



Review

Visual attention: The past 25 years

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ABSTRACT

This review focuses on covert attention and how it alters early vision. I explain why attention is considered a selective process, the constructs of covert attention, spatial endogenous and exogenous attention, and feature-based attention. I explain how in the last 25 years research on attention has characterized the effects of covert attention on spatial filters and how attention influences the selection of stimuli of interest. This review includes the effects of spatial attention on discriminability and appearance in tasks mediated by contrast sensitivity and spatial resolution; the effects of feature-based attention on basic visual processes, and a comparison of the effects of spatial and feature-based attention. The emphasis of this review is on psychophysical studies, but relevant electrophysiological and neuroimaging studies and models regarding how and where neuronal responses are modulated are also discussed.

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1. Introduction

In his short story *Funes el memorioso* [Funes the memorious] the great Argentine author Jorge Luis Borges depicts a character with absolute memory and absolute perception. The tale shows how this prodigious character is, in important ways, unable to think, and unable to see. Forgetting, Borges suggests, is what enables remembering and thinking; perceiving absolutely everything, without selection and interpretation, leads, according to the logic of the short story, to a form of paralysis, a kind of blindness. Borges's insights are on point: Each time we open our eyes we are confronted with an overwhelming amount of information. Despite this, we experience a seemingly effortless understanding of our visual world. This requires separating the wheat from the chaff, selecting relevant information out of irrelevant noise. Attention is the key to this process; it is the mechanism that turns looking into seeing. In perception, ignoring irrelevant information is what makes it possible for us to attend to and interpret the important parts of what we see. Attention allows us to selectively process the vast amount of information with which we are confronted, prioritizing some aspects of information while ignoring others by focusing on a certain location or aspect of the visual scene.

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The topic of visual attention is vast and could not be duly reviewed in a single paper. The interest in visual attention has grown so much that a PubMed search (keyword: 'visual attention' in the title or the abstract) yields about 2400 articles dealing with visual attention since 1980. Almost half of these articles were published since 2005, with over 250 published in 2010 alone (Fig. 1a). Of these, slightly more than half were behavioral studies (cognitive and psychophysical), and slightly less than half were neurophysiological. Several reviews on visual attention have been published in the last 25 years in the *Annual Review of Psychology* (Chun, Golomb, & Turk-Browne, 2011; Egeth & Yantis, 1997; Johnston & Dark, 1986; Kinchla, 1992; Logan, 2004; Pashler, Johnston, & Ruthruff, 2001; Posner & Rothbart, 2007) and *Annual Review of Neuroscience* (Bisley & Goldberg, 2010; Colby & Goldberg, 1999; Desimone & Duncan, 1995; Kastner & Ungerleider, 2000; Knudsen, 2007; Posner & Petersen, 1990; Reynolds & Chelazzi, 2004).

The first paper in *Vision Research* that identified attention as a key word was published in 1976, and only 6 more papers were published during the 1980s. The number of articles on attention published since the 1980s is about 330. The rate of publication has steadily increased with time, the number of publications more than doubling every 5 years from 1970 through 2005. This expansion has continued, although not as pronouncedly, with about 50% more papers published in 2005–2010 than in 2000–2005 (Fig. 1b). These

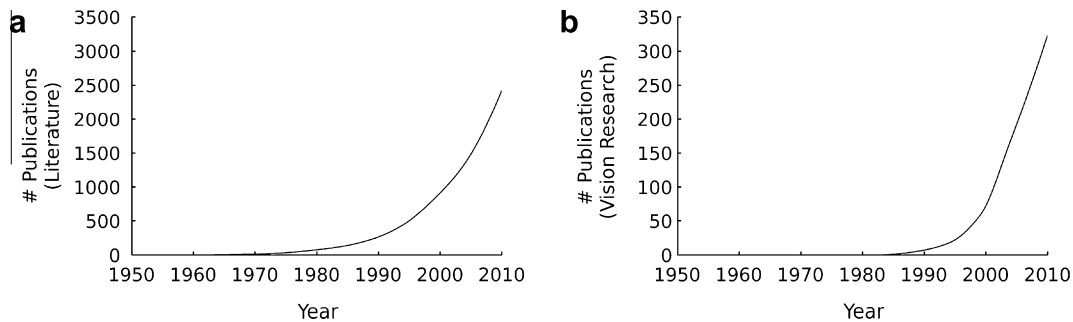


Fig. 1. Number of articles on visual attention published as a function of year in (a) all scientific journals and (b) in *Vision Research*.

