a negative effect on performance when a current target was an ignored distractor on a previous trial. Therefore it is also referred to as negative priming from ignored distractor (Christie & Klein, 2008; Fox, 1995). Tipper (2001) proposed that negative priming is a manifestation of inhibitory mechanisms of attention. Distractors are usually inhibited by attention and this inhibition can be transferred to subsequent trials if a previous distractor becomes a target, thus causing a negative priming effect. But this proposition of residual inhibition of attention was challenged by some other findings. For example, Fox and De Fockert (1998) manipulated intensity contrast between letter displays and their background. Letter displays were presented with either high contrast (white letters against a black background) or low contrast (dark gray letters against a black background). They

15

found that negative priming is maximal when prime and probe displays shared the same intensity contrast. The results indicated that greater similarity between prime and probe displays results in improved retrieval of prime display information, thus causing larger negative priming if retrieved information is incongruent with current inputs. The results are consistent with an episodic retrieval account of negative priming. An episodic retrieval account of negative priming suggests that incongruence between retrieved information and current inputs is the cause of negative priming. A more recent study showed that a so called negative priming effect is an IOR in disguise (Christie & Klein, 2008). Though negative priming may be caused by something other than an inhibitory mechanism of attention, no solid evidence can completely rule out residual inhibition of attention model (Tipper, 2001).

Feature-based selection of attention

Though the cuing paradigm is valuable in revealing the nature of spatial attention (location-based attentional selection), it is ecologically confined in that people usually do not have prior knowledge of where to look when they search in a cluttered scene. Instead, people usually have prior knowledge of a target-defining feature (e.g. the color red when looking for a friend wearing a red baseball hat). In the last two decades, studies have demonstrated that selective attention can operate upon a specific feature of target objects, such as orientation (Haenny, Maunsell & Schiller, 1988; Haenny & Schiller, 1988; Maunsell, Sclar, Nealey & DePriest, 1991), color and luminance (Folk, Leber & Egeth, 2002; McAdams & Maunsell, 2000; Motter, 1994a & 1994b; Serences, Shomstein, Leber, Golay, Egeth & Yantis, 2005; Serences & Yantis, 2007), and direction of motion

(Serences & Boynton, 2007; Treue & Maunsell, 1996, 1999), sometimes even complicated figures (Chelazzi, Duncan, Miller & Desimone, 1998).

More interestingly, an effect of feature-based attention is able to override that of location-based attention. For example, Motter (1994a & 1994b) showed that prior knowledge of target color can enhance the neural response of many V4 cells which selectively respond to the target color and whose RF spreads across the whole visual field. Consistent with this line of physiological evidence, many behavioral studies revealed similar dominance of feature-based attention over location-based attention (Du & Abrams, 2008, 2009; Folk, Leber & Egeth, 2002; Folk, Remington & Johnston, 1992; Folk, Remington & Wright, 1994; Serences et al., 2005). We will further discuss the effect of feature-based attention in Chapter 3.

Biased competition theory

Coexistence of attentional facilitation and inhibition calls for a theoretical model of attention beyond an excitatory model such as the spotlight metaphor. This call has been adequately answered by a biased competition theory (Desimone, 1998; Desimone & Duncan, 1995). In the presence of multiple stimuli, a competition between multiple stimuli for neural representation is a critical challenge to the visual system. According to the biased competition theory, a competition between many stimuli is solved by biasing neural representation toward a behaviorally relevant stimulus and inhibiting other behaviorally irrelevant stimuli. This attentional bias can be guided by either physical salience (stimulus-driven salience) or behavioral relevance of stimuli. The current section reviews the biased competition theory, starting with an introduction of two visual

pathways with dissociable functions, then discussing evidence about neural competition in visual pathways, and finally ending with a review of studies supporting attentional bias.

Ventral and Dorsal visual pathways

Anatomical and physiological studies on monkeys have shown that the visual cortex of monkeys is organized into two functionally specialized processing pathways (Ungerleider & Mishkin 1982, Desimone & Ungerleider 1989). The occipitotemporal pathway, or ventral stream, originates in the primary visual cortex (V1) and goes through the extrastriate cortex including V2 and V4, further extending into the inferior temporal cortex (IT). The ventral stream is also known as the "what" pathway because it plays an essential role for identifying objects. By contrast, the occipitoparietal pathway, or dorsal stream, extends from V1 through the extrastriate cortex (V2 and V3) to the middle temporal (MT) area, and then to the parietal cortex. The dorsal stream, also known as the "where" pathway, is crucial for the appreciation of the spatial relations among objects as well as for the visual guidance of movements toward objects in space (Ungerleider & Mishkin 1982, Goodale & Milner 1992).

A remarkably similar organization within the human visual cortex has been revealed by functional brain imaging studies. Haxby and colleagues have tested the functional dissociation of two visual pathways by having subjects perform object-identity and spatial-localization tasks (Haxby et al 1994, Ungerleider & Haxby 1994). These studies showed that regions of the ventral stream activate in object-identity tasks, whereas regions of the dorsal stream activate in spatial-localization tasks. Other brain imaging studies have shown that neural activation correlated with the perception of color and faces mainly occurs in the vicinity of V4, as well as in areas of inferior temporal lobe

(Zeki et al 1991, Haxby et al 1994, Kanwisher, McDermott & Chun, 1997). On the contrary, areas associated with the dorsal stream, particularly in a region that seems homologous to monkey MT, shows selective activation during perception of motion (Zeki et al 1991, Watson et al 1993, Tootell et al 1995).

Other results from lesion studies and single-cell recordings are also consistent with this functional specialization of two visual pathways. For example, neurons in areas V4 and IT of the ventral stream show selective response for important stimulus attributes such as shape and color (Desimone & Ungerleider 1989; Zeki et al, 1991). More interestingly, different neurons in IT are specialized for recognizing faces and many other complex forms (Rolls & Tovee, 1995; Wachmuth et al, 1994; Kanwisher et al, 1997; Desimone & Ungerleider, 1989). By contrast, neurons in the middle temporal (MT) area are primarily devoted to motion processing because they show response selectivity for the speed and direction of stimulus motion (Newsome & Pare, 1988; Andersen et al 1997).

Competition among multiple stimuli within visual pathways

Multiple objects in a scene compete for a neural representation when they are presented in a single RF. Single-cell recording studies on monkeys have shown that the response to a pair of stimuli within a single RF is a weighted average of the responses to each individual stimulus presented alone (Chelazzi, Duncan, Miller & Desimone, 1998; Desimone, 1998; Moran & Desimone 1985, Reynolds et al 1999; Sato, 1989). These results indicate that two stimuli present at the same time within a neuron's RF interact with each other in a mutually suppressive way. This sensory suppressive interaction among multiple stimuli presented within the same RF has been interpreted as a manifestation of neural competition between multiple stimuli.

The competition among multiple stimuli within a single RF has been shown to occur in many levels of the ventral stream. For example, Kastner and his colleagues presented subjects with four stimuli in four nearby locations either sequentially or simultaneously while subjects were counting letter T or L at central fixation. It was predicted that activation in the simultaneous presentation should be less than that in the sequential presentation because sensory suppression among stimuli can only take place in simultaneous presentation. Although the BOLD signals in V1 were similar in the two presentation conditions, the activation in V2 was reduced in the simultaneous condition compared with the sequential condition, and this reduction was even more pronounced in V4 and temporo-occipital cortex (TEO), as predicted if the sensory suppression is scaled to the RF size of neurons in visual cortex. That is, the small RFs of neurons in V1 and V2 would encompass only a small portion of the visual display, thus less sensory suppression. However, the larger RFs of neurons in V4 and TEO would encompass all four stimuli, causing more sensory suppression (Kastner, De Weerd, Maisog, Desimone & Ungerleider, 1997).

The idea that sensory suppressive interactions are scaled to RF size was directly examined by manipulating the spatial separation between four stimuli in some follow-up studies (Kastner, De Weerd, Desimone & Ungerleider, 1998; Pinsk et al 1999). According to the RF hypothesis, the magnitude of sensory suppression should be inversely related to the degree of spatial separation among the stimuli. In agreement with this idea, separating the stimuli by 4˚ abolished sensory suppressive interactions in V2, reduced them in V4 but did not affect them in TEO. Separating the stimuli by 6˚ led to a

further reduction of sensory suppression in V4, but again had no effect in TEO (Kastner et al 1998, Pinsk et al 1999).

Neural mechanism of attentional bias

Some of the strongest support for the biased competition theory came from studies of neurons in inferior temporal (IT) cortex of macaque monkeys (Chelazzi et al. 1993, 1998). In these studies, the monkeys were rewarded for making an eye movement to a target object in an extrafoveal array of multiple stimuli. Among the search array of stimuli, one stimulus was a `good' stimulus for the cell (i.e. it would elicit a strong response when presented alone) and one or more stimuli were `poor' stimuli for the cell (i.e. it would elicit little or no response when presented alone). Attentional modulation is revealed by a differential response to the good stimulus on trials when it was the target compared with trials when the same good stimulus was a distractor (when the poor stimulus was the target). The results showed the initial population responses to a two stimulus choice array were the same, regardless of whether the good or poor stimulus was the target. Thus, several stimuli appearing in the visual field initially activate their cortical representations in parallel, consistent with the biased competition model. But about 200ms after the onset of the choice array, the responses diverge dramatically depending on which stimulus was the target. When the good stimulus is the target, the response to the good stimulus (also relevant with task goal) in the array remains high until the time of the eye movement. In contrast, when the poor stimulus is the target, the response to the good stimulus (now irrelevant with task goal) in the array becomes strongly suppressed over the course of approximately 100 ms. By the time monkeys overtly selected a target, cells respond as though the irrelevant good stimulus has been filtered from the visual field. These results

illustrated some of the basic components of the biased competition model, including an initial parallel activation of cortical representations of multiple stimuli in the visual field, and the ultimate suppression of responses to the behaviorally irrelevant stimuli.

If there is no attentional modulation, however, multiple stimuli in a single RF interact with each other in a mutually suppressive way. For example, the single cell response to both a `good' stimulus and a `poor' stimulus within a single RF is a weighted average of the responses to each individual stimulus presented alone (Chelazzi, et al., 1998; Desimone, 1998; Moran & Desimone 1985, Reynolds et al 1999; Sato, 1989). The results indicate that neurons cannot effectively discriminate a stimulus from another without help of attentional modulation.

Consistent with the finding of attentional bias in IT cortex, selective attention also biases neural responses in V2 and V4 to a relevant stimulus when two stimuli compete within a same receptive field (Moran & Desimone 1985; Luck et al. 1997; Reynolds, Chelazzi, Luck & Desimone, 1994; Reynolds, Nicholas, Chelazzi, & Desimone, 1995). If the good stimulus for a cell is attended, the response is strong. If the poor stimulus is attended, the response to the good stimulus in the receptive field is greatly suppressed.

Attentional bias has also been reported to operate in the dorsal stream of the visual system (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996, 1999). Researchers used the same strategy that had been used in V4 and IT cortex to study attentional selection of one of two competing stimuli in the cells of middle temporal cortex (MT) and medial superior temporal cortex (MST). They chose one stimulus to be a good stimulus for the recorded cell (moving in its preferred direction) and the other to be a poor stimulus (moving in the opposite direction). The response to

22

the good stimulus, when it was attended, was compared with the response when it was an irrelevant distractor. When both good and poor stimuli were in the same receptive field of cells in either MT or MST, the response of the cell was almost completely determined by the attended stimulus (direction of motion), similar to what has been found in V2, V4, and IT cortex. The response was good when the animal attended to the stimulus moving in the preferred direction of the cell and poor when animal attended to the stimulus moving in the opposite direction. A smaller effect of attention was found when one of the two stimuli was moved outside the receptive field, presumably reducing local suppressive interactions in these areas. This inverse dependence of an attentional effect on the spatial separation between the stimuli is inconsistent with any simple facilitatory model of attention but is compatible to the biased competition theory.

In addition, many studies revealed that spatial attention modulates neural responses of cells in different areas (including V1, V2 and V4) of visual cortex of monkeys in a way consistent with the biased competition theory (Desimone & Duncan, 1995; Moran & Desimone, 1985; Motter, 1993; Luck, Chelazzi, Hillyard & Desimone, 1997). For example, Motter (1993) found more than one third of neurons in V1, V2 and V4 showed different tuning curves to orientations when attention was directed toward versus away from the location of receptive field. More specifically, spatial attention can either enhance neural response in some cells or produce inhibitory effects on orientation tuning curves in other cells. Moreover, this attentional modulation on orientation tuning curves is more prominent when the target is accompanied by competing distractors in the same receptive field than when target is presented alone (Moran & Desimone, 1985; Motter, 1993; Luck et al., 1997). Consistent with Motter's finding, Luck et al (1997) suggested

that modulation of spatial attention should be understood as an attentional bias toward a relevant location. When multiple stimuli are present simultaneously in a receptive field, instead of simply enhancing everything in receptive field, spatial attention actually biases the neural response to an attended stimulus by inhibiting other unattended stimuli. However, when multiple stimuli are presented sequentially, a relative weak yet robust enhancement for an attended stimulus compared with an unattended stimulus has been observed too (Luck et al., 1997).

Many studies reported attentional modulation on direction tuning curves in MT and MST of the dorsal pathway (Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996, 1999). For example, Treue and his colleagues found that directing attention into a RF caused a median of 19% firing rate increase in MT cells and 40% enhancement for MST cells (Treue & Maunsell, 1996). And the effect of attention is much larger when there are two moving stimuli competing with each other in the same RF, which is consistent with biased competition theory (Treue & Maunsell, 1996, 1999). There is other evidence supporting the biased competition theory. For example, even stronger average enhancements (70% in MT and 100% in MST) have been observed when spatial attention was switched from a stimulus moving in the non-preferred direction inside the receptive field to another stimulus in the receptive field that was moving in the preferred direction (Treue & Maunsell, 1999).

A multiplicity of attention

So far, I discussed four functions attention may serve: (a) attended stimuli receive preferential access to central bottleneck such as short term consolidation and response

selection; (b) attended stimuli are given great weight in perceptual processing; (c) attended stimuli are processed at higher gain than are ignored stimuli; (d) ignored stimuli are inhibited. A lot of studies have tried to argue that attention can be explained exclusively by one of these four functions. However, "it seems much more likely that the term attention applies to many separable processes, each of which operates within different cognitive subsystem and in a manner that reflects the representational structure and processing demands of that cognitive subsystem." (page 261, Luck & Vecera, 2002) In other words, all aforementioned effects of attention are true effects of separate mechanisms that are all given the same label of attention.

This multiplicity of attention provides an explanation for many controversial results from studies of attention. This multiplicity may be the key to settle debates about pre-perceptual selection vs post-perceptual selection, location-based selection vs feature-based selection, and a facilitatory effect vs an inhibitory effect. Those seemingly contradictory effects of attention are not mutually exclusive and coexist in different subsystems or at different stages.

Top-down guidance and bottom-up saliency

Selective attention plays a vital role in visual information processing because the visual system has multiple bottlenecks. Now we know that attentional modulation can occur at multiple processing stages. And the effect of attention can be either excitatory or inhibitory. But an essential question remained untouched in this review. How does selective attention decide which object in the scene is most important? Most theories of selective attention proposed that the attentional selection is under the guidance of two

driving forces: goal-directed prioritization (top-down guidance) and stimulus-driven

saliency (bottom-up saliency) (Corbetta & Shuman, 2002; Theeuwes, 1991, 1994, 2004).

Top-down guidance of attention relies on a control setting of attention which depends

on observers' prior knowledge of a target location or sought-for features such as color

and luminance. As I discussed in the section of "spatial attention and spotlight metaphor",

behavioral studies convincingly showed that selective attention enhances information

processing at a cued location when observers know the target location in advance

(Eriksen & Eriksen, 1974; Henderson, 1991; Posner, 1980; Posner, Snyder & Davidson,

1980; Vierck & Miller, 2008). More evidence from physiological studies showed that

spatial attention can dramatically increase neural activity of cells whose RFs overlap with

a cued location (Mangun, 1995; Mangun & Buck, 1998). Moreover, spatial attention can

increase baseline firing rate of neurons even when there is no visual stimulus in the RF,

which reflects a pure form of top-down modulation of spatial attention driven by prior

knowledge of target location (Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999;

Luck et al. 1997).

Attention can be also guided by sought-for features such as orientation (Haenny,

Maunsell & Schiller, 1988), color and luminance (Chelazzi, Miller, Duncan & Desimone,

1993; Du & Abrams, 2008; McAdams & Maunsell, 2000; Motter, 1994a), and direction

of motion (Serences & Boynton, 2007; Treue & Maunsell, 1996, 1999). For example,

studies showed that neural response to a sought-for color in V4 can be greatly enhanced

if the preferred color of V4 neurons happens to match the sought-for color (Motter,

1994a). Results from behavioral studies are also consistent with this idea of top-down

guidance for a specific sought-for feature (feature-based attention). For example, Folk

and colleagues found that uninformative pre-cues captured attention if and only if they matched the target-defining feature (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). Conversely, salient events such as color or motion singletons, often fail to capture attention if they do not match the features that define the target (Bacon & Egeth, 1994; Gibson & Kelsey, 1998; Hillstrom & Yantis, 1994; Jonides & Yantis, 1988; Todd & Kramer, 1994).

In addition to top-down guidance, deployment of attention can be governed by stimulus-driven salience which is purely decided by intrinsic properties of the stimulus (e.g. onset of stimulus, color or luminance contrast, and motion onset). The onset capture of attention in visual search is perhaps the prototypical example of stimulus-driven selection (Yantis & Jonides, 1984, 1990; Yantis, 1993). In visual search, an onset target usually can be found more quickly than a non-onset target, indicating that irrelevant onset of a new object involuntarily pulls attention to itself. The onsets of a new object capture attention not only during visual search but also in a change-detection task and Posner cuing task (Cole, Kentridge, Gellatly, & Heywood, 2003; Cole, Kentridge, Heywood, 2004; Pratt & McAuliffe, 2001; Schreij, Owens & Theeuwes, 2008). It has also been demonstrated that a completely irrelevant onset can nevertheless capture attention and result in interference in visual search (Forster & Lavie, 2008; Schreij, Owens & Theeuwes, 2008; Theeuwes, 1991, 1994, 1995).

There was a hot debate about the mechanism underlying onset capture. Initially onset capture was explained as the consequence of luminance increment (Yantis & Jonides, 1984). But this luminance increment account was invalidated by the finding that the onset of a new perceptual object captures attention in visual search even when the object is

equiluminant with its background and thus exhibits no luminance increment when it appears (Yantis & Hillstrom, 1994). Moreover, Yantis et al (1994) also showed that a salient luminance increment alone without the appearance of a new object is insufficient to capture attention (Yantis & Hillstrom, 1994). Noticing that a non-onset stimulus was always preceded by a placeholder whereas an onset stimulus was not, Gibson (1996) proposed that onsets of a new object capture attention simply because the new object is not masked by a placeholder as the non-onset stimuli are. This explanation was undermined by another study in which Yantis and Jonides (1996) found an onset capture effect when each stimulus in the target display was masked by preceding placeholders. In that study, six placeholders were initially presented for 800ms, and then a new placeholder onset abruptly. 200ms after the new placeholder onset, all seven placeholders were replaced by letter stimuli. In this case, every stimulus was masked by a preceding placeholder. But attention was captured by the onset of a new placeholder. As a result, RT to target was the fastest when a target letter spatially overlapped with the new placeholder (Yantis & Jonides, 1996). Thus Yantis et al. (1996) proposed that the appearance of a new perceptual object, instead of a luminance increment or pre-masking, is the origin of onset capture.

A recent study indicated that the capture effect of onsets may be due to the luminance transient associated with the event (Franconeri, Hollingworth, & Simons, 2005). But it has been showed that new objects can capture attention even without a unique luminance transient (Davoli, Suszko, & Abrams, 2007). In real-world scenes, the onset of a new object also yields prioritization even when it occurs during a saccade (Brockmole & Henderson, 2005). But when there is no luminance transient available for guidance of

28

attention, observers rely heavily on their working memory representation of spatial location to guide visual search (Brockmole & Henderson, 2005).

In addition to the capture of covert attention, a new object has been demonstrated to capture gaze when presented around the time of an eye movement (Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999).

In addition, studies also showed that other salient events can capture attention in a stimulus-driven fashion. For example, an irrelevant feature singleton such as a color singleton can disrupt visual search for a shape singleton (Theeuwes, 1994, 2004). Surprisingly, the onset of motion rather than continuous motion grabs attention reflexively (e.g., Abrams & Christ, 2003, 2005). Even the emergence of a new perceptual grouping is able to capture attention (Christ & Abrams, 2006b).

Interaction between stimulus-driven saliency and goal-directed guidance

Admittedly dichotomizing attention into stimulus-driven process and goal-directed guidance was very useful in developing theories of attention. However the dichotomy does not mean that stimulus-driven saliency and goal-directed guidance are mutually exclusive. On the contrary, they interact with each other in a very complex way. And it is the joint effect of stimulus-driven saliency and goal-directed guidance that determine allocation of attention. The first line of evidence supporting this joint effect came from studies of contingent capture. Folk and his colleagues proposed that stimulus-driven capture is contingent upon a top-down control setting for a sought-for feature rather than being completely blind to top-down control. For example, an irrelevant onset fails to capture attention when targets are defined by a specific color and succeeds in capturing

attention when targets are defined by onsets (Du & Abrams, 2008; Folk, Leber & Egeth, 2002; Folk, Remington & Johnston, 1992; Folk, Remington & Wright, 1994; see also Gibson & Kelsey, 1998).