articles have largely focused on behavioral research, with roughly one in six articles having a focus on neurophysiology. In line with this growth in interest, three special issues on visual attention have been published in *Vision Research* during the last decade (Baldassi, Burr, Carrasco, Eckstein, & Verghese, 2004; Carrasco, Eckstein, Verghese, Boynton, & Treue, 2009; Spekreijse, 2000).

The appeal of visual attention seems to be related to an observation that is likely to disconcert a traditional vision scientist: changing an observer's attentional state while keeping the retinal image constant can affect perceptual performance and the activity of 'sensory' neurons throughout visual cortex. For over a century, the study of visual attention has attracted some of the greatest thinkers in psychology, neurophysiology and perceptual sciences, including Hermann von Helmholtz, Wilhelm Wundt and William James. More recently (1960–1980s), many psychologists, including Michael Posner, Anne Treisman, Donald Broadbent and Ulric Neisser, have provided distinct theories and developed experimental paradigms to investigate what attention does and what perceptual processes it affects. Initially, there was a great deal of interest in categorizing mechanisms of vision as pre-attentive or attentive. The interest in that distinction has waned as many studies have shown that attention actually affects tasks that were once considered pre-attentive, such as contrast discrimination, texture segmentation and acuity.

In the past 25 years, and especially within the last 15, there has been a growing interest in the mechanisms of visual attention: how visual attention modulates the spatial and temporal sensitivity of early perceptual filters, how attention influences the selection of stimuli of interest, how and where the neuronal responses are modulated, what neural computations underlie the selection processes, and how attention and eye movements interact. Our understanding of visual attention has advanced significantly during this epoch due to a number of factors: (1) psychophysical research on humans has systematically characterized distinct attentional systems and their effects on perception; (2) single-unit neurophysiological research in monkeys has yielded a precise estimate of local activity, and has enabled researchers to study how and at what processing stage attention modulates neuronal responses (see Appendix A); (3) neuroimaging studies, e.g., functional magnetic resonance imaging (fMRI), event-related potentials (ERPs), steady-state visual evoked potentials (SSVEP), and magnetoencephalography (MEG) have allowed the study of the human brain while it is engaged in attention tasks (see Appendix A); (4) advances in eye-tracking technology in the last ~20 years have enabled high-resolution imaging of eye movements during tasks involving perception and attention; and (5) computational modeling has taken into account psychophysical findings and neurophysiological constraints and implemented plausible brain mechanisms and architectures underlying attention effects on perception.

Furthermore, neurophysiological studies have yielded insights into the global structure of the neural networks employed in selec-

tive information processing, and have enabled the identification of cortical and subcortical brain areas involved in attention. Neuroimaging data have revealed three networks related to different aspects of attention: alerting, orienting, and executive control (Posner & Petersen, 1990). Alerting is defined as maintaining a state of high sensitivity to incoming stimuli, and is associated with the frontal and parietal regions of the right hemisphere (Marrocco & Davidson, 1998). Orienting is the selection of information from sensory input, and it is associated with posterior brain areas including the superior parietal lobe (related to the lateral intraparietal area in monkeys), the temporal parietal junction and the frontal eye fields (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Posner, 1980). Lastly, executive control is defined as involving the mechanisms for resolving conflict among possible responses. It activates the anterior cingulate and the lateral prefrontal cortex (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Bush, Luu, & Posner, 2000).¹ This attention network impacts visual processing, which is one of the most efficient ways to enhance the stimulus representation for the purpose of selection.

In general, the influence of attention increases along the hierarchy of the cortical visual areas, resulting in a neural representation of the visual world affected by behavioral relevance of the information, at the expense of an accurate and complete description of it (e.g., Treue, 2001). Realizing that behavioral relevance modulates neural representation led to a reconceptualization of areas that had been considered to be 'purely sensory'. For instance, four important fMRI studies of attention published in 1999, showed that spatial attention affect primary visual cortex, V1 (Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999), which, until then, had been considered a purely sensory area. It is likely that attention effects in V1 reflect feedback activity originating in higher level extrastriate areas (for a review see Hopf, Heinze, Schoenfeld, & Hillyard, 2009).