Besides top-down guidance based on a sought-for feature, top-down selection based on location exerts an influence upon stimulus-driven capture such as onset capture. For example, Theeuwes (1991) tried to manipulate the size of the attentional spotlight by presenting a central arrow cue either before or after stimuli. He found that the size of the attentional spotlight influences the occurrence of onset capture. Only onsets within the attentional spotlight can capture attention. However, other studies showed that an onset across the whole visual field can be suppressed if observers know the target location in advance (Yantis & Jonides, 1990; but see Christ & Abrams, 2006a). These results indicate that stimulus-driven capture can be contingent upon a control setting for a specific location.

Consistent with the idea of contingent capture, Bacon & Egeth (1994) found that a specific search strategy can influence attentional capture in a fashion similar to top-down guidance. More specifically, according to them there are two visual search modes. One is the singleton detection mode in which observers search for a local feature discontinuity. The other is the feature search mode in which observers look for a specific target-defining feature. Surprisingly, they found that an irrelevant color singleton was able to capture attention only when observers were searching for a shape singleton-- presumably using a singleton detection mode. But when observers were required to search for a particular shape among multiple heterogeneous shapes, they successfully inhibited an

irrelevant color singleton because they were using a feature search mode in this case (Bacon & Egeth, 1994; but see Theeuwes, 2004).

Although onset capture can be suppressed if onsets are inconsistent with a top-down control setting of attention (Folk, Remington, & Johnston, 1992; Yantis & Jonides, 1990), some recent results reveal important synergistic interactions between goal-directed and stimulus-driven selection (Richard, Wright & Ward, 2003; Ludwig & Gilchrist, 2002; Ludwig & Gilchrist, 2003). In particular, Ludwig and Gilchrist (2002) studied both onset capture and color-based contingent capture in a saccadic and a manual pointing task. During both tasks, Ludwig and Gilchrist (2002) presented a distractor that either did or did not match the target in color. Distracters appeared either with or without an abrupt onset. Ludwig and Gilchrist found that subjects produced more inappropriate saccades to the color-matched distracters than to the color-unmatched ones, and more saccades were also made erroneously to distracters that abruptly onset. But most importantly, participants were most likely to fixate irrelevant onsets when they shared the target color. Error rates in that condition were more than the sum of the individual error rates for onset and color-match alone. These results thus revealed an important interactive effect of top-down and bottom-up attentional mechanisms (Ludwig & Gilchrist, 2003).

Despite findings such as those just discussed, there has been relatively little work in which both top-down and bottom-up attentional factors have been manipulated simultaneously. Two more recent studies employing an RSVP task did manipulate both stimulus-driven and goal-directed factors. Lamy, Leber, & Egeth (2004) extended a task initially developed by Folk, Leber & Egeth (2002). In the task, subjects were required to identify a uniquely colored target letter in a rapid stream of letters presented at fixation.

31

Folk et al. (2002) showed that subjects were impaired in identifying the target at fixation if a distractor suddenly appeared in the periphery—but only if the distractor matched the target color. They called the impairment a "spatial blink" because the color-matched distractor involuntarily pulls attention to a location of the display known to be irrelevant to the task. Because the effect of the distractor is contingent upon the color match between target and distractor (mismatching colors did not impair performance), the effect serves as an example of contingent attentional capture. Importantly, because subjects could easily ignore the peripheral distractor if it did not match the sought-for color, it appears that stimulus-driven saliency contribute minimally to the task.

In a subsequent study by Lamy et al. (2004), a stimulus-driven factor was manipulated in addition to the manipulation of top-down attentional set. Lamy et al. found that a color-matched distractor (a top-down influence) produced a larger spatial blink at a 100 msec distractor-target interval when it was a color singleton (a bottom-up influence) than did the same distractor when mixed with heterogeneously colored distracters. Another more recent study (Du & Abrams, 2008) found that onsets of irrelevant distractors alone are incapable of capturing attention, but onsets do enhance the capturing effect of color-matched distractor (larger spatial blink). Thus, the spatial blink, initially presumed to reflect only goal-directed guidance, may also depend somewhat on stimulus-driven saliency. The aforementioned results convincingly revealed synergistic interactions between top-down and bottom-up factors involved in attentional capture.

Chapter 3: Feature-based Attention

As it is mentioned in Chapter 2, a top-down control setting of a sought-for feature enhances the neural response of visual neurons which prefer the same sought-for feature such as color and luminance (McAdams & Maunsell, 2000; Motter, 1994a & 1994b), orientation (Haenny, Maunsell & Schiller, 1988; Maunsell, Sclar, Nealey & DePriest, 1991), direction of motion (Martinez-Trujillo & Treue, 2004; Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996, 1999), and even complex shapes (Chelazzi et al. 1998). Chapter 3 reviews evidence supporting feature-based attentional selection, starting from the color-based contingent capture and its neural mechanism in visual cortex, then a discussion about selective enhancement of neural response contingent upon direction of motion, finally ending with a review of orientation analysis and orientation-based modulation of attention.

In addition, I list three research questions in Chapter 3. To address these three research questions, a general method and four experiments will be proposed.

Color-based contingent capture and its neural correlates

More than sufficient evidence shows that attention can be involuntarily captured by a distractor when its color matches the sought-for color. This involuntary capture of attention is contingent upon the sought-for feature, thus first labeled *contingent capture* by Folk and his colleagues (Folk, Remington & Johnston, 1992; Folk, Remington & Wright, 1994). Folk et al (1992) found that when observer search for a red target in a visual display, an irrelevant flash of four red dots shortly before the onset of the search display pulls attention involuntarily to the location of red dots, resulting in a performance

cost for identifying the red target. But a flash of green dots, which is as physically salient as red dots, does not attract attention at all. Thus Folk et al suggested that subjects maintain a control setting for a sought-for feature. Only a stimulus matching the same sought-for feature receives a high priority in processing, thus capturing attention involuntarily (Folk, Remington & Johnston, 1992).

Studies on spatial blink provide evidence consistent with the idea of contingent capture (Du & Abrams, 2008; Folk, Leber & Egeth, 2002; Lamy, Leber, & Egeth, 2004). In the task, participants are required to identify a uniquely colored target letter in a rapid stream of letters presented at fixation. Folk et al. (2002) showed that the participants were disrupted in identifying the target at fixation if an irrelevant distractor suddenly appeared in the periphery—but only if the irrelevant distractor matched the target color. The impairment by an irrelevant color-matched distractor was labeled as a spatial blink. Because the effect of the distractor was contingent upon the color match between target and distractor (mismatching colors did not impair performance), it appears that stimulus-driven factors contributed minimally to the spatial blink. As a result, the spatial blink effect initially serves as an example of contingent attentional capture. However, some recent studies showed that stimulus-driven factors such as an onset or a color singleton do contribute to so called spatial blink and enhance the contingent capture effect (Du & Abrams, 2008; Lamy, Leber, & Egeth, 2004).

Importantly, the aforementioned results indicated that an irrelevant distractor possessing the sought-for color can override spatial control of attention, and pulls attention to the distractor's location even though the distracting element appears in a location of the display known to be irrelevant to the task (Folk et al., 2002; Serences et al.,

34

2005). Thus a distracting stimulus possessing a sought-for feature can be preferentially selected in parallel across the whole visual field. This conclusion is corroborated by several single cell recording studies. For example, Motter (1994a) trained monkeys to select a bar based on color or luminance and then to discriminate the angular tilt of the selected bar. He found that the majority of V4 neurons (74%) were selectively activated when the color or luminance of a stimulus in the receptive field matched the color or luminance of the cue. The activity was attenuated when there was not a match between the stimulus and the cue. Across the population of V4 neurons, optimal stimuli that matched the sought-for color or luminance elicited about twice the activity as stimuli that did not match the sought-for feature. The differential activation is based on the presence or absence of a match between preferred stimulus features and sought-for features. Moreover, this differential activation spread across the whole population of V4 neurons, thus it is independent of spatial location.

Admittedly, human subjects usually have to perform visual search based on feature representations in their memory. When subjects are told to search for a red target letter, they do not need to see a red cue but instead they can simply rely on a representation of red in memory (Folk et al., 2002). So Motter (1994b) followed up his previous study (Motter, 1994a) and removed color cues during the trial. He found that the differential activation depending on a match or mismatch between the sought-for color and the stimulus color was unchanged even when the cue was removed and monkeys had to perform the task based on their memory of the sought-for color (Motter, 1994b). More interestingly, when the sought-for color was switched from one color to another in the middle of a trial, differential activation reversed over the course of 150-300ms. If the

stimulus in the receptive field contained a sought-for feature that is newly selected, V4 neurons become activated without concomitant physical change in the stimulus. Across the topographic map of V4 the activity associated with the newly selected feature pop out, whereas the activity of the deselected feature faded to the background levels of other background objects. This pattern of result indicated that monkeys were continuously updating their top-down control setting for a sought-for color (Motter, 1994b).

In conclusion, humans and monkeys can maintain a top-down control setting of a specific color. And colors are processed in parallel across the whole visual field and the attentional modulation based on a specific sought-for color is independent of spatial location. But these findings do not mean that the feature-based attentional selection and the location-based attentional selection are mutually exclusive. McAdams and Maunsell (2000) found that some V4 neurons manifest both location-based and feature-based modulation of attention. More specifically, V4 neurons' response to optimal orientation within RF was attenuated more when monkeys attended to a color patch outside RF (both a location switch and a feature switch were involved) than when they attended to a gabor patch outside RF (only a location switch was involved).

Attentional effect contingent upon motion direction

Attentional modulation based on motion direction has been reported in many single cell recording studies (Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Treue & Martinez-Trujillo, 1999). When a monkey attends to a stimulus moving in a particular direction, MT neurons whose preferred direction matches the attended direction show enhanced sensory gains on their direction tuning curves, whereas MT neurons whose

preferred direction is opposite to the attended direction are suppressed (Treue &

Martinez-Trujillo, 1999).

Thus Treue and his colleagues argued that (1) feature-based attention exerts a

multiplicative modulation upon neuronal responses and that the strength of this

modulation depends on the similarity between the attended feature and the cell's

preferred feature, in line with the feature similarity gain model, and (2) at the level of the

neuronal population, feature-based attention increases the selectivity for attended features

by increasing the responses of neurons which prefer the sought-for feature while

decreasing the responses of neurons which tune to the opposite feature (Martinez-Trujillo

& Treue, 2004), and (3) This ''feature-similarity gain'' mechanism influences the firing

rate of all neurons tuned to the attended feature, even when neurons are being driven by a

stimulus outside the focus of spatial attention (Bichot, Rossi & Desimone, 2005;

Martinez-Trujillo and Treue, 2004; Saenz et al., 2002; Treue and Martinez Trujillo, 1999).

This motion-direction-based modulation of attention has been observed in MT even

without actual visual motion (Serences & Boynton, 2007). Serences et al. (2007) found

that motion-direction-based attentional modulation spreads across the visual field—even

to regions of the scene that do not contain a stimulus. They proposed that the spread of

feature-based attention to empty regions of space may facilitate the perception of

unexpected but behaviorally relevant stimuli at all locations in the visual field.

The motion-based modulation of attention was consistent with findings of a study of

contingent capture. Folk et al. (1994) found that attentional capture can be contingent

upon apparent motion. They used a variant of a cuing paradigm and presented rotating

dots around placeholder. They found that a placeholder with rotating dots produced a RT

cost in visual search if the target was defined by a motion signal (different types of motion and even onsets). But the same placeholder with rotating dots produced no performance cost in visual search if the target was defined by a static feature of color (Folk, Remington & Wright, 1994).

Visual analysis of orientation and Orientation-based selection of attention

The analysis of orientation begins in the primary visual cortex (V1), where orientation selectivity emerges in individual neurons. Extrastriate visual cortex (including V2, V3 and V4) also contains many orientation selective neurons. As we know, contours and textures are important attributes of object surfaces and critical for object recognition. They are often described by combinations of local orientations in visual images. Therefore, it is essential for our visual system to analyze orientations in local regions and determine their spatial relationships. The orientation analysis is critical not only for representing contours and textures but also for segmenting surfaces to segregate figures from the background. However, our understanding of orientation-specific control of attention is relatively poor compared with our knowledge of color-based modulation of attention. So it is important for us to examine how a top-down control setting for a specific orientation works.

Most theories of attention assume that visual analysis of orientation occurs in a pre-attentive stage. So it is supposed to be relatively insensitive to the top-down modulation of attention and highly effortless. However, studies showed that spatial attention can influence visual analysis of orientation by improving either spatial resolution (Yeshurun & Carrasco, 1998) or sensory gain (Luck, Chelazzi, Hillyard & Desimone, 1997; Motter,

1993). For example, Motter (1993) showed that spatial attention is able to modulate neurons' orientation tuning curve in early levels of visual cortex such as V1, V2 and V4. And this attentional modulation is more prominent when there are multiple competing stimuli in the scene. These aforementioned studies indicated that orientation analysis is under a top-down modulation of attention. In addition, another hallmark of orientation analysis – automaticity has also been challenged. A study showed that the so called "preattentive" detection of an orientation oddball is impaired during the attentional blink. This result indicates that orientation analysis requires attentional resources and is not truly automatic (Joseph, Chun & Nakayama, 1997). Therefore, orientation analysis is affected by attentional modulation and can be used to investigate attentional capture.

Single cell recording of monkeys demonstrated that a cue of specific sought-for orientation does modulate neural responses of cells in visual cortex. For example, Haenny et al. had a monkey match an orientation stimulus to a orientation sample (Haenny, Maunsell & Schiller, 1988). They found that a neuron's response to a particular orientation was affected by whether or not it was the orientation for which the monkey was looking. Over half the neurons in V4 (110/192) responded differently to visual stimuli when the animal was cued to look for different orientations. The selectivity for the combinations of stimulus and cue orientation were varied and complex. For a tactile-visual match task, 44% (67/152) of the neurons had significant sensitivity for both cue orientation and stimulus orientation. Moreover, about two thirds of 67 cells showed an interaction between cue and stimulus orientation tuning (the neural responses were enhanced only when the monkey saw a particular pair of cue and stimulus orientation). A large proportion (46%) of neurons that showed an interaction between both stimulus and

cue orientation tuning responded best to a combination that represented one of four matching conditions. For example, a cell responded best when both cue and stimulus orientation were vertical (a matching condition). Relatively smaller percentage of neurons responded best to each of 12 non-matching conditions. For example, a cell responded best when cue orientation was horizontal but stimulus orientation was vertical (a non-matching condition). They found a similar response pattern in both a visual-visual match task and a tactile-visual match task. This result indicates that a top-down control setting for a specific orientation is not only applicable to the visual modality but also the tactile modality.

Following the studies of Haenny et al., Maunsell et al. (1991) confirmed that a sought-for orientation acts as a top-down control signal, modulating monkeys' neural responses to stimulus orientation. But in the Maunsell study, the distribution of preferred combinations was uniform across all four matching conditions and twelve non-matching conditions, unlike Haenny study which found more neurons responding best to one of the four matching conditions than those responding best to one of twelve non-matching conditions. So they proposed that greater preference for a matching combination between a cue orientation and a stimulus orientation might be a result of individual preference (Maunsell, Sclar, Nealey & DePriest, 1991). If their argument can be applied to humans, we would predict that prioritization of an irrelevant stimulus that matches a sought-for feature varies across subjects too. There may be great individual differences in orientation-specific contingent capture.

40

Goals of the dissertation

Previous studies have confirmed an important role for color in attention: During search for a target in a specific color, human subjects' attention will be involuntarily captured by an irrelevant distractor possessing the sought-for color. And when monkeys perform a similar search, neural responses of V4 cells which prefer the sought-for color are selectively enhanced.

As we know, orientation analysis is critical for recognizing objects. But our understanding of orientation-based capture of attention is relatively poor compared with our knowledge of color-based capture of attention. In summary, single cell recordings from monkeys seems to indicate an orientation-based modulation of neural response. However, this orientation-based modulation appears to influence neural responses to any orientation rather than specifically targeting a sought-for orientation (Haenny, Maunsell & Schiller, 1988; Maunsell, Sclar, Nealey & DePriest, 1991). Thus it is impossible to predict the behavioral consequence of such an orientation-based modulation of neural response. In addition, no study ever examined whether human subjects' attention can be involuntarily captured by an irrelevant stimulus in a sought-for orientation. Therefore, the major question I am interested in is whether an irrelevant distractor that matches the sought-for orientation can capture attention involuntarily. If an orientation-matched distractor does capture attention, the present study will be the first one to show orientation-specific capture of attention, and provide important new insights into the mechanisms underlying orientation-based control of attention.

In addition, recent studies showed that stimulus-driven saliency of distractors can influence the magnitude of contingent capture (Du & Abrams, 2008; Lamy, Leber, &

Egeth, 2004). For example, Du and Abrams (2008) already showed that abrupt appearance of distractors can significantly enhance color-based contingent capture even though abrupt appearance alone is unable to induce a capture effect. So I hope to examine whether an orientation-specific capture of attention, if any, can be influenced by stimulus-driven saliency of an orientation singleton.

General method

    The spatial blink paradigm which was initially developed by Folk et al (2002) will be used in the present study as the main research paradigm to examine the effect of orientation-based attention for two reasons. First, the spatial blink paradigm is a well established research paradigm that produces a consistent and robust attentional capture effect contingent upon a sought-for color. For example, in a typical spatial blink study, subjects are presented with a stream of color letters rapidly at the center of the display and required to identify a target letter in a designated color. Researchers have repeatedly found that a peripheral distractor known to be irrelevant to the task interferes with the identification of the central target letter only if the distractor matches the target color. So a typical spatial blink effect supposedly reflects an attentional capture effect contingent upon color. If an orientation-specific contingent capture works in the same way as a color-specific contingent capture, I would expect to observe a similar capture effect (an impairment of central letter identification) contingent upon an orientation-match between distractor and target. Second, a typical color-based spatial blink effect spreads across the whole visual field, clearly indicating that a top-down control of spatial attention is violated under the situation of color-based contingent capture of attention. That finding is

consistent with single cell recording data that the color-based modulation of attention is independent of the spatial locus of attention. If an orientation-specific contingent capture also spreads across the whole visual field, the orientation-based modulation of attention would also be location-independent just like the color-based modulation of attention.

To study orientation-specific contingent capture, I developed a variant of the spatial blink paradigm. The sequence of events on a trial in either Experiment 1 or 2 is illustrated in Figure 1. As Figure 1 shows, letters were presented sequentially at the center of display at a rate of 10 items/sec. Every letter was in the same color. Each letter was presented within a gray bar which was in the same orientation as the letter. Letters could be vertical, horizontal, 45º clockwise or counterclockwise from vertical. Half of the participants were required to identify the sole oblique letter 45º clockwise from vertical. The rest of the participants were required to identify the sole oblique letter 45º counterclockwise from vertical.

Two sets of three white bars flanked the central letter stream either shortly before or after the target letter. Figure 1 illustrates all the five distractor conditions in either Experiment 1 or 2. For example, there is no peripheral bar in the ***Null*** condition which serves as a baseline condition of no irrelevant distractor. In the ***Vertical*** condition, all six bars are vertical. But the ***Horizontal*** condition contains a single horizontal bar with five vertical bars. In the ***Matched*** condition, one of peripheral bars is in the same orientation as target, and the other five are vertical. In the ***Orthogonal*** condition, one peripheral bar is perpendicular to the target orientation and the other five are vertical. Those distractor conditions are varied across four experiments. Further details of procedures in each experiment are discussed in the method of each experiment.