The processing of sensory input is facilitated by knowledge and assumptions about the world, by the behavioral state of the organism, and by the (sudden) appearance of possibly relevant information in the environment. Indeed, numerous studies have shown that directing attention to a spatial location or to distinguishing features of a target can enhance its discriminability and the evoked neural response. Many human psychophysical studies, as well as monkey single-unit recording studies, have likened attending to increasing visual salience. The combination of advances in psychophysics, neurophysiology, neuroimaging and modeling has begun to provide a mechanistic characterization of attention, which lies at the crossroads between perception and cognition. Attention is currently a central topic in vision research and cognitive

¹ Results from the attention network test (ANT), which is designed to evaluate alerting, orienting, and executive attention in adults, children, patients, and monkeys, has suggested that the efficiencies of these three networks are uncorrelated (Fan, McCandliss, Sommer, Raz, & Posner, 2002).

neuroscience, bringing together scientists from psychophysics, cognitive psychology, neuroimaging, computational neuroscience, neurophysiology and neuropsychology. Understanding the mechanisms of attention is a fundamental challenge in all of these disciplines. We have now developed a fairly good idea of the basics of attentional selection, its spatial and temporal characteristics, its effects on various aspects of visual performance, and we have some ideas about the underlying neural substrates. Still, we are far from a consensus on how visual attention works.

There are three main types of visual attention: (1) spatial attention, which can be either overt, when an observer moves his/her eyes to a relevant location and the focus of attention coincides with the movement of the eyes, or covert, when attention is deployed to relevant locations without accompanying eye movements; (2) feature-based attention (FBA), which can be deployed covertly to specific aspects (e.g., color, orientation or motion direction) of objects in the environment, regardless of their location; and, (3) object-based attention in which attention is influenced or guided by object structure (object-based attention will not be discussed further in this review; for reviews see [Olson, 2001](#); [Scholl, 2001](#)).² By focusing on different kinds of information, these types of attention optimize our visual system: whereas spatial attention guides an observer to a particular location, FBA guides an observer to particular features in the visual scene. For instance, when waiting to meet a friend at a café we may deploy spatial attention to the door (where he is likely to appear) and deploy FBA to orange objects (because he often wears an orange jacket). Attention can affect perception by altering performance – how well we perform on a given task – and/or by altering the subjective appearance of a stimulus or object.

The term attention has been widely used, but unfortunately it has not always been defined explicitly. In fact, in some studies, it is not clear whether or how the construct has been operationalized. Here, I will review studies of covert attention that conform to the view that attention is a selective process, which is usually conceptualized as being related to limited cognitive and brain resources. I will focus on psychophysical studies of visual attention and I will refer to related electrophysiological and/or neuroimaging studies. Note that studies of visual attention also include topics covered in other reviews of this special issue, such as the interaction between the covert and overt systems of attention [see review on eye movements by [Kowler, 2011](#)], the use of ideal observer to model covert and overt orienting of attention [see contributions of ideal observer theory to vision research by [Geisler, 2011](#)], visual search [see review on visual search by [Nakayama & Martini, 2011](#)], and visual cognition, executive functions and memory [see review on visual cognition by [Cavanagh, 2011](#)]. Consistent with the scope of *Vision Research*, this review focuses on the effect of attention on basic visual dimensions where the best mechanistic understanding of attention to date has been achieved, such as contrast sensitivity and spatial resolution [see review on spatial vision by [Graham, 2011](#)] and also includes attention effects on motion processing [see review by [Burr & Thompson, 2011](#) on motion processing]. The visual system can separate This is due to the existence of models of these visual dimensions, as well as to the confluence of psychophysical, single-unit recording, neuroimaging studies, and

computational models, all indicating that attention modulates early vision.