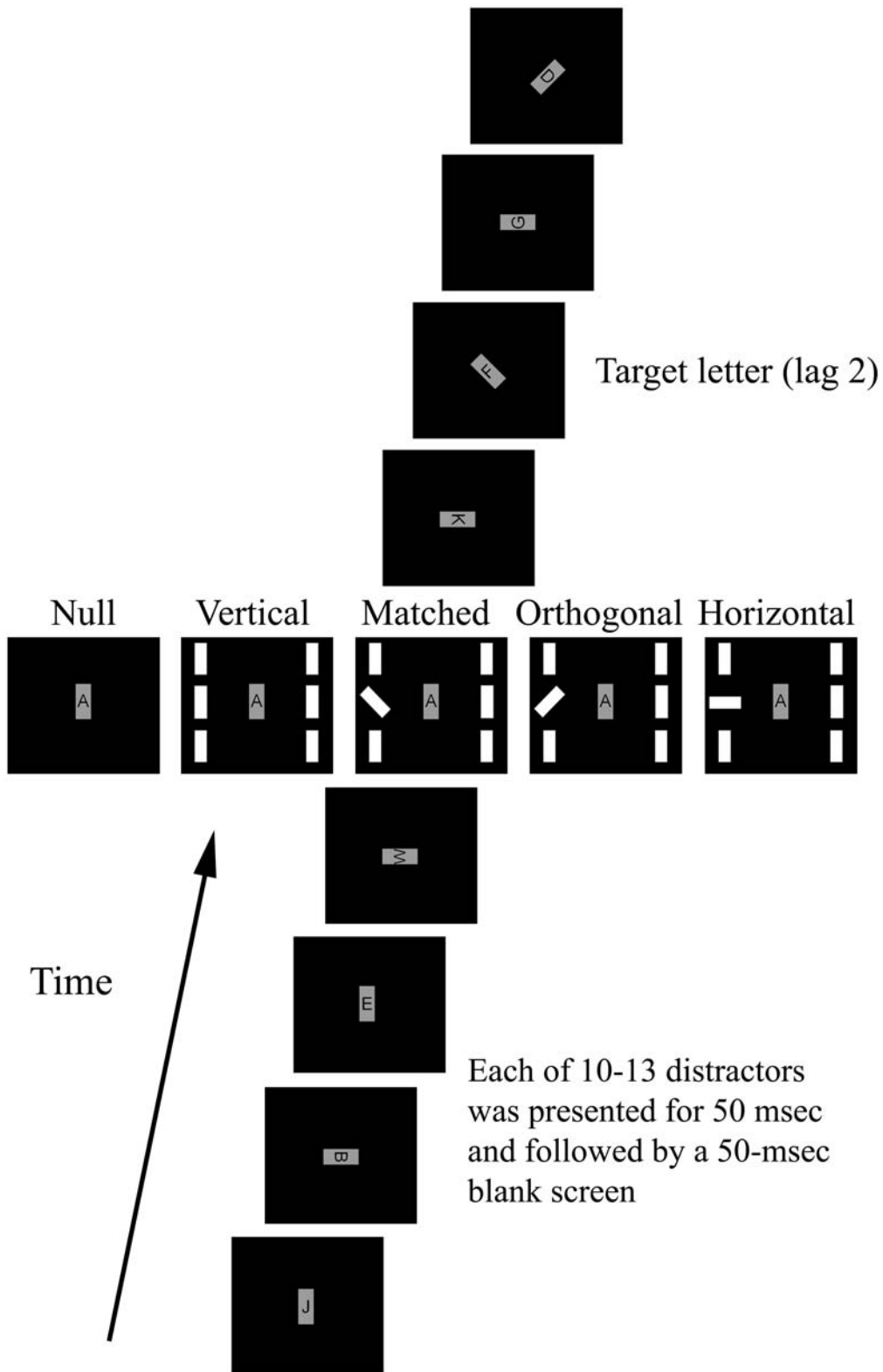Figure 1. Schematic representation of events in Experiments 1 and 2.

Null   Vertical   Matched   Orthogonal   Horizontal

Target letter (lag 2)

Time

Each of 10-13 distractors
was presented for 50 msec
and followed by a 50-msec
blank screen

44

Chapter 4: Experiment 1

Though single cell recording data showed that a sought-for orientation can modulate orientation tuning curves in neurons of monkeys' visual cortex, it is still unknown whether an irrelevant stimulus that matches a sought-for orientation can capture human subjects' attention involuntarily. The present experiment is designed to examine whether attention can be captured by an irrelevant distractor in a sought-for orientation. If an orientation-specific contingent capture (a spatial blink effect contingent upon a specific orientation) occurs, it would indicate the existence of a top-down attentional control setting for a particular orientation. In addition, the occurrence of a spatial blink would indicate that the orientation-specific contingent capture is location-independent too.

As I explained in the general method, half of the participants were asked to search for a letter tilted 45º clockwise from vertical at the center of the display. The other half of the participants looked for a letter tilted 45º counterclockwise from vertical. There were four distractor conditions with different peripheral distracting bars in Experiment 1. In the *Null* condition, there was no peripheral bar. In the *Vertical* condition, all six bars were vertical bars. In the *Matched* condition, one of the peripheral bars was in the same orientation as the target, and the other five bars were vertical. In the *Orthogonal* condition, one peripheral bar was perpendicular to the target orientation and the other five bars were vertical. If an orientation-specific control setting of attention works in the same way as a color-based control setting, only an orientation singleton that matches the sought-for orientation will capture attention when it appears prior to the target, resulting in an impairment of central target identification (also known as a spatial blink).

Method

Participants

Forty-four undergraduate students from Washington University participated in a half

hour long experiment for course credit. All had normal or corrected-to-normal visual

acuity. No participants had experience in similar experiments.

Apparatus and Procedure

All stimuli were presented on a 19-in. monitor with a 100 Hz refresh rate in a dimly

lit room at a distance of 56 cm. The sequence of events on a trial is illustrated in Figure 1.

Each trial began with a 500-msec presentation of a gray fixation cross in the center of the

screen, followed by the sequential presentation of 20 upper case letters at the center. The

letters were selected randomly without replacement from the English alphabet, with the

exception of "I". Every letter was presented in a gray bar which was in the same

orientation as the letter. Letters were vertical, horizontal, 45º clockwise or

counterclockwise from vertical. Letters were 1.0º in width and 1.3º in height. The gray

background bars were 1.3º in width and 4.5º in height. Like a classical spatial blink

experiment, each letter was presented for 50 msec, followed by a 50-msec blank interval,

yielding an SOA of 100 msec. One half of the participants were required to identify an

oblique letter 45º clockwise from vertical. The other half of the participants searched for

an oblique letter 45º counterclockwise from vertical. There were two oblique letters

which were perpendicular to each other in each trial. Across trials, the target letter (either

45º clockwise or counterclockwise from vertical) appeared in the 10th through 14th

frame of the letter sequence. And the other oblique letter was presented either 4 frames

before or after the target letter. The color of all letters was black. Participants reported the target letter by pressing the corresponding key after each trial.

There were four conditions for peripheral distracting bars. On one-fourth of the trials, there was no white distracting bar in the periphery. This was the ***Null*** condition serving as a baseline in which there was no distracting stimulus in the periphery. On the rest of the trials, one of the letters in the 8th through 15th frames, randomly chosen with equal chance, was flanked by two sets of white bars (three vertical bars in each set) whose inner edges appeared 6º right or left of the center of display. Each bar was 0.7º in width and 2.5º in height. These trials were evenly distributed in three conditions (Vertical, Matched and Orthogonal conditions). In the ***Vertical*** condition, all six peripheral bars were vertical bars so that the ***Vertical*** condition served as another baseline in which there was neither an orientation singleton nor a distractor matched to the target orientation. In the ***Matched*** condition, however, one bar either to the left or right of the central letter was an oblique bar which was in the same orientation as the target letter. The other five peripheral bars in the ***Matched*** condition were vertical. Thus there was an orientation singleton matching the sought-for orientation in the ***Matched*** condition. On the contrary, there was an oblique bar perpendicular to target letter in the ***Orthogonal*** condition. The rest of the bars in the ***Orthogonal*** condition were also vertical. Thus the ***Orthogonal*** condition had an orientation singleton that was perpendicular to the target orientation. If attentional capture is contingent upon a specific sought-for orientation, only the ***matched*** condition should produce a significant amount of capture effect, whereas the ***Orthogonal*** and ***Vertical*** conditions should not capture attention.

On half of the trials containing peripheral distracting bars, the frame containing the peripheral distracting bars appeared two frames before that containing the target (distractor-target lag of 2). On the other half of the trials, the frame containing peripheral distracting bars appeared two frames after the target frame (lag of -2).

Design

The four distracting conditions (Null, Vertical, Matched and Orthogonal) were mixed up and presented to each subject in a random order. The experiment contained 24 replications of each combination of four distractor-conditions and two distractor-target lags, for a total of 192 trials. Participants first served in one block of 16 trials for practice. They then completed the test trials. After every 64 trials, they received a brief break.

Results

The accuracy of target identification is plotted in Figure 2 as a function of distractor-target lag and the distractor condition. There were three main findings. First, we found a main effect of lag, with lower accuracy as lag increased, $F(1,43)=14.049, p=0.001, \eta_p^2 = 0.246$. Next, there was a main effect of distractor condition, with lower accuracy in the ***Matched*** and ***Orthogonal*** conditions, $F(3,129)= 10.213, p<0.001, \eta_p^2 = 0.192$. Finally, the effects of lag and distractor condition interacted ($F(3,129)=11.803, p<0.001, \eta_p^2 = 0.215$), reflecting the fact that performance was impaired only in the ***Matched*** and ***Orthogonal*** conditions and only at lag 2. The impairment at lag 2 is indicative of the spatial blink.
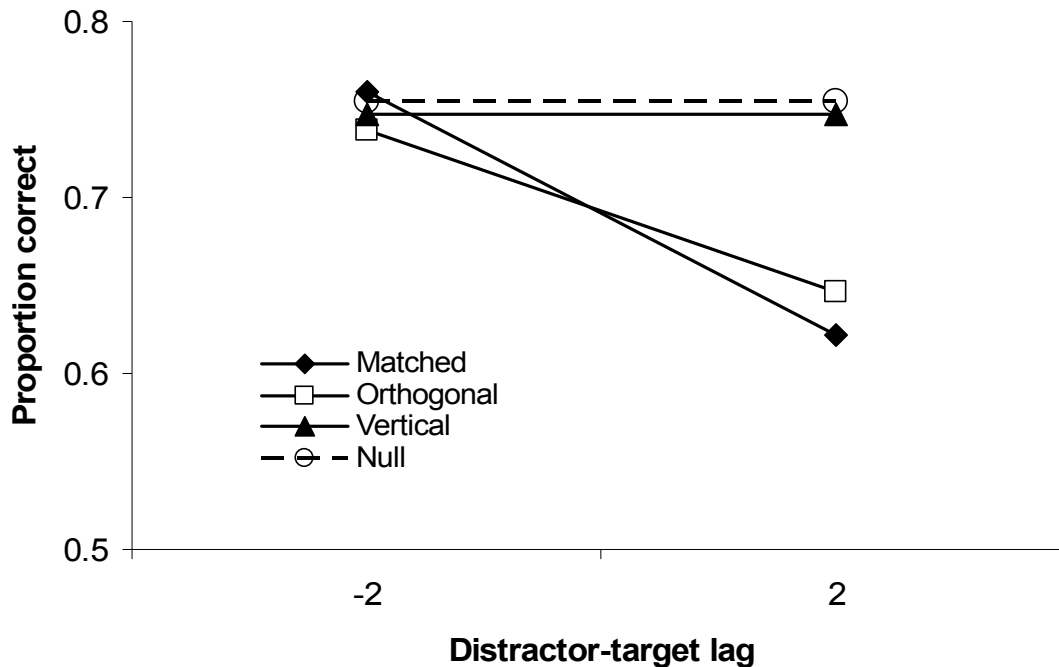
Figure 2. The accuracy of target identification in Experiment 1.

The accuracy difference between two lags for each condition was divided by the sum of the accuracy of two lags to represent the magnitude of attentional capture for that condition. There was no difference between accuracy at the two lags in the *Null* condition. Therefore, the magnitude of attentional capture in the *Null* condition was zero. The magnitude of attentional capture for the other three conditions is plotted in Figure 3.

A further comparison of the magnitude of the spatial blink between the *Matched* condition and the *Null* condition (zero) confirmed the presence of a spatial blink in the *Matched* condition, t(43) = 4.072, *p<0.001;* Similarly, a comparison between the *Orthogonal* condition and the *Null* condition confirmed the presence of a spatial blink in the *Orthogonal* condition, t(43) = 3.043, *p=0.004.* Thus, both the *Matched* condition and the *Orthogonal* condition induce large spatial blinks. And most surprisingly, the spatial blink caused by the orientation-matched singletons in the *Matched* condition was

not different from that in the ***Orthogonal*** condition, t(43) = 1.27, *p=0.211,* as can be seen in Figure 3.
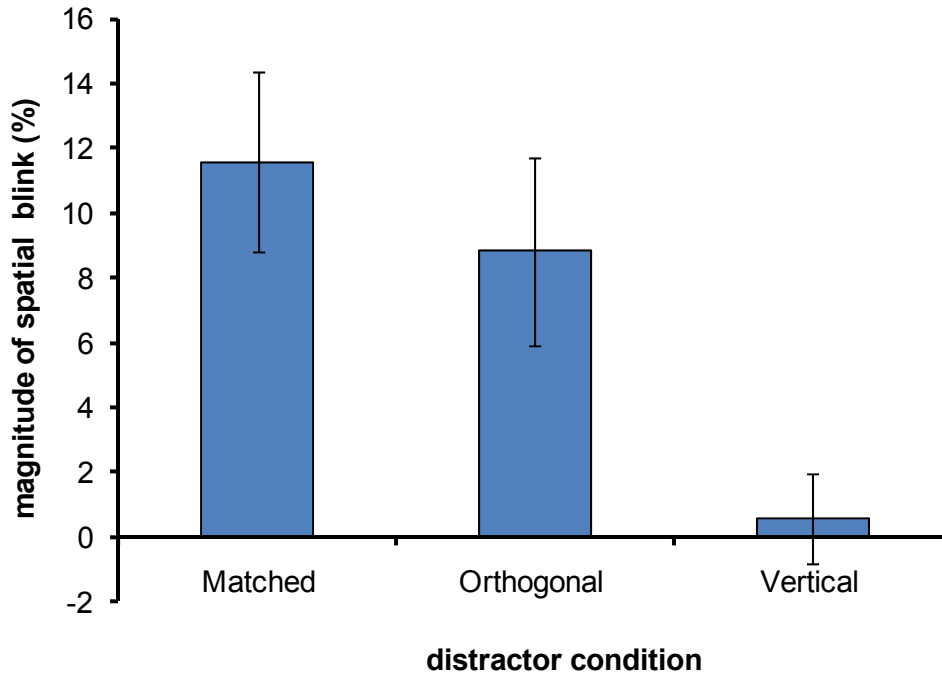

Figure 3. The magnitude of the spatial blink in each condition of Experiment 1

But the spatial blink in the ***Vertical*** condition was not significantly different from that of the ***Null*** condition, t(43) = 0.421, *p=0.676*: Presenting six vertical bars in the ***Vertical*** condition did not induce any capture effect compared to the Null condition.

Discussion

The present experiment found that an irrelevant orientation singleton in the periphery of the visual field that matches a sought-for orientation can involuntarily capture attention, resulting in impaired performance of target identification at fixation. These results are the first to show that a top-down control setting for a sought-for orientation can be established to influence involuntary attentional capture during visual search. But

surprisingly, an irrelevant orientation singleton that was perpendicular to the sought-for orientation also captured attention. Why does an orientation-specific control setting prioritize two orientations that are 90º apart? The answer may lie in a recent single cell recording study of the structure of receptive fields of visual neurons in monkeys. The study showed that many V2 and V3 neurons in monkeys have receptive fields containing many subregions which are tuned to different orientations, most commonly about 90˚ apart (Anzai, Peng & Van Essen, 2007). If a top-down control setting for orientation activated these neurons with bimodal orientation tuning curves then that would explain why subjects appear to have prioritized two orientations perpendicular to each other.

However, there are some alternative explanations of the results from the present experiment. Both the ***Matched*** condition and the ***Orthogonal*** condition had an orientation singleton in the distractor display, whereas the other conditions (the Vertical condition and the Null condition) did not have an orientation singleton. Though it is impossible for a color singleton to induce a spatial blink (Du & Abrams, 2008; Folk, Leber & Egeth, 2002), it may still be possible that an orientation singleton would pull attention away from identifying the target in a stimulus-driven fashion. In that case, the present results would not indicate the presence of any specific attentional set for orientation, but instead would reflect bottom up capture by a salient orientation singleton.   Experiment 2 was designed to test whether the capture effect (spatial blink) observed in Experiment 1 can be accounted for by the stimulus-driven saliency of an orientation singleton.

Another alternative explanation is that participants might treat the two oblique orientations as a special group different from vertical or horizontal bars because each of the two oblique letters only occurred once in the central stream. Experiments 4 and 5

were designed to rule out this possibility by presenting two letters orthogonal to the target

letter in the central stream.

Chapter 5: Experiment 2

Experiment 1 clearly showed that an irrelevant orientation singleton that matched a sought-for orientation captured attention and impaired target identification. This capture effect may be well explained by contingent attentional capture theory. But why did an irrelevant distractor that was perpendicular to the sought-for orientation also capture attention? Of course, one possibility is that this capture effect by the unmatched orientation singleton is a side effect when a top-down control setting for a specific orientation selectively activates visual neurons which prefer two orientations 90˚ apart. In that way, contingent capture may be determined not only by a top-down control setting but also by the feature preferences of visual neurons.

However, there are a few other possibilities. One possible explanation is that participants adopted a control setting to prioritize *any* oblique bars irrespective of their specific orientations. This possibility seems very unlikely because there were two oblique letters whose orientations were perpendicular to each other in the central letter stream. If participants maintained a top-down control setting for all oblique letters, they would report either the target letter or the orthogonal letter with equal chance. Of course, another alternative explanation exists: The distracters in both the ***Matched*** condition and the ***Orthogonal*** condition contained an orientation singleton, and that was not true for the other distractor types. It might be the orientation singletons in both of those conditions that captured attention in a stimulus-driven fashion in Experiment 1.

To examine that possibility, one single vertical bar in the ***Vertical*** condition of Experiment 1 was replaced with a horizontal bar in the present experiment. By doing so, I can set up a new ***Horizontal*** condition in which a horizontal orientation singleton appears.

The horizontal singleton should be equally salient, if not more, as those orientation singletons in the *Matched* condition and the *Orthogonal* condition. According to the stimulus-driven saliency account, the horizontal singleton should capture attention and interrupt target identification in the same way as the orientation singletons in the *Matched* and the *Orthogonal* conditions of Experiment 1. On the contrary, if the activation of visual neurons that have a bimodal orientation tuning curve with two peaks 90˚ apart accounts for the capture effect in Experiment 1, the horizontal singleton here is expected to be ineffective in capturing attention because the orientation of the horizontal singleton is 45˚ from the target orientation.

In addition, the finding that an irrelevant orientation singleton perpendicular to the target orientation captures attention is quite a deviation from my original prediction. Therefore, both the *Matched* condition and the *Orthogonal* condition were included in Experiment 2 in order to replicate the results of Experiment 1.

Method

Participants

Forty-four undergraduate students from Washington University participated in a half hour long experiment for course credit. All had normal or corrected-to-normal visual acuity. No participants had experience in similar experiments.

Apparatus and Procedure

The sequence of events in a trial is illustrated in Figure 1. All stimuli and procedures were the same as those of Experiment 1 with one exception. In Experiment 2, peripheral bars in the *Horizontal* condition were not homogenously vertical bars any more. One bar

54

either to the left or right of the center was horizontal so that the ***Horizontal*** condition of Experiment 2 contained a horizontal orientation singleton that was 45º from either of the two target orientations (see the ***Horizontal*** condition in Figure 1).

Design

The four distracting conditions (Null, Horizontal, Matched and Orthogonal) were mixed up and presented to each subject in a random order. The present experiment contained 24 replications of each combination of four distractor-conditions and two distractor-target lags, for a total of 192 trials. Participants first served in one block of 16 trials for practice. They then completed the test trials. After every 64 trials, they received a brief break. One half of the participants were asked to report a tilted letter 45º clockwise from vertical. The other participants searched for an oblique letter 45º counterclockwise from vertical.

Results

The accuracy of target identification is plotted in Figure 4 as a function of distractor-target lag and the distractor condition. There were three main findings. First, we found a main effect of lag, with lower accuracy as lag increased, $F(1,43)=25.035$, $p<0.001$, $\eta_p^2 = 0.368$. Next, there was a main effect of distractor condition, with accuracy lowest in the *Matched* and *Orthogonal* conditions, $F(3,129)= 18.070$, $p<0.001$, $\eta_p^2 = 0.296$. Finally, the effects of lag and distractor condition interacted ($F(3,129)=15.881$, $p<0.001$, $\eta_p^2 = 0.270$), reflecting the fact that the impairment caused by either orientation-matched distractors or orthogonal distractors occurred mainly for lag 2. This is the pattern indicative of the spatial blink.
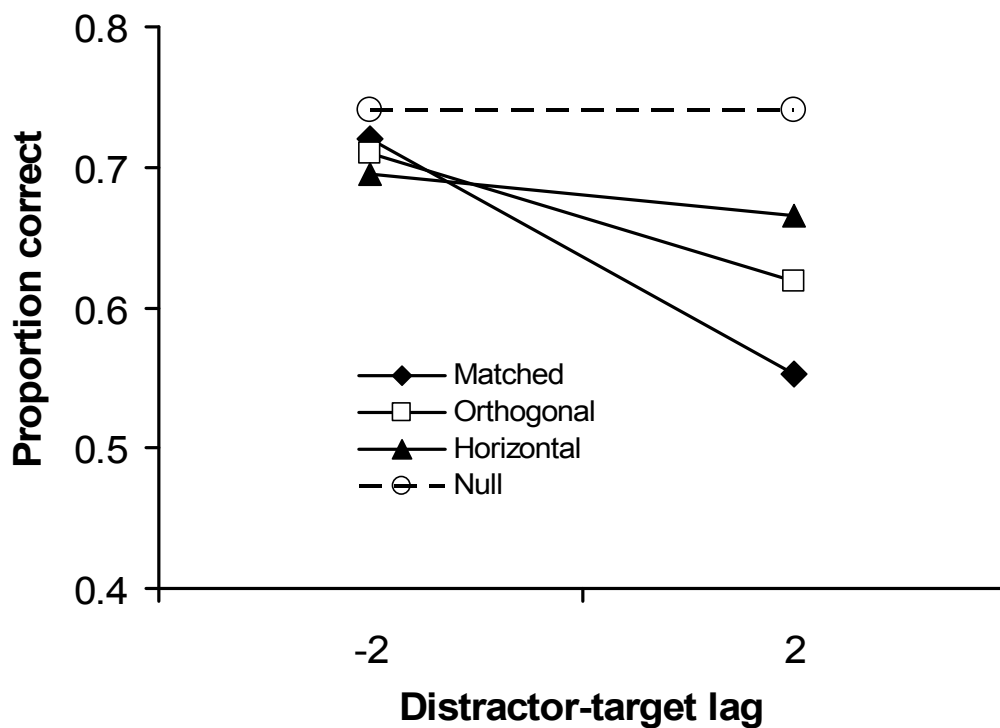
Figure 4. The accuracy of target identification from Experiment 2.