In the following pages, I will review literature that explores why attention is considered to be a selective process, that describes how spatial covert attention affects various aspects of early visual processing (e.g. contrast sensitivity and spatial resolution), and that studies how the manner in which attention affects perception sometimes depends on the type of attention being deployed (endogenous or exogenous). Then I will describe studies that analyze how FBA affects early vision and that compare the effects of spatial- and FBA on vision. For each Section, I will characterize the behavioral effects of attention, followed by the potential physiological substrates, and complementary models.

2. Attention as a selective process

Attention is a selective process. Selection is necessary because there are severe limits on our capacity to process visual information. These limits are likely imposed by the fixed amount of overall energy available to the brain and by the high-energy cost of the neuronal activity involved in cortical computation. The metabolic cost of brain activity is largely dominated by neuronal activity, for which energy usage depends strongly on firing rates ([Attwell & Laughlin, 2001](#)). Given that the amount of overall energy consumption available to the brain is essentially constant ([Clarke & Sokoloff, 1994](#)), the high bioenergetic cost of spikes requires the use of efficient representational codes relying on a sparse collection of active neurons ([Barlow, 1972](#)), as well as the flexible allocation of metabolic resources according to task demands. These energy limitations, which allow only a small fraction of the machinery to be engaged concurrently, provide a neurophysiological basis for the idea that selective attention arises from the brain's limited capacity to process information ([Lennie, 2003](#)).

The notion that stimuli compete for limited resources ([Broadbent, 1958](#); [Kinchla, 1980, 1992](#); [Neisser, 1967](#); [Treisman, 1960](#)) is supported by electrophysiological, neuroimaging and behavioral studies (for reviews see [Beck & Kastner, 2009](#); [Desimone & Duncan, 1995](#); [Reynolds & Chelazzi, 2004](#)). According to the biased-competition hypothesis, stimuli in the visual field activate populations of neurons that engage in competitive interactions, most likely at the intracortical level. When observers attend to visual stimulation at a given location, such competition is biased in favor of the neurons encoding information at the attended area. Thus, neurons with receptive fields at that location either remain active or become more active, while others are suppressed (for a review, see [Desimone & Duncan, 1995](#)). In most neural implementations of the biased competition model, nodes within each processing stage compete by inhibiting the output activity generated by neighboring nodes (e.g., [Corbich & Deco, 2002](#); [Deco & Rolls, 2005](#)).

Single-cell physiology and neuroimaging studies indicate that multiple simultaneous stimuli within a neuron's receptive field (RF) interact with each other in a mutually suppressive way. Neural responses have been compared when a single visual stimulus is presented alone in a RF and when another stimulus is presented simultaneously with that stimulus within the same RF, in several ventral and dorsal areas in the monkey brain (e.g., [Luck, Chelazzi, Hillyard, & Desimone, 1997](#); [Miller, Gochin, & Gross, 1993](#); [Moran & Desimone, 1985](#); [Recanzone, Wurtz, & Schwarz, 1997](#); [Reynolds, Chelazzi, & Desimone, 1999](#); [Snowden, Treue, Erickson, & Andersen, 1991](#)). Evidence shows that the responses to the paired stimuli are a weighted average of the individual responses ([Reynolds et al., 1999](#); see Section 4.5).

In the human brain, evidence for neural competition has been found using an fMRI paradigm in which multiple stimuli are

² A seminal theory of visual attention related space-based and object-based attention. [Logan \(1996\)](#) proposed the CODE theory of visual attention (CTVA) that integrates space-based and object-based approaches to attention and interfaces visual spatial attention with other kinds of attentional selection and with higher-level processes that apprehend relations between objects. This theory combines the COntour DETector (CODE) theory of perceptual grouping by proximity ([Compton & Logan, 1993](#); [van Oeffelen & Vos, 1982](#); [van Oeffelen & Vos, 1983](#)) and Bundesen's ([Bundesen, 1990](#)) theory of visual attention (TVA). However, I will not elaborate on this theory in this review because it neither includes object-based attention nor does it focus on attention's interaction with higher-level processes, core elements of the CODE theory.

presented in close proximity at distinct peripheral locations of the visual field either sequentially or simultaneously, while observers maintain fixation. Several studies show that simultaneous presentations evoke weaker responses than sequential presentations and that response differences increase in magnitude from striate to ventral and dorsal extrastriate areas (Beck & Kastner, 2005, 2007; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner et al., 2001; Luck, Chelazzi, et al., 1997; Miller et al., 1993; Moran & Desimone, 1985; Pinsk, Doniger, & Kastner, 2004; Recanzone et al., 1997; Reynolds et al., 1999; Snowden et al., 1991). Also in line with the idea of biased competition, fMRI experiments reporting a retinotopically-specific signal enhancement at the focus of attention have also reported a signal reduction at the same location when attention is allocated elsewhere (Beck & Kastner, 2009; Slotnick, Schwarzbach, & Yantis, 2003; Somers, Dale, Seiffert, & Tootell, 1999; Tootell, Hadjikhani, Mendola, Marrett, & Dale, 1998). Similarly, directing attention to a specific location leads to widespread baseline-activity reduction throughout the remaining visual field (Smith, Singh, & Greenlee, 2000). These results are consistent with the idea that selective attention results in greater resource allocation to the attended location, at the cost of available resources at the unattended location. Moreover, as attention is distributed across a larger region, the extent of activated retinotopic visual cortex increases, but the level of neural activity in any given subregion decreases compared to the activation attained when attention is distributed across a smaller region (Muller, Bartelt, Donner, Villringer, & Brandt, 2003).

The focus of spatial attention has been likened to a spotlight (Posner, 1980), a zoom lens (Eriksen & Yeh, 1985), or a Gaussian gradient (Downing & Pinker, 1985), which enhances processing of visual stimuli within a circumscribed region of space. There is general agreement that the size of this attended region may be adjusted voluntarily.³ Behavioral studies have shown that when attention is distributed over a larger region of the visual field, rather than being focused on one location, there is a corresponding loss in spatial resolution and processing efficiency for any given subregion of the attended region (e.g., Castiello & Umiltà, 1990, 1992; Eriksen, 1990; Eriksen & Murphy, 1987; Eriksen & Schultz, 1979; Eriksen & St. James, 1986; Eriksen & Yeh, 1985; Shulman & Wilson, 1987). Usually we think of the need to selectively process information in cluttered displays with different colors and shapes (i.e., in 'Where's Waldo'-like displays). However, psychophysical evidence shows that even with very simple displays, attention is involved in distributing resources across the visual field. There are processing tradeoffs for simple, non-cluttered displays, in which only two stimuli are competing for processing; the benefit brought about at the attended location for contrast sensitivity and acuity has a concomitant cost at the unattended location (Barbot, Landy, & Carrasco, 2011; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Montagna, Pestilli, & Carrasco, 2009; Pestilli & Carrasco, 2005; Pestilli, Viera, & Carrasco, 2007). These findings suggest that trade-offs are a basic characteristic of attentional allocation and that such a mechanism has a general effect across different stimulus and task conditions. Hence, these findings are inconsistent with the idea that perceptual processes have unlimited capacity (e.g., Eckstein, Thomas, Palmer, & Shimozaki, 2000; Palmer, Verghese, & Pavel, 2000; Solomon, 2004).

To conclude, attention allows us to optimize performance in visual tasks while overcoming the visual system's limited capacity. Attention optimizes the use of the system's limited resources by enhancing the representations of the relevant, while diminishing

the representations of the less relevant, locations or features of our visual environment. Selective attention thus enables us to gather relevant information and guides our behavior – key factors for the evolutionary success of an organism.

3. Spatial covert attention

Attention can be allocated by moving one's eyes toward a location (overt attention) or by attending to an area in the periphery without actually directing one's gaze toward it (covert attention). The deployment of covert attention aids us in monitoring the environment and can inform subsequent eye movements. Psychophysical, electrophysiological and neuroimaging studies provide evidence for the existence of both overt and covert attention in humans, human infants and non-human primates.

Whereas covert attention can be deployed to more than one location simultaneously ("in parallel"), eye movements are necessarily sequential ("serial"); they can only be directed to one location at a given time. Many studies have investigated the interaction of overt and covert attention, and the order in which they are deployed. The consensus is that covert attention precedes eye movements, and that although the effects of covert and overt attention on perception are often similar, this is not always the case [see reviews on eye movements by Kowler, 2011 and on visual search by Nakayama & Martini, 2011].