The accuracy difference between two lags for each condition was divided by the sum of the accuracy of two lags to represent the magnitude of attentional capture for that condition. There was no difference between accuracy at the two lags in the ***Null*** condition. Therefore, the magnitude of attentional capture in the ***Null*** condition was zero. The magnitude of the spatial blink for the other three conditions is plotted in Figure 5.

A further comparison of the magnitude of the spatial blink between the ***Matched*** condition and the ***Null*** condition confirmed the presence of a spatial blink in the ***Matched*** condition, t(43) = 5.722, *p<0.001;* Similarly, a comparison between the ***Orthogonal*** condition and the ***Null*** condition confirmed the presence of a spatial blink in the ***Orthogonal*** condition, t(43) = 3.579, *p=0.001.* Thus, both the ***Matched*** condition and the ***Orthogonal*** condition induced large spatial blinks. But slightly different from the

results of Experiment 1, the spatial blink caused by the orientation-matched distractors in the *Matched* condition was larger than that in the *Orthogonal* condition, $t(43) = 3.493$, *p=0.001,* as can be seen in Figures 4 and 5.
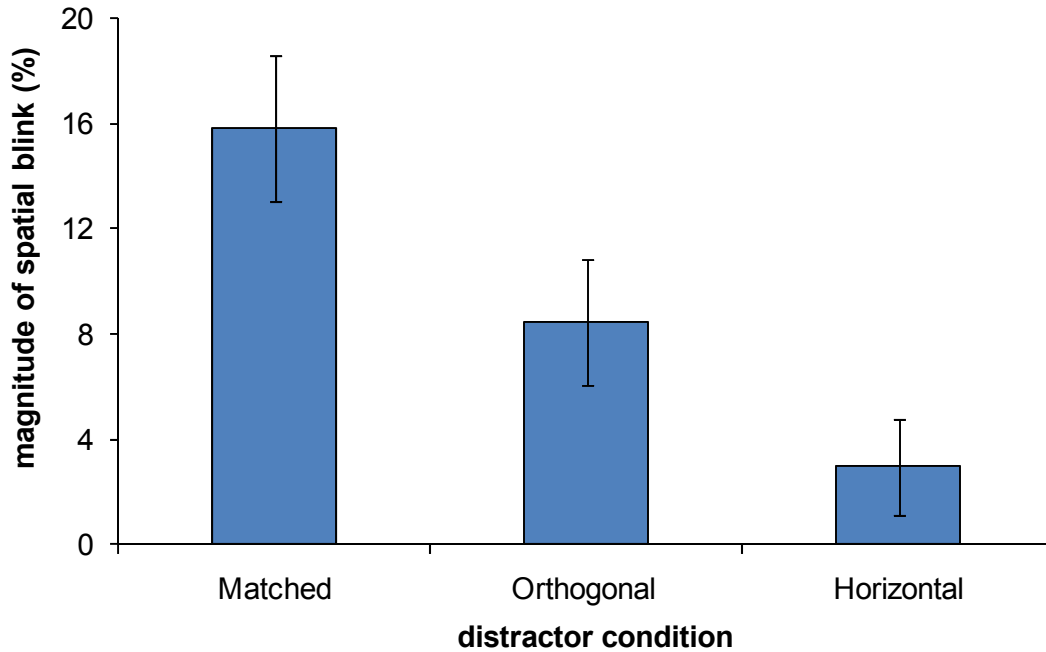

Figure 5. The magnitude of the spatial blink in each condition of Experiment 2

Although a horizontal singleton in the *Horizontal* condition caused reduced accuracy across both lags compared to the *Null* condition, this impairment was not the same as the spatial blink in either the *Matched* condition or the *Orthogonal* condition. Actually the spatial blink in the *Horizontal* condition was not significantly different from that of the *Null* condition, $t(43) = 1.662$, *p=0.104*. Therefore, presenting a horizontal singleton among five vertical bars in the *Horizontal* condition did not induce any capture effect.

Discussion

Experiment 2 found that an irrelevant orientation singleton that either matches the sought-for orientation or is perpendicular to the sought-for orientation can involuntarily capture attention, resulting in impaired performance of central target identification at lag 2 (a spatial blink). These results replicate the findings of Experiment 1. But most importantly, the present experiment found that a horizontal singleton only slightly interrupted target identification at fixation--and in a way different from either an orientation-matched singleton (*Matched* condition) or an orientation-unmatched singleton (*Orthogonal* condition). The irrelevant orientation singleton in either the *Matched* condition or the *Orthogonal* condition mainly produced attentional capture effects at lag 2, whereas the horizontal condition interrupted central target identification at both lags, and to a less severe level than both the *Matched* condition and the *Orthogonal* condition at lag 2. Since a salient horizontal singleton did not capture attention to the same extent as an orientation singleton in either the *Matched* condition or the *Orthogonal* condition, the attentional capture effects observed in the *Matched* and *Orthogonal* conditions of Experiments 1 and 2 cannot be solely explained by the stimulus-driven saliency of the orientation singletons there. Thus the present results rule out the stimulus-driven saliency account of Experiment 1.

The present results were also slightly different from those of Experiment 1 in that the magnitude of attentional capture in the *Matched* condition was somewhat larger than that of the *Orthogonal* condition here, while they were equal in Experiment 1. The reason for this difference is unclear. But these results are still consistent with the bimodal tuning curve account of visual neurons (Anzai, Peng & Van Essen, 2007). As I previously

58

suggested, the attentional capture effect by an orientation singleton being perpendicular to the sought-for orientation is a side effect when a top-down control setting for a specific orientation selectively activates visual neurons which prefer two orientations 90° apart. Therefore, the current results indicate that contingent capture of attention may be not only decided by a top-down control setting but also influenced by the feature preferences of visual neurons.

Though a horizontal singleton was different from an orientation singleton in both the *Matched* and *Orthogonal* conditions in capturing attention at lag 2, a horizontal singleton did disrupt central identification slightly across both lag -2 and lag 2 in the present experiment. This pattern of results indicates that stimulus-driven saliency of an orientation singleton might account for a part of the attentional capture effect observed in the *Matched* and *Orthogonal* conditions of Experiments 1 and 2. As I mentioned in Chapter 2, many previous studies suggested that allocation of attention is determined by a joint effect of stimulus-driven saliency and top-down guidance from a control setting (Du & Abrams, 2008, 2009; Lamy et al. 2004; Ludwig & Gilchrist, 2002, 2003). The next experiment was designed to examine whether there is a synergistic effect between the stimulus-driven saliency of an orientation singleton and the top-down prioritization for a sought-for orientation.

Chapter 6: Experiment 3

Previous studies showed that an increase in the stimulus-driven saliency of distractors can significantly enhance the contingent capture effect even though a salient distractor alone is insufficient to induce attentional capture (Du & Abrams, 2008; Lamy et al. 2004). For example, Lamy et al. (2004) found that an irrelevant distractor that matches the target color (when the target was defined by color) is more effective for capturing attention when it is a color singleton than when it is embedded among heterogeneous items of different colors. Du and Abrams (2008) also found that abrupt onsets of distractors actually increased the effect of contingent capture caused by a distractor whose color matched the sought-for color. But onsets of a non-target-color distractor failed to capture attention. It is unknown, however, whether there is a synergistic effect between the stimulus-driven saliency of an orientation singleton and the top-down prioritization for a sought-for orientation.

More specifically, the present experiment is designed to examine whether an orientation singleton can enhance attentional capture contingent upon a sought-for orientation in a stimulus-driven fashion. If the stimulus-driven saliency of an orientation singleton does contribute to the spatial blink based on a sought-for orientation, an orientation singleton that matches the sought-for orientation should be more effective in capturing attention than a non-singleton distractor that also matches the sought-for orientation.

Method

Participants

Forty-eight undergraduate students from Washington University participated in a half hour long experiment for course credit. All had normal or corrected-to-normal visual acuity. No participants had experience in similar experiments.

Apparatus and Procedures

The sequence of events on a trial is illustrated in Figure 6. As Figure 6 shows, the present experiment kept three distractor conditions of Experiment 1 intact. These three distractor conditions included the *Vertical* condition, the *Matched* condition and the *Orthogonal* condition. Two new distractor conditions were added to examine whether the orientation-specific contingent capture effect would be diminished as the stimulus-driven saliency of the orientation-matched distractor is reduced. Thus, the number of orientation-matched distractors was manipulated to make orientation-matched distractors either an orientation singleton, as in the *Matched* condition, or five non-singleton distractors, as in the *Multi-matched* condition. More specifically, in the *Multi-matched* condition, five out of six bars were tilted bars that matched the sought-for orientation. The remaining one was a vertical bar that constituted an orientation singleton. As we know, the vertical orientation singleton competes with the multiple orientation-matched bars, perhaps reducing the stimulus-driven saliency of those orientation-matched bars compared with the orientation-matched singleton in the *Matched* condition. Similarly in the *Multi-orthogonal* condition, five out of six bars were tilted bars that were perpendicular to the sought-for orientation. The remaining one was a vertical bar that constituted an orientation singleton. Therefore, the stimulus-driven saliency of the

61

multiple orthogonal distractors in the ***Multi-orthogonal*** condition was also reduced compared with the orthogonal singleton in the ***Orthogonal*** condition.

   Other parameters of the stimuli were same as those in the Experiment 1.

Design

   Five distractor conditions (Vertical, Matched, Orthogonal, Multi-matched and Multi-orthogonal) were mixed up and presented to each subject in a random order. The present experiment contained 24 replications of each combination of five distractor-conditions and two distractor-target lags (lag of 2 and -2) for a total of 240 trials. Participants first served in one block of 16 trials for practice. They then completed the test trials. After every 80 trials, they received a brief break.

Results

   The accuracy of target identification is plotted in Figure 7 as a function of distractor-target lag and distractor condition. There were three main findings. First, we found a main effect of lag, with lower accuracy as lag increased, $F(1,47)=20.640, p<0.001, \eta_p^2 = 0.305$. Next, there was a significant main effect of distractor condition, with accuracy lowest in the ***Matched*** condition, $F(4,188)= 3.668, p=0.007, \eta_p^2 = 0.072$. Finally, the effects of lag and distractor condition interacted ($F(4,188)=6.157, p<0.001, \eta_p^2 = 0.116$), reflecting the fact that the impairment caused by either orientation-matched distractors or orthogonal distractors occurred mainly for lag 2. This is the pattern indicative of the spatial blink.
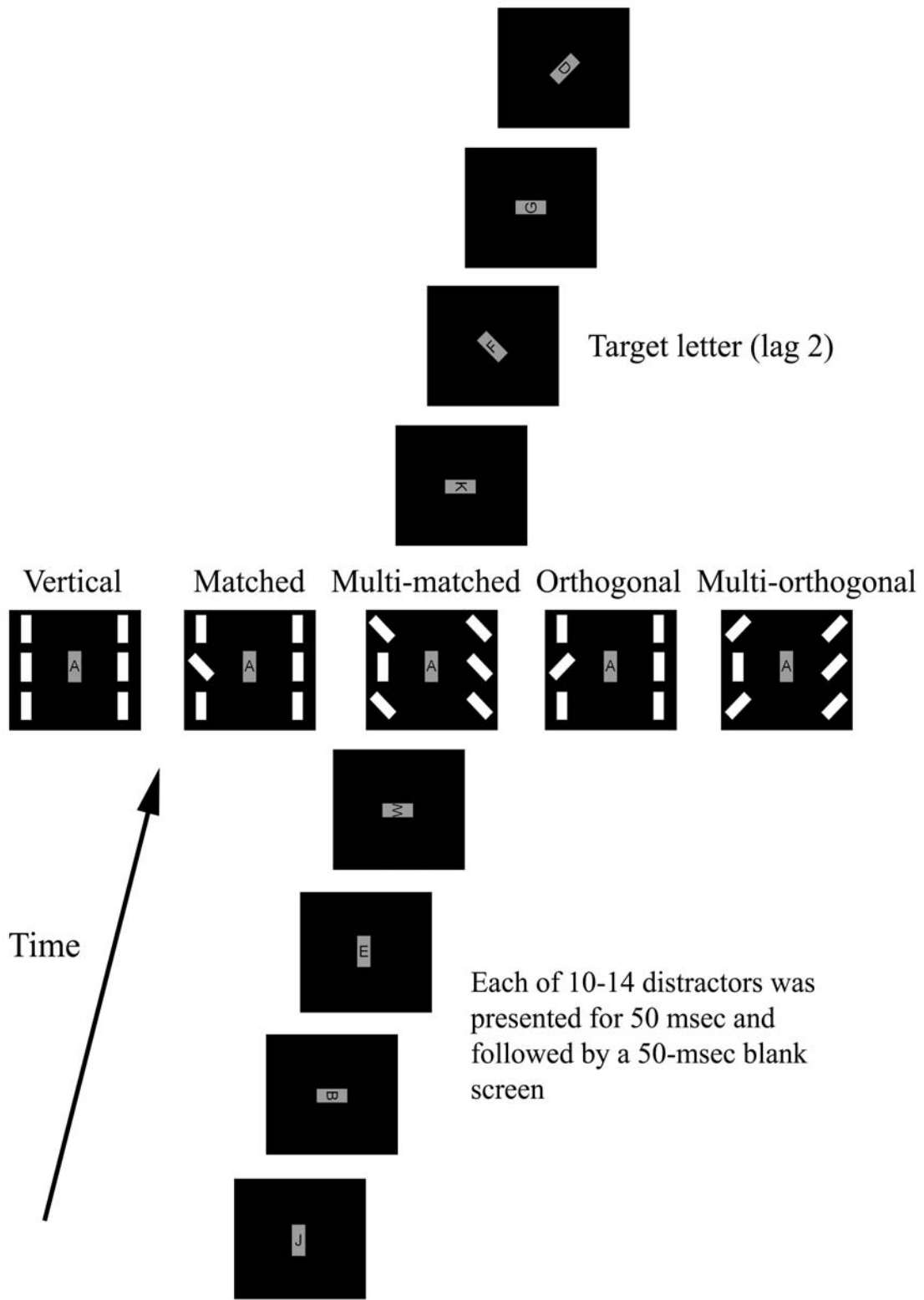
Figure 6. Schematic representation of events in Experiment 3.

The accuracy difference between two lags for each condition was divided by the sum of the accuracy of two lags to represent the magnitude of attentional capture for that condition. The magnitude of the spatial blink for all five conditions is plotted in Figure 8.
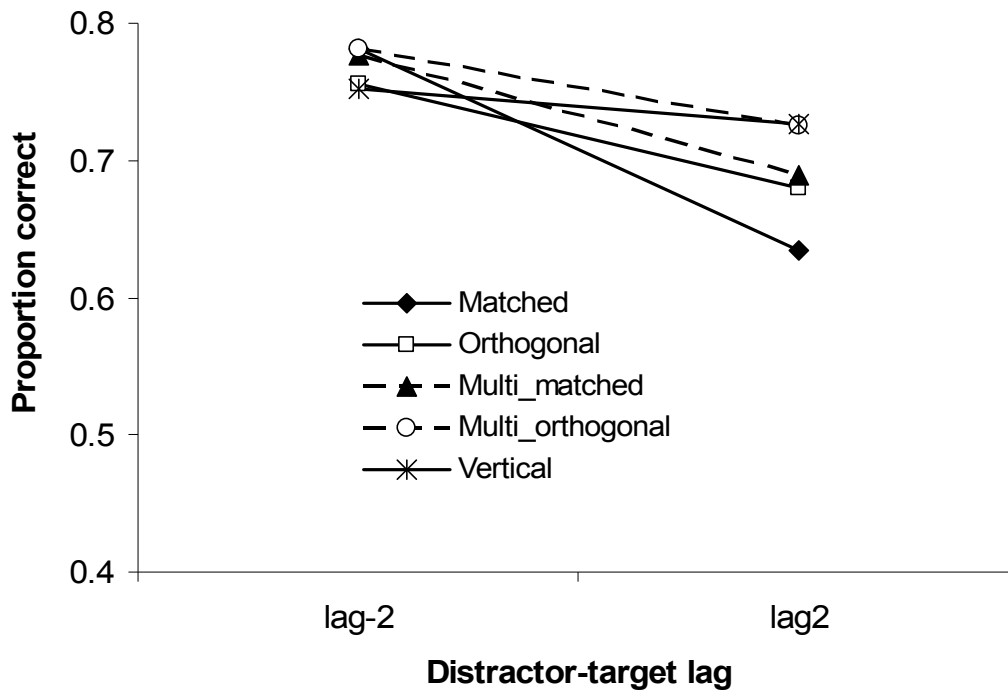

Figure 7. The accuracy of target identification from Experiment 3.

A comparison of the magnitude of the spatial blink between the *Matched* condition and a theoretical baseline of zero, as in the Null condition of the previous experiments, confirmed the presence of a spatial blink in the *Matched* condition, $t(47) = 4.598$, $p<0.001$. Similarly, a comparison between the *Orthogonal* condition and a theoretical baseline of zero confirmed the presence of a spatial blink in the *Orthogonal* condition, $t(47) = 3.10$, $p=0.003$. Thus, both the *Matched* condition and the *Orthogonal* condition induced a large spatial blink. And consistent with the results of Experiment 2, the spatial

blink caused by the orientation-matched distractors in the *Matched* condition was larger than that in the *Orthogonal* condition, $t(47) = 3.096$, *p=0.003,* as can be seen in Figure 8.
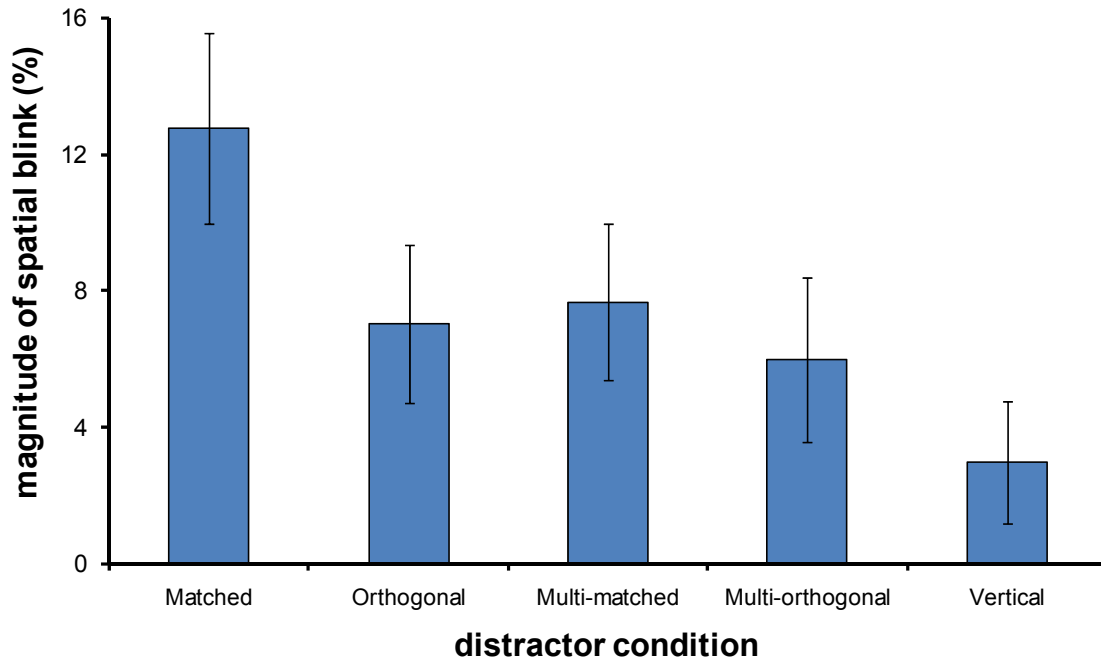

Figure 8. The magnitude of the spatial blink in each condition of Experiment 3

When the spatial blink in the *Multi-matched* condition was compared to the theoretical baseline of zero, there was a spatial blink in the *Multi-matched* condition, $t(47) = 3.281$, *p=0.002*. A similar comparison between the *Multi-orthogonal* condition and a theoretical baseline of zero also confirmed the presence of a spatial blink in the *Multi-orthogonal* condition, $t(47) = 2.515$, *p=0.015;* Thus both the *Multi-matched* condition and the *Multi-orthogonal* condition caused a spatial blink. But the spatial blink in the *Vertical* condition was not significantly different from zero, $t(47) = 1.663$, *p=0.103*.

In order to examine the synergistic effect of stimulus-driven saliency and top-down guidance, a planned comparison between the *Multi-matched* condition and the *Matched* condition was performed. The results showed that the spatial blink of the *Matched*

condition was lager than that of the ***Multi-matched*** condition, t(47) = 2.476, *p=0.017*. Thus an orientation-matched singleton in the ***Matched*** condition is more effective in capturing attention than multiple orientation-matched bars in the ***Multi-matched*** condition. But a similar comparison between the ***Multi-orthogonal*** condition and the ***Orthogonal*** condition found no difference between the two, t(47) = 0.511, *p=0.611*.