Hermann von Helmholtz is considered to be the first scientist to provide an experimental demonstration of covert attention (ca. 1860) (Helmholtz, 1896), cited in (Nakayama & Mackeben, 1989). Looking into a wooden box through two pinholes, Helmholtz would attend to a particular region of his visual field (without moving his eyes in that direction). When a spark was lit to briefly illuminate the box, he found he got an impression of only the objects in the region he had been attending to, thus showing that attention could be deployed independently of eye position and accommodation.

Humans deploy covert attention routinely in many everyday situations, such as searching for objects, driving, crossing the street, playing sports and dancing. Covert attention allows us to monitor the environment and guides our eye movements (overt attention) to locations of the visual field where salient and/or relevant information is. Moreover, covert attention plays an important role in social situations, for example, in competitive situations (such as sports activities). Moving the eyes also provides a cue to intentions that the individual wishes to conceal, a predicament solved by covert attention.

To investigate covert attention, it is necessary to ensure that observers' eyes remain fixated at one location, and to keep both the task and stimuli constant across conditions while manipulating attention. Unfortunately, many studies have inferred the role of attention, without actually defining it or manipulating it. In this review, I include studies in which attention has been manipulated experimentally. As shown below, covert attention improves perceptual performance – accuracy and speed – on many detection, discrimination and localization tasks. Moreover, covert attention affects performance and the appearance of objects in several tasks mediated by dimensions of early vision, such as contrast sensitivity and spatial resolution.

3.1. Types of covert spatial attention: endogenous and exogenous

William James described two different kinds of attention (James, 1890); one is passive, reflexive, involuntary, while the other is active and voluntary. We now refer to these as exogenous/transient attention and endogenous/sustained attention. A growing body of behavioral evidence has demonstrated that there

³ However, it has long been debated whether the spotlight of spatial attention has a unitary "beam" or whether it can be divided flexibly to disparate locations (for a recent review see Jans, Peters, and De Weerd (2010) and a comment by Cave, Bush, and Taylor (2010).

are two covert attention systems that facilitate processing and select information: 'endogenous' and 'exogenous'. The former is a voluntary system that corresponds to our ability to willfully monitor information at a given location; the latter is an involuntary system that corresponds to an automatic orienting response to a location where sudden stimulation has occurred. Endogenous attention is also known as 'sustained' attention and exogenous attention is also known as 'transient' attention. These terms refer to the temporal nature of each type of attention: It takes about 300 ms to deploy endogenous attention. Whereas observers seem to be able to sustain the voluntary deployment of attention to a given location for as long as is needed to perform a task, the involuntary deployment of attention is transient, meaning it rises and decays quickly, peaking at about 100–120 ms (Cheal, Lyon, & Hubbard, 1991; Hein, Rolke, & Ulrich, 2006; Ling & Carrasco, 2006a; Liu, Stevens, & Carrasco, 2007; Muller & Rabbitt, 1989a; Nakayama & Mackeben, 1989; Remington, Johnston, & Yantis, 1992). A single-unit recording study has demonstrated that in macaque area MT exogenous attention has a faster time course than endogenous attention (Busse, Katzner, & Treue, 2008). In addition, when observers know that a target is likely to appear at a certain time, they can allocate their endogenous attention accordingly (e.g., Coull & Nobre, 1998). The different temporal characteristics and degrees of automaticity of these systems suggest that they may have evolved for different purposes and at different times – the exogenous/transient system may be phylogenetically older, allowing us to automatically respond to environmental demands and react quickly to stimuli that are likely to provide behaviorally relevant information. Note that the terms endogenous attention and sustained attention have been used interchangeably by different authors and, at some times, even by the same authors. The terms exogenous and transient attention have also been used as synonyms although, strictly speaking, the term exogenous should be used only when the cue is uninformative regarding the target location, whereas the term transient does not necessarily imply that such is the case. In the remainder of the review, I will use the terms endogenous and exogenous, except in cases where the authors used a transient cue instead of an exogenous cue.

A seminal procedure in the study of attention is the Posner cueing paradigm, in which observers have to respond as quickly as possible to a peripheral target, which is preceded by a central or peripheral cue (Posner, 1980). This paradigm allows the comparison of performance in conditions where attention is deliberately directed to either a given location (attended condition), away from that location (unattended condition) or distributed across the display (neutral or control condition). I explain this cueing procedure in detail below (Section 3.3). In both endogenous and exogenous conditions, performance in detecting or discriminating a target is typically better (faster, more accurate or both) in trials in which the target appears at the cued location than at uncued locations. After attention has been directed to a peripheral location with a peripheral cue, there is delayed responding to stimuli subsequently displayed at that location. This inhibitory aftereffect, first described by Posner and Cohen (Posner & Cohen, 1984) and later labeled 'inhibition of return', encourages orienting towards novel locations and hence might facilitate foraging and other search behaviors (for reviews see Wang & Klein, 2010).

Whereas the shifts of attention prompted by central/sustained cues appear to be under conscious control and observers can allocate resources according to cue validity (Giordano, McElree, & Carrasco, 2009; Kinchla, 1980; Mangun & Hillyard, 1990; Sperling & Melchner, 1978), it is extremely difficult for observers to ignore peripheral/transient cues (Cheal et al., 1991; Giordano, McElree, & Carrasco, 2009; Jonides, 1981; Nakayama & Mackeben, 1989; Yantis & Jonides, 1996). Involuntary transient shifts of attention occur even when the cues are known to be uninformative and

irrelevant (Barbot et al., 2011; Montagna, Pestilli, & Carrasco, 2009; Muller & Rabbitt, 1989b; Pestilli & Carrasco, 2005; Pestilli et al., 2007; Prinzmetal, McCool, & Park, 2005; Yeshurun & Rashal, 2010), and when responding to the cues may even impair performance (Carrasco, Loula, & Ho, 2006; Hein et al., 2006; Talgar & Carrasco, 2002; Yeshurun, 2004; Yeshurun & Carrasco, 1998, 2000; Yeshurun & Levy, 2003; Yeshurun, Montagna, & Carrasco, 2008).

Endogenous attention and exogenous attention show some common perceptual effects (Hikosaka, Miyauchi, & Shimojo, 1993; Suzuki & Cavanagh, 1997); however, they also show some unique perceptual effects. For instance, with peripheral cues, but not with central cues, the effects of attention are larger for a conjunction search than for a feature search in a letter search task (Briand, 1998; Briand & Klein, 1987; Hikosaka et al., 1993; Suzuki & Cavanagh, 1997). Moreover, comparing the effects of endogenous and exogenous attention under low-noise vs. high-noise conditions, has revealed that endogenous attention affects performance only under high-noise conditions, but not under low-noise conditions (Doshier & Lu, 2000a, 2000b; Lu & Doshier, 1998, 2000), whereas exogenous attention can operate under both low- and high-noise conditions (Lu & Doshier, 1998, 2000). Subsequent studies, however, have shown that both types of attention increase contrast sensitivity, even in low-noise conditions (Ling & Carrasco, 2006a). Furthermore, transient attention improves performance in a texture segmentation task at peripheral locations but impairs it at central locations (Carrasco, Loula, et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2008) whereas sustained attention improves performance at all eccentricities (Yeshurun et al., 2008).

Some studies dealing with the effects of attention on temporal aspects of processing also show differential effects for endogenous and exogenous attention. For instance, endogenous allocation of attention impairs temporal order judgment, whereas exogenous allocation of attention improves it (Hein et al., 2006). Differences have also been reported during vigilance (Maclean et al., 2009) and during inhibition of return (Chica & Lupiáñez, 2009). Furthermore, a study employing a speed-accuracy trade-off procedure, which enables conjoint measures of discriminability and temporal dynamics, showed that with peripheral cues, the attentional benefits of endogenous attention increased with cue validity while costs remained relatively constant. However, with peripheral cues, the benefits and the costs of exogenous attention in discriminability and temporal dynamics were comparable across the range of cue validities, that is, they were not more pronounced with higher cue validity (Giordano, McElree, & Carrasco, 2009).