Discussion

As I predicted, when the stimulus-driven saliency was reduced in the ***Multi-matched*** condition compared to the ***Matched*** condition, a vertical singleton with multiple orientation-matched bars in the ***Multi-matched*** condition produced a smaller capture effect than an orientation-matched singleton in the ***Matched*** condition. Therefore the salience of the orientation singleton did account for a part of the attentional capture observed in Experiments 1 and 2, though an orientation singleton alone was insufficient to capture attention there. As the stimulus-driven saliency was reduced in the ***Multi-orthogonal*** condition compared to the ***Orthogonal*** condition, the spatial blink in the ***Multi-orthogonal*** condition was numerically smaller than that in the ***Orthogonal*** condition.

The results of the present experiment suggest a synergism between top-down attentional control and stimulus-driven saliency. This is consistent with some previous studies on color-based contingent capture (Du & Abrams, 2008; Lamy et. al., 2004) which showed a synergetic effect between top-down control (target-defining color) and stimulus-driven salience (either a salient color singleton or a salient event of onset). More specifically, the human visual system apparently deploys attention based on both

stimulus-driven saliency and top-down guidance from control settings. These two forces work in a synergistic fashion. When they work together, their effect is larger than the sum of their individual effects. The current study showed that an orientation singleton could boost the contingent capture effect of an orientation-matched distractor (indexed by a larger spatial blink) much like the color singleton did in the earlier studies. Thus these results extended this synergistic mechanism into a new visual domain: orientation-based contingent capture of attention.

In addition, the present experiment found that an orientation singleton in either the *Matched* or *Orthogonal* condition captured attention, disrupting identification of the central target. This pattern of results replicated the main findings from Experiments 1 and 2. Thus both an orientation singleton that matches target orientation and an orientation singleton that is perpendicular to the target consistently capture attention. As I discussed in Experiment 2, attentional capture in either the *Matched* or *Orthogonal* condition was not due to the stimulus-driven saliency of an orientation singleton in those conditions because a horizontal singleton cannot capture attention.

Experiments 1-3 showed that an orientation singleton that was perpendicular to the target orientation captured attention. That could have occurred if participants adopted a crude control setting to prioritize any oblique letters irrespective of their specific orientations—and not just the target orientation. But this possibility seems unlikely because participants were explicitly told to ignore any letters that were not in the same orientation as the target letter. In addition, there were two oblique letters whose orientations were perpendicular to each other in the central letter stream on each trial. If participants maintained a control setting to prefer all oblique letters, they would equally

likely to report either the target letter or the orthogonal letter, resulting in an overall accuracy of nearly 50%. Nevertheless, Experiment 4 was designed to further examine this possibility by always presenting an orientation-unmatched oblique letter before the target letter.

There is also another alternative explanation. Although participants would be unlikely to adopt a top-down control setting for all oblique letters, they could have treated the two oblique letters differently from the other letters because each of the two oblique letters was never repeated in the central stream. Since the orthogonal letter that was perpendicular to the target only appeared once in the central stream, it might have been prioritized for its single occurrence. To examine this possibility, two orthogonal letters which are perpendicular to the target letter will be presented in the central stream in the next experiment. If a single occurrence of the orthogonal letter that is perpendicular to the target accounts for the spatial blink in the **Orthogonal** condition in Experiments 1 - 3, then the spatial blink in the **Orthogonal** condition in the new experiment should be greatly reduced or even eliminated when orthogonal letters that are perpendicular to the target appear twice in the central stream.

Chapter 7: Experiment 4

Experiments 1 to 3 found that an irrelevant orientation singleton that matched the sought-for orientation involuntarily captured attention, resulting in impaired performance of central target identification at lag 2. But homogenously vertical bars in the Vertical condition of Experiment 1 and a horizontal singleton in the Horizontal condition of Experiment 2 did not produce an attentional capture effect. Therefore the capture effects observed in the Matched condition of Experiments 1 and 2 were mainly due to the prioritization of a top-down control setting rather than bottom-up saliency of an orientation singleton.

However, it remains unknown why an irrelevant orientation singleton that was perpendicular to the sought-for orientation also captured attention. A possible explanation is that the orientation singleton in the *Orthogonal* condition captured attention in a stimulus-driven fashion. This stimulus-driven saliency account was ruled out because a horizontal singleton did not capture attention in Experiment 2. Thus an orthogonal singleton does not capture attention in a purely stimulus-driven fashion. However, two other alternative explanations need further examination. One possibility is that the capture effect in the *Orthogonal* condition was a side effect of a top-down control setting for a specific sought-for orientation. When this top-down control setting selectively activates visual neurons which have bimodal tuning curve with two peaks 90° apart, both the sought-for orientation and the irrelevant orthogonal orientation (perpendicular to the sought-for orientation) are prioritized automatically by those visual neurons. Another alternative explanation is that the two oblique letters in the central stream were treated as a group because each of them was the sole letter tilted in a unique orientation and only

appeared once in the central stream. Being the sole oblique letter other than the target letter might have caused participants to prioritize that orientation in addition to the target, thus resulting in a capture effect in the ***Orthogonal*** condition.

To examine these possibilities, Experiment 4 presented two oblique letters that were perpendicular to the target letter in each trial (one before the target letter, one after the target letter) while keeping everything else the same as Experiment 2. By doing so, oblique letters that were perpendicular to the target letter were not as special as the target letter any more. And the capture effect would be expected to diminish in the ***Orthogonal*** condition if the explanation suggested above is correct.

In addition, in the present experiment one of the oblique letters that was perpendicular to the target letter always appeared before the target letter. Therefore, the present experiment served another important purpose: to force participants to narrow their top-down control setting to a specific target orientation. If participants were searching for any oblique letters instead of a specifically tilted letter, they might report the first oblique letter they encountered, thus severely impairing performance across all conditions irrespective of the different peripheral distractors. If the present experiment replicates the results of Experiment 2, the possibility that participants were maintaining a top-down control setting for any oblique letters can be confidently ruled out.

Method

Participants

Forty-eight undergraduate students from Washington University participated in a half hour long experiment for course credit. All had normal or corrected-to-normal visual

acuity. No participants had experience in similar experiments.

Apparatus and Procedure

All stimuli and procedures were the same as those of Experiment 2 with one exception. In Experiment 2, there was only one oblique letter that was orthogonal to the target. It could either appear before the target letter or after the target letter. However, in the present experiment, there were two oblique letters which were perpendicular to the target letter in the central stream. One of them appeared 4 frames before the target letter and the other appeared 4 frames after the target letter.

Design

The present experiment had a four distracting conditions (Null, Horizontal, Matched and Orthogonal) by two lags within-subject design which was exactly same as that of Experiment 2.

Results

The accuracy of target identification is plotted in Figure 9 as a function of distractor-target lag and the distractor condition. There were three main findings. First, we found a main effect of lag, with lower accuracy as lag increased, $F(1,47)=18.443, p<0.001, \eta_p^2 = 0.282$. Next, there was no main effect of distractor condition, $F(3,141)= 1.977, p=0.120, \eta_p^2 = 0.040$. But most importantly, the effects of lag and distractor condition interacted ($F(3,141)=6.424, p<0.001, \eta_p^2 = 0.120$), reflecting the fact that the impairment caused by either orientation-matched distractors or orthogonal distractors occurred mainly for lag 2, replicating results from Experiments 1-3. This was the pattern indicative of the spatial blink.
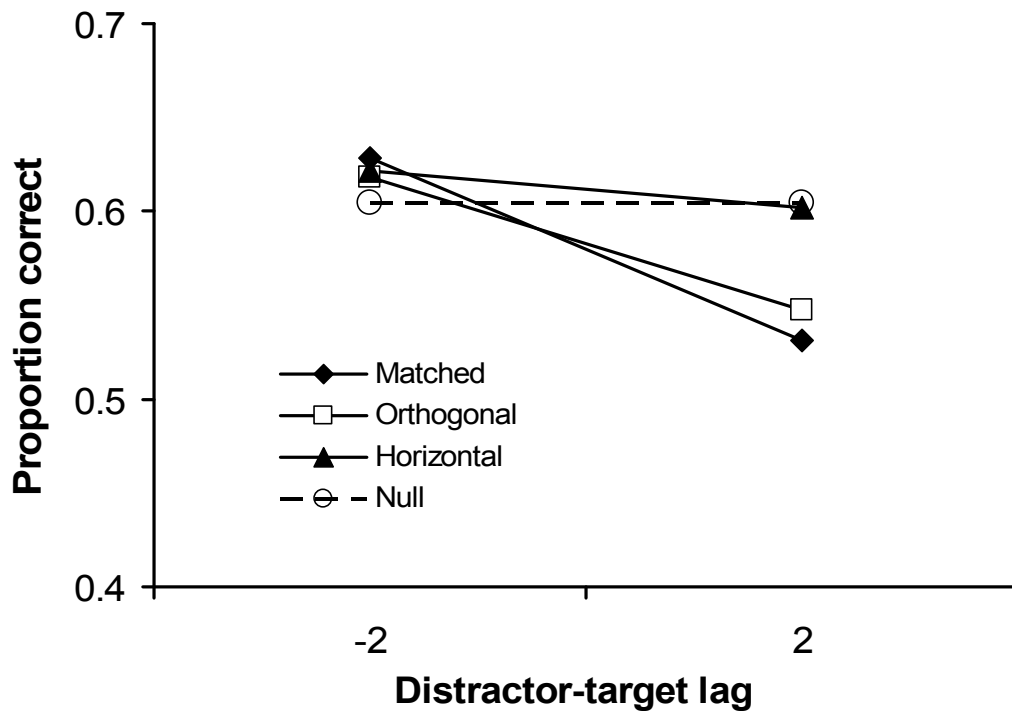
Figure 9. The accuracy of target identification from Experiment 4.

The accuracy difference between two lags for each condition was divided by the sum of the accuracy of two lags to represent the magnitude of attentional capture for that condition. There was no difference between accuracy at the two lags in the *Null* condition. Therefore, the magnitude of attentional capture in the *Null* condition was zero. The magnitude of the spatial blink for the other three conditions is plotted in Figure 10.

A further comparison of the magnitude of the spatial blink between the *Matched* condition and the *Null* condition confirmed the presence of a spatial blink in the *Matched* condition, $t(47) = 4.116$, *p<0.001*. Similarly, a comparison between the *Orthogonal* condition and the *Null* condition confirmed the presence of a spatial blink in the *Orthogonal* condition, $t(47) = 3.066$, *p=0.004*. Thus, both the *Matched* condition and the *Orthogonal* condition induced large spatial blinks. And consistent with the results of

Experiment 1, the spatial blink caused by the orientation-matched distractors in the *Matched* condition was not significantly different from that in the *Orthogonal* condition, $t(47) = 0.246$, *p=0.807,* as can be seen in Figure 10.
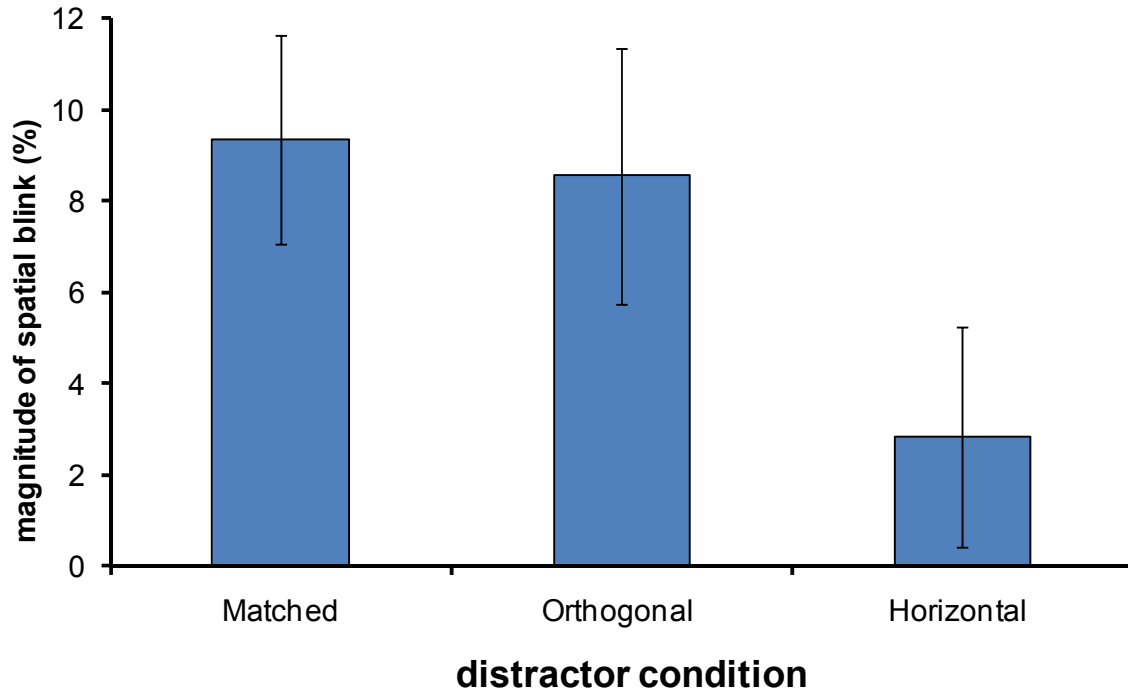

Figure 10. The magnitude of the spatial blink in each condition of Experiment 4

Also consistent with Experiment 2, a horizontal singleton in the *Horizontal* condition did not cause a spatial blink because the spatial blink in the *Horizontal* condition was not significantly different from that of the *Null* condition, $t(47) = 1.177$, *p=0.245*. Therefore, presenting a horizontal singleton among five vertical bars in the *Horizontal* condition did not induce any capture effect.

Discussion

Even with two orthogonal letters being perpendicular to target in the central stream in the present experiment, both an irrelevant orientation singleton that matched the sought-

for orientation (the *Matched* condition) and an irrelevant orientation singleton that was perpendicular to the sought-for orientation (the *Orthogonal* condition) captured attention and produced the spatial blink. And also consistent with Experiment 2, participants did not produce the spatial blink in the *Horizontal* condition. Over all, the present experiment replicated the results of Experiment 2. Therefore, two seemingly plausible explanations can be confidently ruled out based on the present results.

First, if participants were maintaining a top-down control setting for all oblique letters, the spatial blink observed in both the *Matched* condition and the *Orthogonal* condition of Experiments 1-3 could be easily explained by such a broad top-down control setting. However, it was not possible for participants to maintain such a broad top-down control setting when an orthogonal letter being perpendicular to the target always appeared prior to the target in the present experiment. If participants truly maintained a broad control setting for all oblique letters, they would have reported the first orthogonal letter they encountered on most trials, resulting in very low accuracy across all conditions. However, relatively high accuracy (above 50% across all conditions) in the present experiment weakens this possibility.

Second, since an irrelevant orientation singleton that is perpendicular to the target orientation appeared only once in the central stream of previous experiments, it was as rare as the target. The single occurrence of such an orthogonal letter might make the orthogonal orientation (that was orthogonal to target) as special as the target orientation. Therefore, when two orthogonal letters that were perpendicular to the target letter were presented in the central stream, the spatial blink in the *Orthogonal* condition might be largely reduced or eliminated, whereas the spatial blink in the *Matched* condition should

74

remain intact or even become larger (the target orientation was more salient than the orthogonal orientation because the target letter was a true singleton in the central stream). Contrary to this prediction, the present experiment showed that the magnitude of spatial blink diminished to a similar level for both the *Matched* condition and the *Orthogonal* condition. Therefore the unexpected prioritization of an orthogonal orientation singleton was not due to the single occurrence of an orthogonal orientation singleton.

In summary, Experiment 2 showed that the stimulus-saliency of an orientation singleton was insufficient to account for the capture effect observed in the *Orthogonal* condition. The present experiment also indicated that the spatial blink in the *Orthogonal* condition was neither due to a broad top-down control setting for all oblique letters nor the single occurrence of an orthogonal letter being perpendicular to the target. Thus only one possibility was left: The capture effect in the *Orthogonal* condition was a side effect of a top-down control setting for a specific sought-for orientation. When this top-down control setting selectively activates visual neurons which have bimodal tuning curves with two peaks 90° apart, the irrelevant orientation singleton being orthogonal to the sought-for orientation is also prioritized as a side effect of the activation of those bimodal visual neurons. This is an important finding because it demonstrates that feature-based attentional capture is not only contingent upon a top-down control setting for a specific feature but also influenced by the feature preferences of visual neurons. Admittedly, the current study did not provide direct neural measurements of individual neurons. So caution should be taken when we explain the spatial blink in the *Orthogonal* condition.

Chapter 8: Experiment 5

The first four experiments of the present dissertation test the existence of an orientation-specific control setting of attention. Human subjects can set up an attentional control setting for a sought-for orientation based on verbal instruction. This top-down control setting for a sought-for orientation selectively enhances neural responses of visual neurons with preference for the same orientation, thus resulting in involuntary prioritization of an orientation-matched distractor at an irrelevant location. But some of those selectively activated visual neurons might have a bimodal orientation tuning curve with two peaks 90˚ apart (Anzai, Peng & Van Essen, 2007). When those neurons are selectively activated, their activation might have a side effect: an irrelevant distractor whose orientation is perpendicular to the sought-for orientation can also be involuntarily prioritized.

However, these conclusions are only based on the study of two specific target orientations (either 45º clockwise from vertical or 45º counterclockwise from vertical). If subjects are required to search for a target in a different orientation such as an upright letter or a horizontal letter, what kind of irrelevant bars will capture attention? If the selective activation of visual neurons with bimodal orientation tuning curves accounts for the effects observed in the earlier experiments then an upright or a horizontal target might cause either a vertical or a horizontal singleton in the periphery to also capture attention. The present experiment was designed to examine whether both a vertical singleton and a horizontal singleton can capture attention when subjects search for a vertical or a horizontal target letter.

Method

Participants

Sixty-two undergraduate students from Washington University participated in a half hour long experiment for course credit. All had normal or corrected-to-normal visual acuity. No participants had experience in similar experiments.

Apparatus, Procedures and Designs

Twenty participants were required to report the sole vertical letter in the central stream. When participants searched for a vertical target, the sequence of events on a trial is illustrated in Figure 11. As Figure 11 shows, there were multiple tilted letters (45º from vertical) and two horizontal letters in the central stream to serve as masks for the target. One horizontal letter was presented before the target. The other horizontal letter was presented after the target.

For the other forty-two participants, they were required to report the sole horizontal letter (half of them looked for a horizontal letter facing left, the other half searched for a horizontal letter facing right. See Figure 12 for the latter condition). When participants searched for a horizontal target facing right, the sequence of events on a trial is illustrated in Figure 12. As Figure 12 shows, there were multiple tilted letters (45º from vertical) and two vertical letters in the central stream to serve as masks for the target. One vertical letter was presented before the target. The other was presented after the target. Other parameters of the stimuli are the same as those in Experiment 1.

There were four conditions of peripheral distracting bars. On one-fourth of the trials, there was no white distracting bar in the periphery. This was the *Null* condition of the present Experiment. On the other three-fourths of trials, one of the letters in the 8th

through 15th frames, randomly chosen with equal chance, was flanked by two sets of white bars (three bars in each set) whose inner edges appeared 6º to the right or left of the center of display. These trials containing peripheral distractors were evenly distributed among three conditions (the *Neutral* condition, the *Matched* condition and the *Orthogonal* condition). In the *Neutral* condition, all six peripheral bars were homogeneously tilted so that the *Neutral* condition had neither an orientation singleton nor a bar that matched the target orientation. In the *Matched* condition, however, one bar either to the left or right of the central letters was either a vertical bar or a horizontal bar that matched the sought-for orientation. The other five peripheral bars were homogeneously tilted (45º from vertical). Thus there was a vertical singleton or a horizontal singleton matching the sought-for orientation in the *Matched* condition. The *Orthogonal* condition had either a horizontal bar or a vertical bar that was orthogonal to the target. The singleton in the *Orthogonal* condition was accompanied by five homogeneously tilted bars (45º from vertical). Thus there was a horizontal singleton or a vertical singleton that was perpendicular to the sought-for orientation in the *Orthogonal* condition. If the same mechanism underlying the results of Experiment 1 works in the present experiment, the singletons in both the *Matched* condition and the *Orthogonal* condition will capture attention.

On half of the trials containing peripheral distracting bars, the frame containing the peripheral distracting bars could appear either two frames before that containing the target (distractor-target lag of 2) or two frames after the target (lag of -2).

Design

Four distractors conditions (Null, Neutral, Matched and Orthogonal) were mixed up and presented to each subject in a random order. The present experiment contained 24 replications of each combination of four distractor-conditions and two distractor-target lags, for a total of 192 trials. Participants first served in one block of 16 trials for practice. They then completed the test trials. After every 64 trials, they received a brief break.
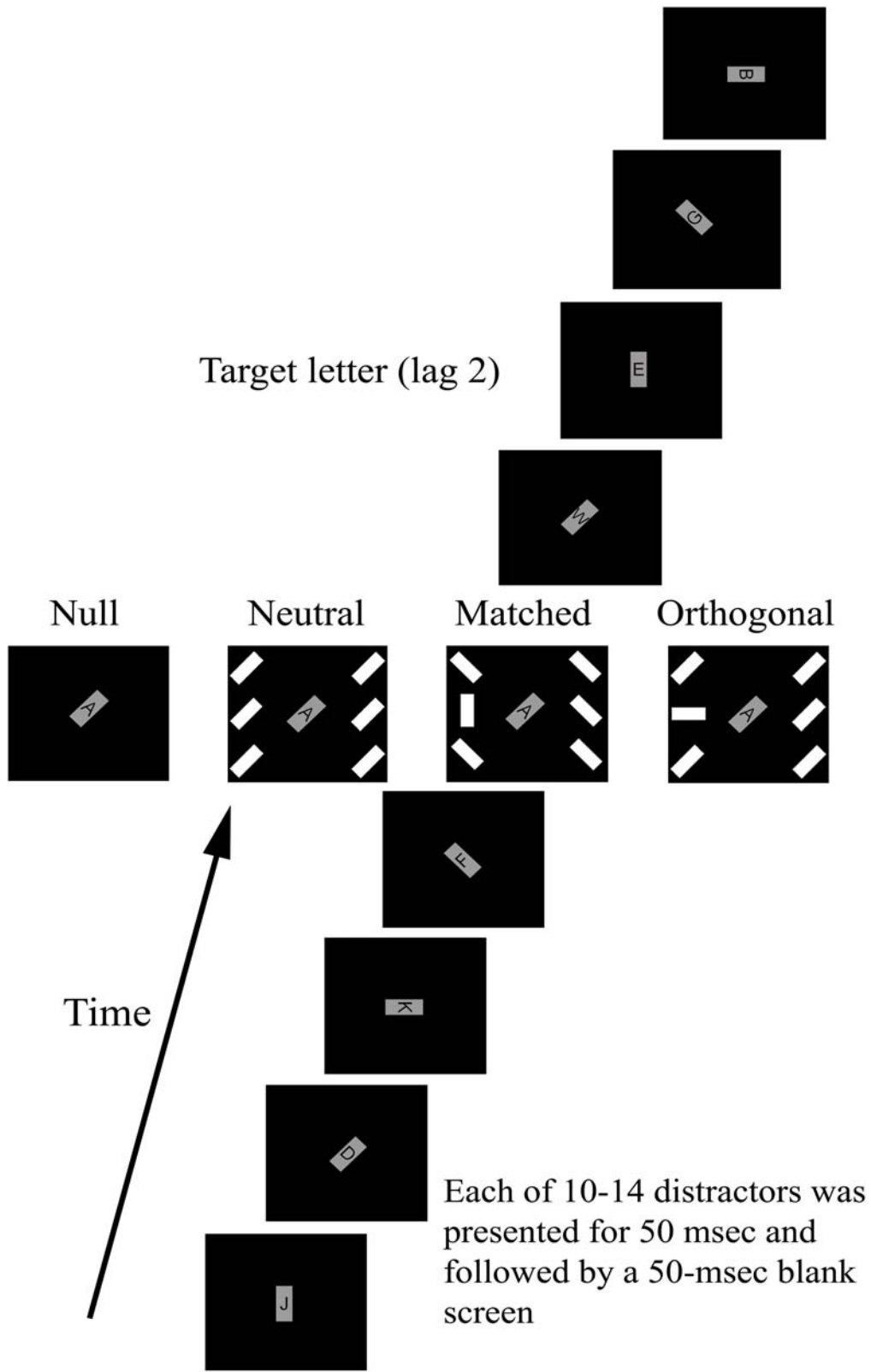
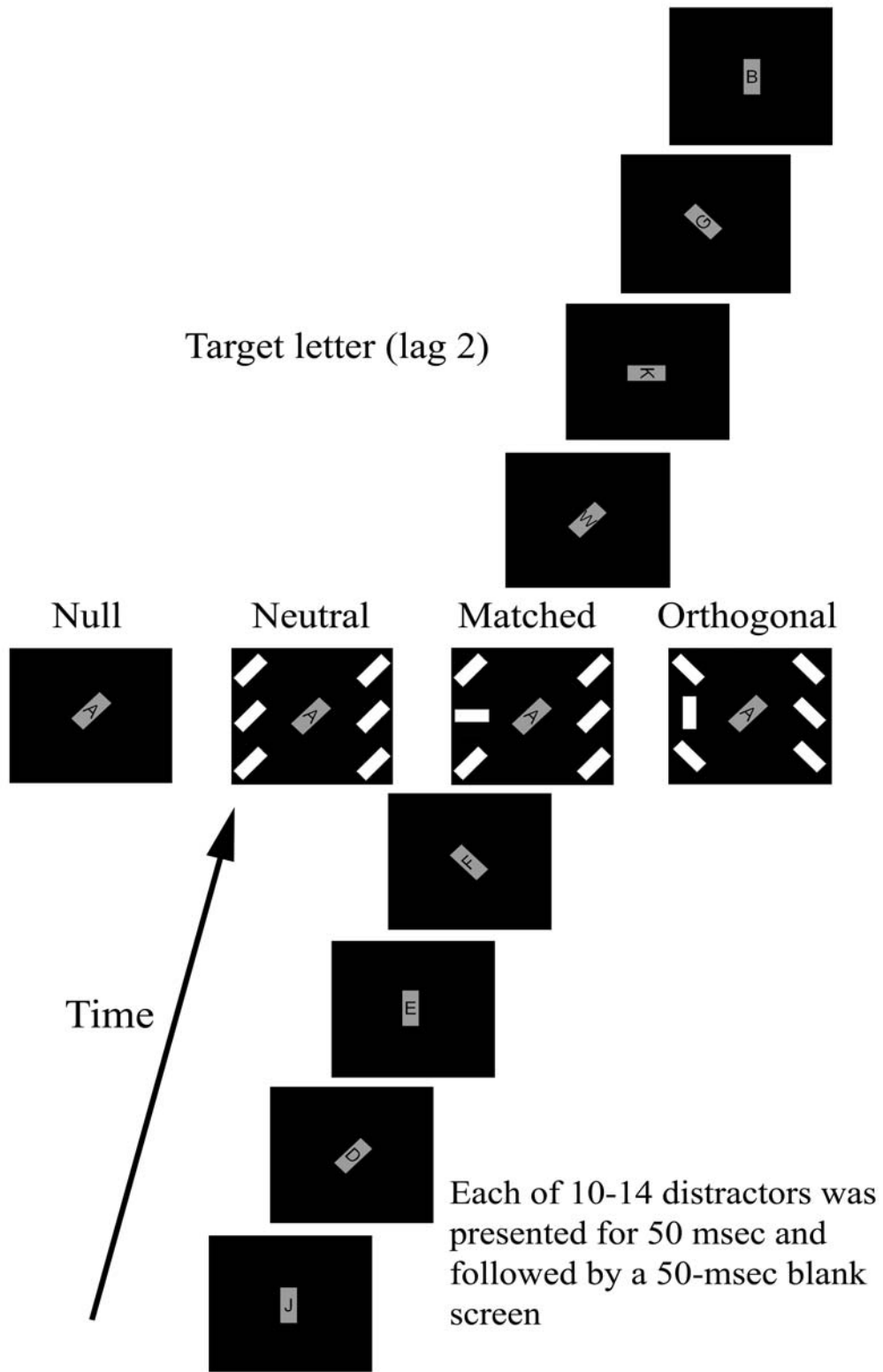**Figure 11**. Schematic representation of events in the vertical target condition of Experiment 5.

Figure 12. Schematic representation of events in the horizontal target condition of Experiment 5.

Results and Discussion

The accuracy of target identification is plotted in Figure 13 as a function of distractor-target lag and the distractor condition. There were three main findings. First, we found a main effect of lag, with lower accuracy as lag increased, $F(1,61)=4.11$, $p=0.047$, $\eta_p^2 = 0.063$. Next, there was a main effect of distractor condition, $F(3,183)= 3.053$, $p=0.03$, $\eta_p^2 = 0.048$. But most importantly, the effects of lag and distractor condition interacted ($F(3,183)=4.723$, $p=0.003$, $\eta_p^2 = 0.072$), reflecting the fact that the impairment caused by either orientation-matched distractors or orthogonal distractors occurred mainly for lag 2. This was the pattern indicative of the spatial blink.
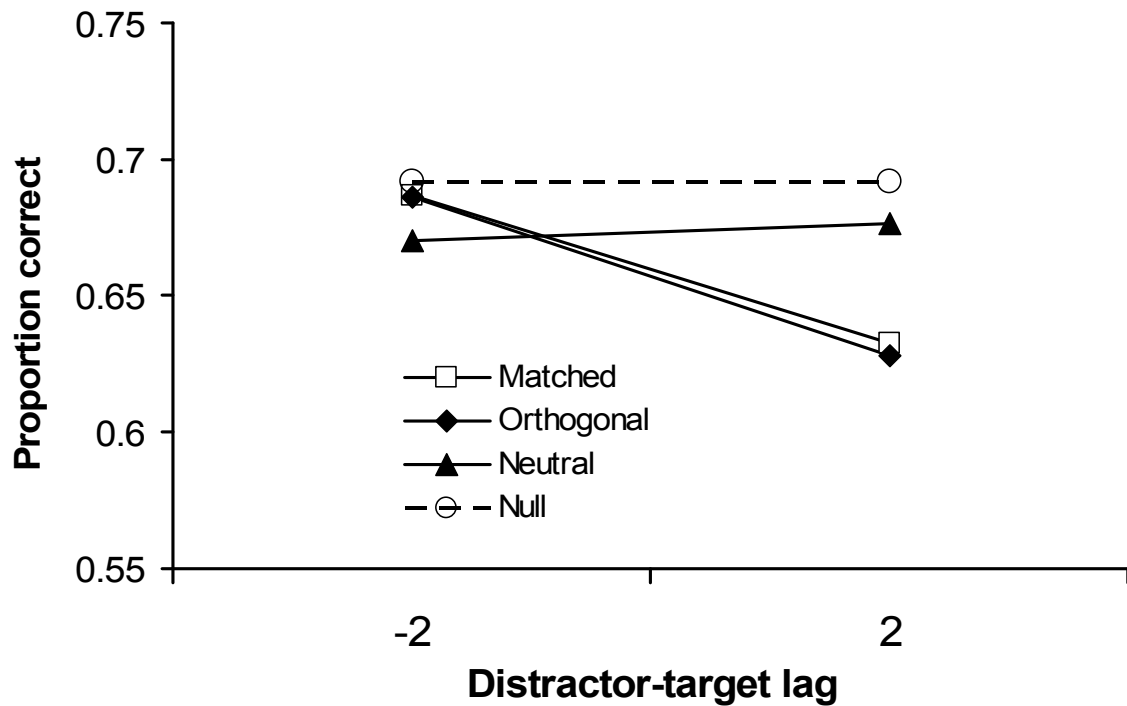

Figure 13. The accuracy of target identification from Experiment 5.

The accuracy difference between two lags for each condition was divided by the sum of the accuracy of two lags to represent the magnitude of attentional capture for that

condition. Again the magnitude of the spatial blink in the *Null* condition was zero. The magnitude of the spatial blink for the other three conditions is plotted in Figure 14.

A further comparison of the magnitude of the spatial blink between the *Matched* condition and the *Null* condition confirmed the presence of the spatial blink in the *Matched* condition, $t(61) = 2.475$, *p=0.016;* Similarly, a comparison between the *Orthogonal* condition and the *Null* condition confirmed the presence of the spatial blink in the *Orthogonal* condition, $t(61) = 2.794$, *p=0.007.* Thus, both the *Matched* condition and the *Orthogonal* condition induce large spatial blinks. And consistent with the results of Experiments 1 and 4, the spatial blink caused by the orientation-matched distractors in the *Matched* condition was not significantly different from that in the *Orthogonal* condition, $t(61) = 0.145$, *p=0.885,* as can be seen in Figure 14.
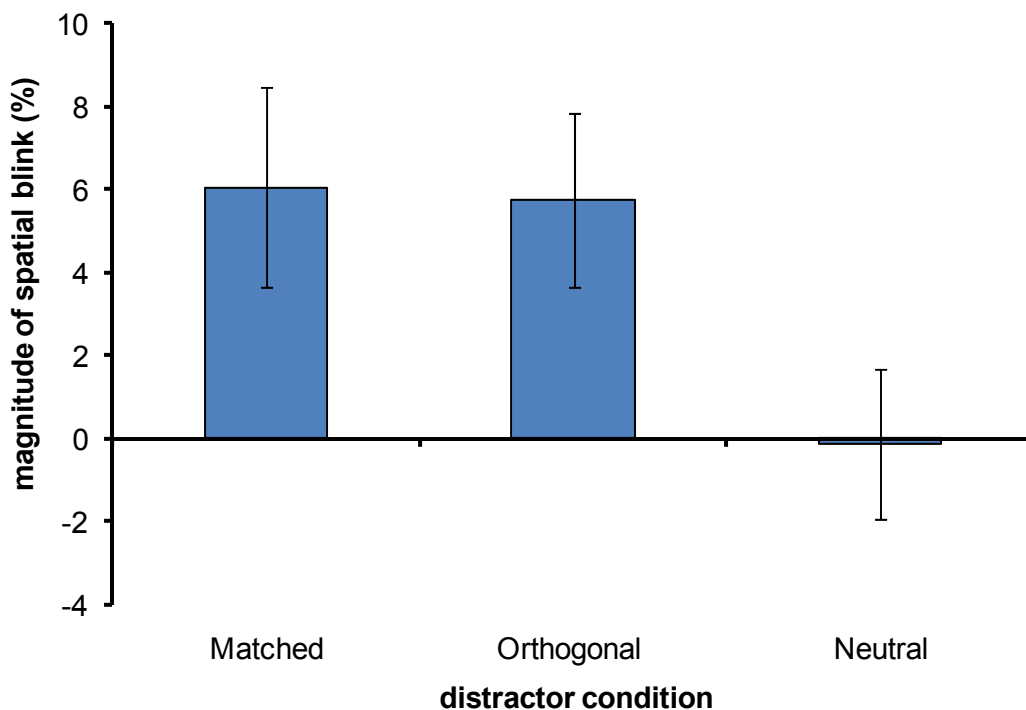

Figure 14. The magnitude of the spatial blink in each condition of Experiment 5

Also consistent with Experiment 1, six homogeneously tilted bars in the *Neutral* condition did not cause a spatial blink because the magnitude of the spatial blink in the *Neutral* condition was not significantly different from that of the *Null* condition, $t(61) = 0.074$, *p=0.941*.

Discussion

When participants were required to identify a vertical letter or a horizontal letter in the present experiment, an irrelevant orientation singleton that matched the sought-for orientation still captured attention involuntarily. In addition, an irrelevant orientation singleton that was perpendicular to the sought-for orientation also captured attention. This general pattern of results is consistent with results from Experiments 1-4. And it indicates that involuntary attentional capture caused by either an orientation-matched singleton in the *Matched* condition or an orthogonal singleton in the *Orthogonal* condition can occur when participants are searching for a vertical target or a horizontal target.

Why does an orthogonal singleton that is perpendicular to the target orientation capture attention in a similar way as an orientation singleton that matches the target orientation? A possibility is that the spatial blink in the *Orthogonal* condition is a side effect of orientation-specific control of attention. When a top-down control setting for a sought-for orientation selectively activates visual neurons which prefer two orientations that are orthogonal to each other, an orientation singleton that matches the target captures attention. And as a side effect, an orthogonal singleton also captures attention because it is perpendicular to the sought-for orientation and is a favorable stimulus to the selectively

activated neurons. The selectively activated neurons with bimodal tuning curves prioritize not only the sought-for orientation but also the irrelevant orientation that is perpendicular to the sought-for orientation. This is an important finding because it shows that allocation of attention is not only determined by a joint effect of stimulus-driven saliency and top-down guidance but also by feature preferences of visual neurons. Of course, there are three alternative possibilities. But the present experiment along with Experiments 1-4 ruled out these possibilities. The possibilities will be further discussed in the general discussion.

One thing worth noting is that the magnitude of spatial blink (attentional capture) in both the *Matched* condition (6.06%) and the *Orthogonal* conditions (5.76%) of Experiment 5 appears to be smaller than those of other four experiments. This is possibly due to less top-down control when participants search for either a horizontal or vertical target. Participants usually are more exposed to either vertical or horizontal letters than 45° tilted letters in daily life, participants may find it easier to search for either a horizontal or vertical target than a 45° tilted target. This was consistent with the results of Experiment 4 and 5. When participants searched for a 45° tilted target in Experiment 4, their average accuracy is 0.595 (See Figure 13). But the average accuracy is 0.67 when participants searched for either vertical or horizontal target in Experiment 5 (See Figure 11). Therefore participants may exert less top-down control upon task when they search for a horizontal or vertical target than a 45° tilted target. As a result, they showed a smaller attentional capture effect in Experiment 5 in relative to the results of other experiments.

Chapter 9: Meta Analysis

Since all five experiments had both the *Matched* condition and the *Orthogonal* conditions, we conducted a meta analysis of the effect size of attentional capture in two conditions (there were 246 participants in five experiments). In addition, three experiments (154 participants) had a conceptually neutral condition which presented 6 homogenously oriented bars in periphery. Two other experiments (92 participants) presented a horizontal singleton in periphery. So that a meta-analysis on the *Neutral* (or *Vertical*) condition and the *Horizontal* condition was also performed to estimate the effect size of attentional capture in these two conditions.

Again, the accuracy difference between two lags was divided by the sum of the accuracy of two lags to represent the magnitude of attentional capture for each condition. The grand average magnitude of attentional capture for each of four conditions is illustrated in the Fig 15.

A comparison of the magnitude of the spatial blink between the *Matched* condition and the theoretical baseline of zero confirmed the presence of the spatial blink in the *Matched* condition, $t(245) = 9.086$, $p<0.001$; Similarly, a comparison between the *Orthogonal* condition and the theoretical baseline of zero confirmed the presence of the spatial blink in the *Orthogonal* condition, $t(245) = 6.993$, $p<0.001$. Thus, both the *Matched* condition and the *Orthogonal* condition produce large spatial blinks. And the spatial blink caused by the orientation-matched distractors in the *Matched* condition was significantly larger than that in the *Orthogonal* condition, $t(245) = 3.010$, $p=0.003$, as can be seen in Figure 15. And the spatial blink in the *Vertical* condition was not significantly different from the theoretical baseline of zero, $t(153) = 1.044$, $p=0.298$.

Presenting six vertical bars in the ***Vertical*** condition did not induce any capture effect. The spatial blink in the ***Horizontal*** condition was not significantly different from the theoretical baseline of zero though it appeared to approach significant difference, $t(91) = 1.913$, $p=0.059$. Thess results indicated that the ***Horizontal*** condition is more distracting than the *Vertical* condition in a purely stimulus-driven fashion.
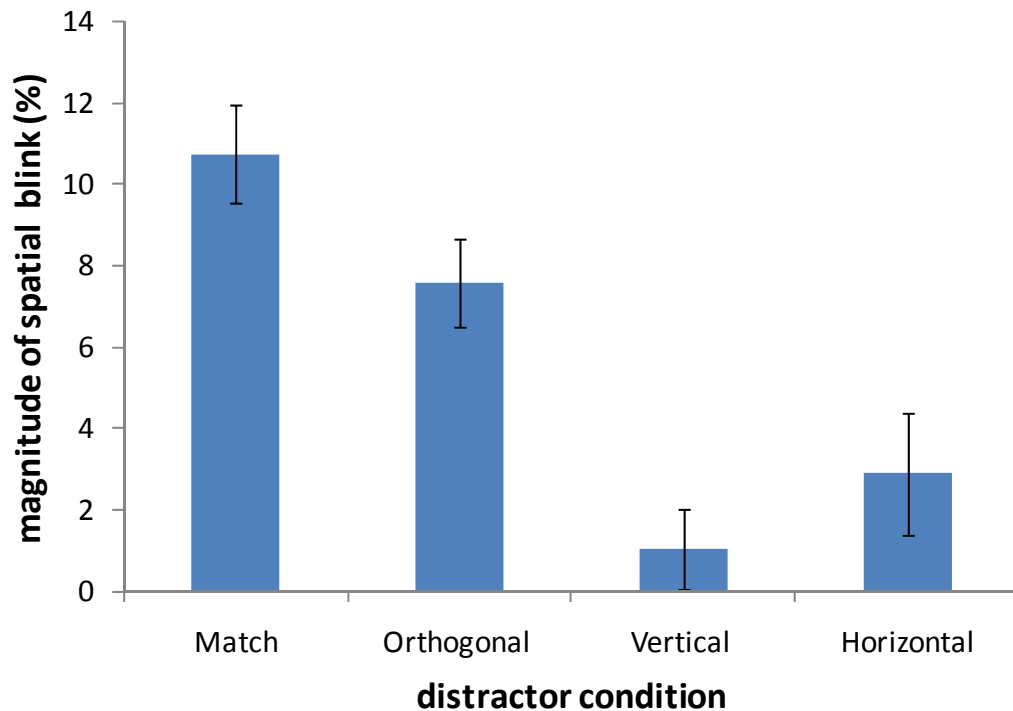
Figure 15. The aggregated magnitude of the spatial blink in each condition of five Experiments

In conclusion, the meta-analysis of five experiments confirmed that both an orientation-matched singleton in the ***Matched*** condition and an orthogonal singleton in the ***Orthogonal*** condition can involuntarily capture attention, resulting in a large impairment in detecting central target (spatial blink). But the orientation singleton in the ***Horizontal*** condition and six homogenous tilted bars in the ***Vertical*** condition are unable to capture attention. This pattern of results is consistent with results of each experiment.

Chapter 10: General Discussion

A summary of results

The present dissertation reported five experiments to examine the consequences of maintaining an attentional set for a specific orientation. Experiment 1 found that an irrelevant orientation singleton in the periphery that matched the sought-for orientation involuntarily captured attention, resulting in a spatial blink (the ***Matched*** condition had impaired target identification at lag 2 compared with the ***Null*** condition). A similar spatial blink was induced by an irrelevant orientation singleton that was perpendicular to the sought-for orientation (the ***Orthogonal*** condition). However, the spatial blink in either the ***Matched*** condition or the ***Orthogonal*** condition was not merely due to the abrupt appearance of distracting peripheral bars because six vertical bars in the periphery (the ***Vertical*** condition) did not produce a spatial blink.

The experimental setting of Experiment 2 was almost the same as that of Experiment 1 with one exception: Experiment 2 included a horizontal bar among five vertical bars in the ***Horizontal*** condition. As expected, Experiment 2 found attentional capture effects (spatial blink) in both the ***Matched*** condition and the ***Orthogonal*** condition, replicating the results of Experiment 1. In addition, Experiment 2 found that a horizontal singleton with five vertical bars in the ***Horizontal*** condition was insufficient to produce a spatial blink. This pattern of results indicates that the spatial blink in both the ***Matched*** condition and the ***Orthogonal*** condition was not due to the stimulus-driven saliency of an orientation singleton.

To estimate the effect of stimulus-driven saliency of an orientation singleton in Experiment 3, peripheral bars were manipulated to be either a tilted singleton with five

vertical bars (*Matched* or *Orthogonal* conditions) or a vertical singleton with five homogenously tilted bars (*Multi-matched* or *Multi-orthogonal* conditions). As in the earlier experiments, Experiment 3 replicated the spatial blink in both the *Matched* condition and the *Orthogonal* condition. But more importantly, it revealed a larger attentional capture effect (spatial blink) in the *Matched* condition compared with that of the *Multi-matched* condition. The *Orthogonal* condition only caused a numerically larger spatial blink than the *Multi-orthogonal* condition. Therefore, the stimulus-driven saliency of an orientation singleton did contribute somewhat to the spatial blink observed in Experiments 1and 2.

In Experiment 4, two oblique letters that were orthogonal to the target letter were presented in the central stream (as opposed to the single orthogonal oblique letter that had been used in the earlier experiments). One appeared prior to the target and the other appeared after the target. This design made it improbable that participants would adopt a control setting for all oblique letters in order to perform the task. Once again, the results showed that both the *Matched* condition and the *Orthogonal* condition produced a spatial blink. Also consistent with Experiment 2, the *Horizontal* condition did not produce a spatial blink. Therefore, the prioritization of an orthogonal singleton was not due to a broad top-down control setting or to the single occurrence of an orthogonal letter in the central stream of Experiments 1-3.

Participants were required to report the sole vertical or horizontal letter in the central stream in Experiment 5. The results showed that there was an attentional capture effect (spatial blink) in both the *Matched* condition and the *Orthogonal* condition (a vertical or horizontal bar among five homogenously tilted bars). But six homogenously tilted bars

did not produce any spatial blink. Therefore, involuntary capture of attention based on a sought-for orientation can not only be applied to a tilted orientation but also to vertical and horizontal orientations.

Contingent Capture and the side effects of orientation-specific control

The contingent attentional capture theory (Folk, Remington & Johnston, 1992) has become an influential theory in the area of attentional capture. Folk and his colleagues proposed that human subjects can adopt a top-down control setting to look for an object with a specific feature (e.g. a target letter in red color). According to the theory, irrelevant distractors can involuntarily capture attention only if they have the same sought-for feature. Most previous studies on the theory have focused on top-down control settings for color. They showed that participants can adaptively maintain either a crude control setting for a color discontinuity (a color singleton) or a more precise control setting for a specific color according to the task setting (Folk, Remington & Johnston, 1992; Folk, Leber, Egeth, 2002). However, much less is known about top-down control settings for orientation even though orientation is one of most important visual features that the human visual system analyzes. Prior to the present dissertation, it was not even known if a top down setting for orientation could even be established.

Experiment 1 found that an irrelevant orientation singleton that matched the sought-for orientation (the *Matched* condition) involuntarily captured attention, resulting in a spatial blink (impaired performance of target identification at fixation). But six vertical bars in the periphery did not produce a spatial blink. These results are consistent with the contingent attentional capture theory (Folk, Remington & Johnston, 1992). It was an

90

orientation match between the sought-for orientation and the orientation of a peripheral bar that triggered involuntary shifts of attention. Moreover, the spatial blink in the ***Matched*** condition was repeatedly observed in all five experiments. Therefore contingent capture based on a sought-for orientation is a robust effect. The results clearly show, for the first time, that it is possible for people to establish a control setting for a specific orientation.

The finding that a spatial blink can be caused by orientation-matched distractors is consistent with previous single cell recording studies (Chelazzi et al. 1998; Haenny, Maunsell & Schiller, 1988; Haenny & Schiller, 1988; Maunsell, Sclar, Nealey & DePriest, 1991; McAdams & Maunsell, 2000; Motter, 1994a & 1994b; Treue & Maunsell, 1996, 1999). These studies provide converging evidence for feature-based attention. They show that neural responses in the visual cortex can be modulated by a feature match between a sought-for feature and the actual stimulus feature, such as a color match (Motter, 1994a & 1994b), an orientation match (Haenny, Maunsell & Schiller, 1988; Haenny & Schiller, 1988; Maunsell, Sclar, Nealey & DePriest, 1991), or a match in motion direction (Treue & Maunsell, 1996, 1999). However, attentional modulation at the level of individual neurons does not necessarily lead to attentional effects on overt behavior. Therefore, it is noteworthy that the present dissertation is the first behavioral study to show that a top-down control setting for a sought-for orientation can also be established to guide attention.

Surprisingly, an irrelevant orientation singleton that was perpendicular to the sought-for orientation (an orthogonal orientation singleton) also captured attention involuntarily, producing a spatial blink. That result is inconsistent with contingent capture theory. Why does an orthogonal orientation singleton capture attention in a similar way as an

91

orientation singleton that matches the sought-for orientation? There are four possibilities--three of which were ruled out in the dissertation. These are discussed next.

First, there was an orientation singleton in the peripheral distractor display in both the *Matched* condition and the *Orthogonal* condition of Experiment 1, whereas there was no orientation singleton in either the *Vertical* condition or the *Null* condition. It is possible that the orientation singleton pulled attention away from identifying the target in a stimulus-driven fashion, resulting in a spatial blink, despite the fact that color singletons are unable to induce a spatial blink under comparable conditions (Du & Abrams, 2008; Folk, Leber & Egeth, 2002). Thus a spatial blink in either the *Matched* condition or the *Orthogonal* condition of Experiment 1 may be due to the stimulus-driven saliency of an orientation singleton instead of a top-down control setting for a specific orientation.

Contradictory to this explanation, Experiment 2 found that a horizontal singleton in the *Horizontal* condition did not capture attention (absence of spatial blink) despite the fact that a horizontal singleton is as salient as an orientation-matched singleton or an orthogonal orientation singleton. However, both an orientation-matched singleton in the *Matched* condition and an orthogonal orientation singleton in the *Orthogonal* condition still captured attention. Therefore, the stimulus-driven saliency of an orientation singleton is insufficient to account for the attentional capture effect (spatial blink) that was observed in either the *Matched* condition or the *Orthogonal* condition of Experiments 1 and 2.

Second, participants might unconsciously adopt a top-down control setting for all oblique letters in the central stream. As a result, a peripheral bar that is either the same as the target orientation or orthogonal to the target orientation would receive the highest

attentional priority because they both match the broad top-down control setting for all oblique letters. A broad top-down control setting for all oblique letters can explain why both the *Matched* condition and the *Orthogonal* condition produced a spatial blink. However this possibility is very unlikely. In Experiments 1-3, there were two oblique letters whose orientations were perpendicular to each other in the central letter stream. Participants were explicitly told to ignore any letters that were not in the same orientation as the target letter. If they had maintained a broad control setting to prefer all oblique letters, they would have been very likely to report the orthogonal letters in the central stream, resulting in severely impaired performance across all lags regardless of the peripheral distractors. Contrary to this prediction, Experiments 1 and 2 showed that an irrelevant singleton interrupted identification of the central target only when it was either the same as the target orientation or orthogonal to the target orientation.

Furthermore, two distracting letters that were orthogonal to the target letter were presented in the central stream in Experiment 4. One was presented prior to the target. The other appeared after the target letter. This experimental design further discouraged participants from adopting a broad control setting for all oblique letters. If they actually had adopted a setting for all oblique letters, they might have been likely to report the orthogonal central letters on many trials. As a result, their identification of the target would be poor regardless of the distractor condition or distractor-target lag. However, Experiment 4 generally replicated the results of Experiments 1 and 2 by showing that both the *Matched* condition and the *Orthogonal* condition had a spatial blink. In addition, Experiment 4 found no spatial blink by a horizontal singleton in the *Horizontal* condition, replicating results from Experiment 2. Therefore, I can confidently rule out the possibility

that participants were maintaining a broad top-down control setting for all oblique letters during the experiments.

In addition, the possibility of a broad control setting for all oblique letters was further weakened by Experiment 5 in which participants were searching for either a vertical or horizontal letter. Experiment 5 showed that both the *Matched* condition and the *Orthogonal* condition produced a spatial blink. It seems highly unlikely for participants to look for both vertical and horizontal letters when they were told to only look for one of those orientations.

Third, participants might have treated the two oblique letters differently from vertical or horizontal letters because each of the two oblique letters was never repeated in the central stream in Experiments 1-3. Since the distracting letter that was perpendicular to the target only appeared once in the central stream of letters, this single occurrence of an orthogonal distracting letter might have increased its relevance to the task goal because it appeared as often as the target letter did. The single occurrence of such an oblique letter might cause the visual system to assign priority to this unique orientation that was perpendicular to the target letter. Moreover, participants might have been able to ignore vertical and horizontal bars in the periphery because vertical and horizontal letters were repeated multiple times in the central stream of letters. To examine this possibility, two oblique letters which were perpendicular to the target letter were presented in the central stream of letters in Experiment 4. If the single occurrence of the distracting letter that is perpendicular to the target accounts for the attentional capture in the *Orthogonal* condition, the spatial blink in the *Orthogonal* condition should have been greatly reduced or even eliminated in the experiment, whereas the spatial blink in the *Matched* condition

should have remained intact or even become larger (a target orientation is more salient than an orthogonal orientation because the target letter was the sole oblique letter in the sought-for orientation). Contrary to this prediction, Experiment 4 showed that the magnitude of the spatial blink diminished to a similar level for both the ***Matched*** condition and the ***Orthogonal*** condition compared to those in Experiments 1 and 2. Therefore the unexpected prioritization of an orthogonal orientation singleton was not due to the single occurrence of an orthogonal orientation singleton.

Finally, the spatial blink in the ***Orthogonal*** condition from Experiments 1 - 5 could have been a side effect of the top-down control setting of a sought-for orientation. This possibility originates from some single cell recording studies of the structure of receptive fields of visual neurons in monkeys. The studies showed that many V2 and V3 neurons in monkeys have receptive fields containing many subregions which are tuned to many different orientations, most commonly with the two most preferred orientations about 90˚ apart (Anzai, Peng & Van Essen, 2007; Felleman & Van Essen, 1987). It is possible that a top-down control setting of a sought-for orientation selectively activates visual neurons which prefer the sought-for orientation in a similar way as a top-down color setting selectively activates neurons which prefer the sought-for color. But many of these visual neurons happen to have a bimodal orientation tuning curve with two peaks 90˚ apart. In other words, a large proportion of selectively activated visual neurons would prefer two orientations that are orthogonal to each other due to the nature of their receptive field. Thus the selective activation of visual neurons with bimodal orientation tuning curves might account for the involuntary prioritization of two orientations perpendicular to each other while only one sought-for orientation is required.

This possibility is consistent with results of all five experiments of the present dissertation. Across all five experiments, bars that were either the same as the target orientation or perpendicular to the target orientation captured attention, thus producing a spatial blink in either the **Matched** condition or the **Orthogonal** condition. However, bars that were 45º from the target orientation were unable to capture attention involuntarily. For instance, six vertical bars in the **Vertical** condition of Experiment 1, a horizontal bar with five vertical bars in the **Horizontal** condition of Experiments 2 and 4, and six homogenously tilted bars in the **Neutral** condition of Experiment 5 did not capture attention. These results indicate that irrelevant bars are not monotonically prioritized in the attentional system based on the angular difference to the target orientation. Instead, when participants are searching for a specific orientation, two orientations are prioritized. One is the sought-for orientation. The other is perpendicular to the sought-for orientation. And this is not decided by a top-down control setting of attention or stimulus-driven saliency of distractors. Instead it is determined by the receptive field characteristic of visual neurons.

Top-down guidance and bottom-up saliency

Selective attention plays a vital role in determining which object in the scene is most important. Most theories of selective attention propose that the attentional selection is under the guidance of a joint effect of two driving forces: goal-directed prioritization (top-down guidance) and stimulus-driven saliency (bottom-up saliency).

The top-down guidance of attention is undeniably a dominant force in determining the deployment of attention. Top-down guidance of attention relies on observers' prior

knowledge of a target location or sought-for features such as color, luminance, orientation and shape. For instance, location-based attention (spatial attention) has been demonstrated to improve accuracy and speed of information processing at a cued location when observers know the target location in advance (Eriksen & Eriksen, 1974; Henderson, 1991; Posner, 1980; Posner, Snyder & Davidson, 1980; Vierck & Miller, 2008). More evidence from physiological studies showed that spatial attention can dramatically increase neural activity of cells whose receptive fields overlap with a cued location (Mangun, 1995; Mangun & Buck, 1998). Moreover, spatial attention can increase the baseline firing rate of neurons even when there is no visual stimulus in the RF, which purely reflects a top-down modulation driven by prior knowledge of target location (Kastner et al, 1999; Luck et al. 1997).

Alternatively, top-down guidance of attention can be driven by sought-for features such as orientation (Haenny, Maunsell & Schiller, 1988), color and luminance (Chelazzi, Miller, Duncan & Desimone, 1993; Du & Abrams, 2008; McAdams & Maunsell, 2000; Motter, 1994a), and direction of motion (Serences & Boynton, 2007; Treue & Maunsell, 1996, 1999). For example, studies showed that neural responses in V4 can be greatly enhanced when the color of a stimulus happens to match the sought-for color (Motter, 1994a). Results from behavioral studies are also consistent with this idea of top-down guidance for a specific sought-for feature (feature-based attention). For example, Folk and colleagues found that uninformative pre-cues captured attention if and only if they matched the target-defining feature (Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). Conversely, salient events such as color or motion singletons, often fail to capture attention if they do not match the features that define the

target (Bacon & Egeth, 1994; Gibson & Kelsey, 1998; Hillstrom & Yantis, 1994; Jonides & Yantis, 1988; Todd & Kramer, 1994).

In addition to top-down guidance, most theories also acknowledged the important role of stimulus-driven salience in determining the deployment of attention. Stimulus-driven salience is purely decided by intrinsic properties of the stimulus. As a result some salient events such as abrupt onset of stimulus, color or luminance contrast, or motion onset can capture attention involuntarily, even if they are totally irrelevant to the task goal. Some single cell recording and FMRI studies shed light on the neural mechanism of stimulus-driven capture of attention (Becker & Kastner, 2005, 2007, 2009; Kastner, Nothdurft & Pigarev, 1999; Knierim, & Van Essen, 1992; Northdurft, Gallant & Van Essen, 1999). For example, a recent FMRI study showed that sensory suppression in extrastriate cortex was eliminated when a stimulus was presented as a feature singleton in a homogenous display, but not when the same stimulus was presented in a heterogeneous display (Becker & Kastner, 2005; Becker & Kastner, 2007). This is consistent with many single cell recording studies which showed that homogenous surrounding texture invokes less suppression in V1 than heterogeneous surrounding texture (Kastner, Nothdurft & Pigarev, 1999; Knierim, & Van Essen, 1992; Northdurft, Gallant & Van Essen, 1999).

The present dissertation provides converging evidence for the effects of stimulus-driven saliency and top-down guidance of attention. For instance, an irrelevant bar that matched the target orientation captured attention, resulting in a spatial blink in the *Matched* condition of all five experiments. The spatial blink effect in the *Matched* condition revealed the robust influence of top-down guidance of the sought-for orientation. Although the effect of stimulus-driven saliency is less pronounced than that

of top-down guidance in the present dissertation, it still manifests in Experiment 2. For instance, in Experiment 2, a horizontal singleton in the ***Horizontal*** condition was more distracting than the ***Null*** condition though its effect differed from attentional capture in either the ***Matched*** condition or the ***Orthogonal*** condition. More importantly, the present dissertation shows that stimulus-driven saliency and top-down guidance work together to determine the deployment of attention, which will be discussed next.

A joint effect of stimulus-driven saliency and goal-directed guidance

Although attention is dichotomized into a stimulus-driven component and a goal-directed component, it is the joint effect of both components that determine the deployment of attention. Recent studies showed that the two components interact with each other in a very complex way. The first line of evidence supporting this joint effect came from studies of contingent capture. Folk and his colleagues proposed that stimulus-driven capture is contingent upon a top-down control setting for a sought-for feature rather than being completely blind to top-down control. For example, an irrelevant onset fails to capture attention when targets are defined by a specific color and succeeds in capturing attention when targets are defined by onsets (Du & Abrams, 2008; Folk, Leber & Egeth, 2002; Folk, Remington & Johnston, 1992; Folk, Remington & Wright, 1994; see also Gibson & Kelsey, 1998).

Consistent with the idea of contingent capture, Bacon & Egeth (1994) found that a specific search strategy can influence attentional capture in a fashion similar to top-down control setting. More specifically, there are two visual search modes. One is the singleton detection mode in which observers search for a local feature discontinuity. The other is

the feature search mode in which observers look for a specific target-defining feature. Surprisingly, they found that an irrelevant color singleton was able to capture attention only when observers were searching for a shape singleton-- presumably using a singleton detection mode. But when observers were required to search for a particular shape among multiple heterogeneous shapes, the irrelevant color singleton did not capture attention because they were using a feature search mode in this case (Bacon & Egeth, 1994; but see Theeuwes, 2004).

Although a top-down control setting of attention seems to suppress stimulus-driven capture of attention in many cases (Folk, Remington, & Johnston, 1992; Yantis & Jonides, 1990), some recent results reveal important synergistic interactions between goal-directed guidance and stimulus-driven selection (Du & Abrams, 2008, 2009; Richard, Wright & Ward, 2003; Ludwig & Gilchrist, 2002; Ludwig & Gilchrist, 2003). For example, two recent studies employing an RSVP task found that the spatial blink, initially presumed to reflect only goal-directed guidance, also depends somewhat on stimulus-driven saliency such as the abrupt appearance of objects or the presence of a color singleton (Du & Abrams, 2008; Lamy, Leber & Egeth 2004).

Consistent with previous studies, the present dissertation showed that attentional capture contingent upon the sought-for orientation is a joint effect of both stimulus-driven saliency of an orientation singleton and top-down guidance of the sought-for orientation. For example, Experiment 3 showed that whether orientation-matched irrelevant bars contain an orientation singleton or not influences the magnitude of the spatial blink. The spatial blink in the ***Multi-matched*** condition was smaller than that in the ***Matched*** condition because the multiple orientation-matched distractors in the ***Multi-matched***

condition were less salient than an orientation-matched singleton in the ***Matched***

condition. Therefore, the present dissertation indicates a synergistic interaction between

top-down and bottom-up factors involved in attentional capture.

Impact of feature preference of visual neurons on Attention

    It is an important finding that the spatial blink can be contingent upon a sought-for

orientation and it is actually due to a joint effect of stimulus-driven saliency and top-

down guidance. Thus the present dissertation expands the contingent capture theory into

a new feature domain: orientation. In addition, the present results also suggest a revision

of classical contingent capture theory: stimulus-driven saliency can be modulated by top-

down guidance but the deployment of attention is not completely contingent upon top-

down guidance.

    The unexpected spatial blink in the ***Orthogonal*** condition of all five experiments was

the most important finding of the present dissertation. The effect could reflect a direct

consequence of a top-down control setting for a specific orientation when this top-down

control setting selectively activates visual neurons with two preferred orientations 90˚

apart from each other (Anzai, Peng & Van Essen, 2007; Felleman & Van Essen, 1987).

In other words, when a large proportion of visual neurons which prefer two orthogonal

orientations are selectively activated by a top-down control setting for a sought-for

orientation, two orthogonal orientations are involuntarily prioritized though only the

sought-for orientation is maintained in the top-down control setting. These results

indicate that attentional capture is not completely determined by a joint effect of

stimulus-driven saliency and top-down guidance. Instead, they reveal an important role of

the innate orientation preferences of visual neurons in determining the effect of orientation-based attentional modulation, thus revealing an important new component that must be accounted for in current theories of attention.

But why have the impacts of neurons' feature preferences not been observed in previous behavioral studies? The reason may be due to differences in the sought-for feature: Most previous studies required participants to search for a target in a particular color, whereas the present experiments used a specific orientation to define the target. The difference between color tuning curves and orientation tuning curves might account for the apparent discrepancy between orientation-based contingent capture and color-based contingent capture. For example, studies showed that a large proportion of visual neurons in V2 and V3 have a bimodal orientation tuning curve, most commonly with two narrow peaks 90˚ apart (Anzai, Peng & Van Essen, 2007; Felleman & Van Essen, 1987). However, few studies have reported a bimodal color tuning curve for visual neurons. Most studies reported color-opponent neurons in the lateral geniculate nucleus (LGN) and double-opponent neurons in the primary visual cortex (Conway, 2001; Conway & Livingstone, 2006; Wachtler, Sejnowski & Albright, 2003). Since visual neurons do not usually have two peaks in their tuning curves in color space, it would not be possible for two distinctive colors (widely separated in color space) to capture attention when participants are required to search for one of those two colors.

Moreover, the opponent process attributes of color vision might also partially account for results of previous studies on color-based contingent capture. Using red-green pairs as an example, some neurons in the LGN and V1 showed an excitatory response to red light and an inhibitory response to green light. But there are some other neurons in LGN and

V1 that showed the opposite response. Thus, when participants searched for a red target, neurons in LGN that preferred red stimuli might be selectively activated and these activated neurons naturally inhibit green distractors because of the opponent process mechanism involving red and green. In fact, most previous studies on color-based contingent capture used red and green targets and distractors. When participants were required to search for a red target, red distractors often captured attention but green distractors did not. When participants searched for a green target, green distractors were much more distracting than red distractors. Thus, the typical findings probably reflect not only a top-down bias for a specific color but also the impact of the (opponent) color preferences of visual neurons.

The present results are also consistent with the biased competition theory of Desimone and collagues (Chelazzi, Duncan, Miller & Desimone, 1998; Desimone, 1998; Moran & Desimone 1985). That theory has implicated the important role of feature preferences of neurons in attentional modulation, although the specific impact of such preferences on attention was not explicitly mentioned. For example, previous single cell studies showed that neural responses to a pair of stimuli (one good stimulus and one poor stimulus) within a single RF is a weighted average of the responses to each individual stimulus presented alone. If the good stimulus is the target, attentional modulation biased neurons' response to their optimal level as if they were responding to a single good stimulus. But if the poor stimulus was the target, attentional modulation biased neural responses to the worst level-- as if they were responding to a single poor stimulus. These single cell recording studies are consistent with the present findings in that effects of attentional modulation may be constrained by the feature preferences of visual neurons.

Conclusion

The present dissertation has three important findings. First, there is a top-down control setting for a specific sought-for orientation. This top-down control setting biases attention toward anything that matches the sought-for orientation. Thus irrelevant distractors that match the target orientation involuntarily capture attention.

Second, both the stimulus-driven saliency of an orientation singleton and the top-down guidance based on a sought-for orientation contribute to the spatial blink. Thus it is a joint effect of stimulus-driven saliency and top-down guidance that determines the deployment of attention.

Last but most important, the feature preferences of visual neurons plays an important role in feature-based attention. Neurons that prefer two orthogonal orientations appear to automatically bias attention to each of the two orientations even when only one orientation is task-relevant.

Chapter 11: References

Abrams, R. A., & Christ, S. E. (2003). Motion onset captures attention. *Psychological Science*, 14, 427-432.

Abrams, R. A., & Christ, S. E. (2005). The onset of receding motion captures attention: Comment on Franconeri and Simons (2003). *Perception & Psychophysics*, 67, 219-223.

Anzai, A., Peng, X. & Van Essen, D. C. (2007) Neurons in monkey visual area V2 encode combinations of orientations. *Nature Neuroscience*, 10, 1313-1321

Bacon, W. F. & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics*. 55. 485-496.

Beck, D. M. & Kastner, S. (2005) Stimulus context modulates competition in human extrastriate cortex. *Nature Neuroscience*, 8, 1110-1116

Beck, D. M. & Kastner, S. (2007) Stimulus similarity modulates competitive interactions in human visual cortex. *Journal of Vision*, 7, 1-12

Beck, D. M. & Kastner, S. (2009) Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research,* 49, 1154-1165

Bichot, N. P., Rossi, A. F. & Desimone, R. (2005) Parallel and Serial Neural Mechanisms for Visual Search in Macaque Area V4. *Science*, 308, 529 - 534.

Bichot, N. P., & Schall, J. D. (2002) Priming in macaque frontal cortex during popout visual search: Feature-based facilitation and location-based Inhibition of Return. *Journal of Neuroscience*, 22: 4675-4685.

Broadbent, D. E. (1958). Perception and Communication. Pergamon Press. New York.

Brockmole, J. R. & Henderson, J. M. (2005). Prioritization of new objects in real-world scenes: evidence from eye movements. *Journal of Experimental Psychology: Human Perception & Performance*. 31, 857-868.

Chelazzi, L., Duncan, J. Miller, E. K., & Desimone, R. (1998) Responses of Neurons in Inferior Temporal Cortex During Memory- Guided Visual Search. *Journal of Neurophysiology*. 80, 2918-2940

Chelazzi, L., Miller, E. K., Duncan, J. & Desimone, R. (1993) A neural basis for visual search in inferior temporal cortex. *Nature*. 363, 345-347.

Chelazzi, L., Miller, E. K., Duncan, J. & Desimone, R. (2001) Responses of Neurons in Macaque Area V4 During Memory-guided Visual Search**.** *Cerebral Cortex***,** 11, 761 - 772.

Christ, S. E. & Abrams, R. A. (2006a). Abrupt onsets cannot be ignored. Psychonomic Bulletin and Review, 13, 875-880.

Christ, S. E. & Abrams, R. A. (2006b). Just like new: Newly segregated old objects capture attention. *Perception & Psychophysics*, 68, 301-309.

Christie, J. J. & Klein, R. M. (2008) On finding negative priming from distractors. *Psychonomic Bulletin & Review,* 15, 866-873

Chun, M. M., & Potter, M. C. (1995). A two-Stage Modal for multiple target detection in Rapid Serial Visual Presentation. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 109-127.

Cole, G. G., Kentridge, R. W., Gellatly, A. R. H. & Heywood, C. A. (2003). Detectability of onsets versus offsets in the change detection paradigm. *Journal of Vision*, 3, 22-31.

Cole, G. G., Kentridge, R. W. & Heywood, C. A. (2004). Visual Salience in the change detection paradigm: the special role of object onset. *Journal of Experimental Psychology: Human Perception & Performance*. 30, 464-477.

Conway, B. R. (2001) Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V1). *Journal of Neuroscience*, 21, 2768-2783.

Conway, B. R. & Livingstone, M. S. (2006) Spatial and temporal properties of cone signals in alert macaque primary visual cortex. *Journal of Neuroscience*, 26, 10826-10846.

Corbetta, M. & Shuman, G. (2002). Control of Goal-Directed and Stimulus-Driven Attention in the Brain. *Nature Reviews*, 3: 201-215.

Davoli, C., Suszko, J., & Abrams, R. (2007). New objects can capture attention without a unique luminance transient. *Psychonomic Bulletin and Review*, 14, 338-343.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society B: Biological Sciences.* 353, 1245-1255

Desimone, R. & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience.* 18: 193-222.

Du, F. & Abrams, R. A. (2008). Synergy of stimulus-driven salience and goal-directed prioritization: Evidence from the spatial blink. *Perception & Psychophysics.* 70, 1489-1503

Du, F. & Abrams, R. A. (2009). Onset capture requires attention. *Psychonomic Bulletin & Review*, 16, 537-541.

Du, F. & Abrams, R. A. (2010). Visual field asymmetry in attentional capture. *Brain & Cognition.* 72, 310-316

Eriksen, B. A. & Eriksen, C. W. (1974) Effects of noise letters upon the identification of a target letter in a non-search task. *Perception & Psychophysics.* 16,143-149

Felleman, D. J. & Van Essen, D. C. (1987) Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *Journal of Neurophysiology*, 57, 889-920

Folk, C. L., Leber, A. B., & Egeth, H. E. (2002). Made you blink! Contingent attentional capture produces a spatial blink. *Perception & Psychophysics.* 64, 741-753.

Folk, C. L., Remington, R. W. & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception & Performance.* 18, 1030-1044.

Folk, C. L., Remington, R. W. & Wright, J. H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset, and color. *Journal of Experimental Psychology: Human Perception & Performance.* 20, 317-329.

Forster, S. & Lavie, N. (2008). Attentional capture by entirely irrelevant distractors. *Visual cognition*, 16, 200-214

Fox, E. (1995) Negative priming from ignored distractors in visual selection: A review. *Psychonomic Bulletin & Review.* 2,145-173

Fox, E. & De Fockert, J. W. (1998) Negative priming depends on prime–probe similarity: Evidence for episodic retrieval. *Psychonomic Bulletin & Review.* 5,107-113

Franconeri, S. L., Hollingworth, A., & Simons, D. J. (2005). Do new objects capture attention? *Psychological Science.* 16, 275 -281.

Gibson, B.S. (1996). Visual quality and attentional capture: A challenge to the special role of abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance,* 22, 1496-1504.

Gibson, B. S., & Kelsey, E. M. (1998). Stimulus-driven attentional capture is contingent on attentional set for displaywide visual features. *Journal of Experimental Psychology: Human Perception & Performance.* 24, 699-706.

Haenny, P.E., Maunsell, J.H., & Schiller, P.H. (1988). State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. *Experimental Brain Research.* 69, 245–259.

Haenny, P.E. & Schiller, P.H. (1988). State dependent activity in monkey visual cortex. I. single cell activity in V1 and V4 on visual tasks. *Experimental Brain Research.* 69, 225–244.

Heinze, H. J., Luck, S. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays. I. Evidence for early selection. *Electroencephalography and Clinical Neurophysiology,* 75, 511-527.

Henderson, J. M. (1991). Stimulus discrimination following covert attentional orienting to an exogenous cue. *Journal of Experimental Psychology: Human Perception & Performance,* 17, 91-106.

Hillstrom, A. P., & Yantis, S. (1994). Visual motion and attentional capture. *Perception & Psychophysics,* 55, 399-411.

Jolicoeur P. & Dell'Acqua R. (1998) The Demonstration of Short-Term Consolidation. *Cognitive Psychology.* 36, 138-202

Jolicoeur P. (1999) Concurrent response-selection demands Modulate the attention blink. *Journal of Experimental Psychology: Human Perception and Performance,* 25(4): 1097~1113

Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics,* 43, 346-354.

Joseph, J., Chun, M., Nakayama, K. (1997). Attentional requirements in a 'preattentive' feature search task. *Nature*, 379, 805-807.

Kanwisher, N., McDermott, J. & Chun, M. M. (1997) The Fusiform Face Area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience* . 17, 4302-4311

Kastner S., De Weerd P., Desimone R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*. 282,108–111

Kastner S., De Weerd P., Maisog J. M., Desimone, R., & Ungerleider, L. G. (1997). Sensory interactions in the human visual system: a functional MRI study. Society for Neuroscience, Abstract. 23,1396

Kastner, S., Nothdurft, H. C., & Pigarev, I. N. (1999). Neuronal responses to orientation and motion contrast in cat striate cortex. *Visual Neuroscience,* 16, 587 – 600.

Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R., and Ungerleider, L.G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron.* 22, 751–761.

Kastner, S. & Ungerleider, L. G. (2000). Mechanisms of Visual Attention in the Human Cortex. *Annual Review of Neuroscience*, 23: 315-341.

Klein, R. (2000). Inhibition of return. *Trends in Cognitive Sciences*. 4, 138-147

Knierim, J. J., & Van Essen, D. C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *Journal of Neurophysiology*, 67, 961 – 980.

Lamy, D. Leber, A. & Egeth, H. E. (2004). Effects of task relevance and stimulus-driven salience in feature-search mode. *Journal of Experimental psychology: Human Perception & Performance.* 30, 1019-1031.

Liu, T., Slotnick, S.D., Serences, J.T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. Cerebral Cortex 13, 1334–1343.

Luck, S. J. (1998). Sources of dual-task interference: Evidence from human electrophysiology. *Psychological Science*, 9, 223-227

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77, 24-42

Luck, S. J. & Vecera, S. P. (2002). Attention. In H. Pashler (Series Ed.) & S. Yantis (Volume Ed.), *Stevens' Handbook of Experimental Psychology: Vol. 1. Sensation and Perception* (3rd ed., pp. 235-286). New York: Wiley.

Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature.* 382. 616-618,

Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*. 32, 4-18

Mangun, G. R. & Buck, L. (1998) Sustained visual-spatial attention produces costs and benefits in response time and evoked neural activity. *Neuropsychologia*, 36, 189-200.

Martinez-Trujillo, J. C. & Treue, S. (2004) Feature-based attention increases the selectivity of population responses in primate visual cortex. *Current Biology*. 744-751

Maunsell, J. H. R., Sclar, G., Nealey, T. A., DePriest, D.D. (1991). Extraretinal representations in area V4 in the macaque monkey. *Visual Neuroscience*. 7, 561-573.

Maunsell, J. H. R. & Treue, S. (2006) Feature-based attention in visual cortex. *Trends in Neuroscience*, 29, 317-322

McAdams, C. J. & Maunsell, J. H. R. (1999). Effects of attention on the orientation tuning functions of single neurons in macaque area V4. *Journal of Neuroscience*. 19, 431-441

McAdams, C. J. & Maunsell, J. H. R. (2000) Attention to both space and feature modulates neuronal responses in macaque area V4. *Journal of Neurophysiology*. 83,1751-1755

Milliken, B., Joordens, S., Merikle, P. M. & Seiffert, A. E. (1998) Selective Attention: A Reevaluation of the Implications of Negative Priming. *Psychological Review*. 105, 203-229

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

Moray, N. (1959). Attention in dichotic listening: Affective cues and influences of instructions. *Quarterly Journal of Experimental Psychology*. 11, 56-60

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presences of competing stimuli. *Journal of Neurophysiology*. 70, 909-919

Motter, B.C. (1994a). Neural correlates of color and luminance feature selection in extrastriate area V4. *Journal of Neuroscience*. 14, 2178-2189.

Motter, B.C. (1994b). Neural correlates of feature selective memory and pop-out in extrastriate area V4. *Journal of Neuroscience*. 14, 2190–2199.

Norman, D. A. (1968). Toward a theory of memory and attention. *Psychology Review*. 7, 522-536.

Northdurft, H. C., Gallant, J. L., & Van Essen, D. C. (1999). Response modulation by texture surround in primate area V1: Correlates of "popout" under anesthesia. *Visual Neuroscience*, 16, 15 – 34.

Osman, A. & Moore, C. M. (1993). The locus of dual-task interference: psychological refractory effects on movement-related brain potentials. *Journal of Experimental Psychology: Human Perception and Performance*. 19, 1292-1312.

Paquet, L. & Lortie, C. (1990). Evidence for early selection: precuing target location reduces interference from same-category distractors. *Perception and Psychophysics*. 48, 382-388

Pashler, H. (1984). Processing stages in overlapping tasks: Evidence for a central bottleneck. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 358-377.

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

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*. 32, 3-25

Posner, M.I. and Cohen, Y. (1984) Components of visual orienting. *In Attention and Performance* Vol. X (Bouma, H. and Bouwhuis, D., eds), pp. 531–556, Erlbaum

Posner, M.I. Rafal, R. D., Choate, L. S. & Vaughan, J. (1985) Inhibition of return: neural basis and function. *Cognitive. Neuropsychology.* 2, 211–228

Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109, 160-174

Pratt, J. & McAuliffe, J. (2001). The effects of onsets and offsets on visual attention. *Psychological Research*. 65, 185-191.

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance.* 18, 849-860.

Reynolds, J., Chelazzi, L., Luck, S. & Desimone, R. (1994) Sensory interactions and effects of selective spatial attention in macaque areaV2. Society for Neuroscience Abstract. 20, 1054.

Reynolds, J., Nicholas, J., Chelazzi, L. & Desimone, R. (1995) Spatial attention protects macaqueV2 and V4 cells from the infuence of non-attended stimuli. Society for Neuroscience Abstract. 21, 1759.

Rolls, E. T. & Tovee, M. J. (1995). Sparseness of the neuronal representation of stimuli in the primate temporal visual cortex. *Journal of Neurophysiology.* 73, 713-726.

Sato, T. (1989) Interactions of visual stimuli in the receptive fields of inferior temporal neurons in awake macaques. *Experimental Brain Research*. 77, 23-30.

Schreij, D., Owens, C. & Theeuwes, J. (2008). Abrupt onsets capture attention independent of top-down control settings. *Perception & Psychophysics*. 70, 208-218.

Serences, J. T. & Boynton, G. M. (2007) Feature-based attentional modulations in the absence of direct visual stimulation. *Neuron*. 55, 301-312.

Serences, J. T., Shomstein, S., Leber, A. B., Golay, X., Egeth, H. E. & Yantis, S. (2005). Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological Science*, 16, 114-122.

Serences, J. T. & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in Cognitive Sciences*. 10, 382-390.

Serences, J. T. & Yantis, S. (2007). Representation of attentional priority in human occipital, parietal, and frontal cortex. *Cerebral Cortex, 17*, 284-293.

Shapiro K L. (1997). Priming from the attentional blink: A failure to extract visual tokens but not visual types. *Psychological Science*. 8, 95-100,

Shapiro, K. L., Caldwell, J., & Sorensen, R. E. (1997). Personal names and the attentional blink: A visual "cocktail party" Effect. *Journal of Experimental Psychology: Human Perception and Performance*. 23, 504-514

Shih, S.-I., & Sperling, G. (1996). Is there feature-based attentional selection in visual search? *Journal of Experimental Psychology: HumanPerception & Performance*, 22, 758-779.

Spitzer, H., Desimone, R. & Moran, J. (1988) Increased Attention Enhances Both Behavioral and Neuronal Performance. *Science*. 240, 338- 340

Theeuwes, J. (1991). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Perception & Psychophysics*, 49, 83-90.

Theeuwes, J. (1994). Stimulus-driven capture and attentional set: Selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception & Performance*, 20, 799-806.

Theeuwes, J. (1995). Temporal and spatial characteristics of preattentive and attentive processing. *Visual Cognition*. 2, 221-233.

Theeuwes, J. (2004). Top-down search strategies cannot override attentional capture. *Psychonomic Bulletin & Review*, 11, 65-70.

Theeuwes, J., Kramer, A.F., Hahn, S. & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: capture of the eyes by new objects. *Psychological Science*, 9, 379-385.

Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D.E. & Zelinsky, G.J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Psychology: Human Perception & Performance*, 25, 1595–1608.

Tipper, S. P. (2001). Does negative priming reflect inhibitory mechanisms? A review and integration of conflicting views. *Quarterly Journal of Experimental Psychology,* 54A, 321-343

Todd, S., & Kramer, A. F. (1994). Attentional misguidance in visual search. *Perception & Psychophysics,* 56, 198-210.

Treisman, A. (1960). Contextual Cues in Selective Listening. *Quarterly Journal of Experimental Psychology.* 12, 242-248.

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

Treue, S., & Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature.* 382, 539-541

Treue, S., & Maunsell, J.H.R. (1999). Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *Journal of Neuroscience.* 19,7591-7602.

Tsal, Y., & Lamy, D. (2000). Attending to an object's color entails attending to its location: Support for location-special views of visual attention. Perception & Psychophysics, 62, 960-968.

Tsal, Y., & Lavie, N. (1988). Attending to color and shape: The special role of location in selective visual processing. Perception & Psychophysics, 44, 15-21.

Tsal, Y., & Lavie, N. (1993). Location dominance in attending to color and shape. Journal of Experimental Psychology: Human Perception & Performance, 19, 131-139.

Turatto, M., Benso, F., Facoetti, A., Galfano, G., Mascetti, G. G. & Umilta, C. (2000). Automatic and voluntary focusing of attention. *Perception & Psychophysics*, 62, 935-952

Vierck, E., & Miller, J. (2006). Effects of task factors on selection by color in the rapid serial visual presentation (RSVP) task. Perception & Psychophysics, 68, 1324-1337.

Vierck, E. & Miller, J. (2008) Precuing benefits for color and location in a visual search task. *Perception & Psychophsics.* 70, 365-373

Vogel, E. K., & Luck, S. J. (2002). Delayed working memory consolidation during the attentional blink. *Psychonomic Bulletin & Review*. 9(4), 739-743

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

Wachtler, T., Sejnowski, T. J. & Albright, T. D. (2003) Representation of color stimuli in awake macaque primary visual cortex. *Neuron*, 37, 681-691.

Weger, U., Abrams, R. A., Law, M. B., & Pratt, J. (2008). Attending to objects: Endogenous cues can produce inhibition of return. *Visual Cognition, 16*, 659-674.

Yantis, S. (1993). Stimulus-driven attentional capture. *Current Directions in Psychological Science*, 2, 156-161.

Yantis, S. (2008). Neural basis of selective attention: Cortical sources and targets of attentional modulation. *Current Directions in Psychological Science, 17,* 86-90.

Yantis, S., & Hillstrom, A. P. (1994). Stimulus-driven attentional capture: Evidence from equiluminant visual objects. *Journal of Experimental Psychology: Human Perception & Performance*. 20, 95-107.

Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: Evidence from visual search. *Journal of Experimental Psychology: Human Perception & Performance*. 10, 601-621.

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception & Performance*. 16, 121-134.

Yantis, S., & Jonides, J. (1996). Attentional capture by abrupt onsets: New perceptual objects or visual masking? *Journal of Experimental Psychology: Human Perception & Performance*. 22, 1505-1513.

Yeshurun, Y. & Carrasco, M. (1998) Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, 396, 72-75

Yoshor, D., Ghose, G.M., Bosking, W.H., Sun, P., Maunsell, J.H.R. (2007) Spatial attention does not strongly modulate neuronal responses in early human visual cortex. *Journal of Neuroscience*. 27, 13205-13209.