Several studies have shown that regions of occipital, parietal and frontal cortex exhibit enhanced responses during endogenous and exogenous shifts of spatial attention (e.g., Brefczynski & DeYoe, 1999; Corbetta et al., 2000; Gandhi et al., 1999; Giesbrecht, Bischof, & Kingstone, 2003; Hopfinger, Buonocore, & Mangun, 2000; Kastner et al., 1999; Liu, Larsson, & Carrasco, 2007; Liu, Pestilli, & Carrasco, 2005; Mayer, Seidenberg, Dorflinger, & Rao, 2004; Nobre, Sebestyen, & Miniussi, 2000; Peelen, Heslenfeld, & Theeuwes, 2004; Rosen et al., 1999; Serences & Yantis, 2007; Serences et al., 2005; Somers et al., 1999; for reviews see Corbetta & Shulman, 2002 and Beck & Kastner, 2009). There is currently no consensus as to whether common neurophysiological substrates underlie endogenous and exogenous attention. Most studies support a view that the networks underlying these two types of attention are partially overlapping but independent (but see Peelen et al., 2004), who reported no difference in the brain networks mediating these systems). Some studies have shown that endogenous attention is cortical in nature, but exogenous attention also recruits subcortical processing (Robinson & Kertzman, 1995; Zackon, Casson, Zafar, Stelmach, & Racette, 1999). Recent studies, however, have shown that endogenous attention also modulates visual responses in the

lateral geniculate nucleus and the thalamic reticular nucleus (McAlonan, Cavanaugh, & Wurtz, 2008; Robinson & Kertzman, 1995; Zackon et al., 1999), and that the superior colliculus, a sub-cortical structure, is necessary for the control of endogenous attention (Lovejoy & Krauzlis, 2010).

Other differences between these two systems are related to the role of feedback. Endogenous attention is mediated by a feedback mechanism involving delayed reentrant feedback from frontal and parietal areas (e.g., Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Buffalo, Fries, Landman, Liang, & Desimone, 2009; Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000; Kastner & Ungerleider, 2000; Lauritzen, D'Esposito, Heeger, & Silver, 2009; Martinez et al., 1999), whereas these regions are not necessarily involved in exogenous attention. In addition, an ERP study in humans has revealed that exogenous attention exerts its effects earlier than does endogenous attention (P1 and P300, respectively, (Hopfinger & West, 2006); and an electrophysiological study in macaque monkeys has demonstrated that exogenous and endogenous attention are controlled by two distinct, but interacting, mechanisms drawing on the same capacity-limited system, with exogenous attention having a much faster time course than endogenous attention (Busse, Katzner, Tillmann, & Treue, 2008)). These two studies dealing with the temporal dynamics of attention further support the idea that the endogenous and exogenous mechanisms represent two attention systems that can affect information processing in distinct ways.

3.2. Mechanisms of covert attention

Although it is well established that covert attention improves performance in various visual tasks, the nature of the attentional mechanisms, and the stages and levels of processing at which they modulate visual activity, are not yet well understood. Explanations of how attention improves perception range from proposals maintaining that the deployment of attention enhances the signal, to those stating that attention improves sensitivity by reducing external noise, to yet others that purport that the effects are due to observers' decision criteria and/or reduction in spatial uncertainty.

Sensory enhancement, noise reduction and efficient selection are not mutually exclusive; rather, all three are likely to contribute to the computational processes by which attention improves performance (Eckstein et al., 2000; Lu & Doshier, 1998, 2000; Palmer et al., 2000; Pestilli & Carrasco, 2005). Thus, it is reasonable to assume that attentional effects in visual tasks reflect a combination of mechanisms such as signal enhancement, external noise reduction and decisional factors. The signal enhancement hypothesis proposes that attention directly improves the quality of the stimulus representation by increasing the gain on the signal within the locus of attentional selection (Bashinski & Bacharach, 1980; Cameron, Tai, & Carrasco, 2002; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Carrasco, Williams, & Yeshurun, 2002; Doshier & Lu, 2000a, 2000b; Downing, 1988; Ling & Carrasco, 2006a; Lu & Doshier, 1998, 2000; Luck, Hillyard, Mouloua, & Hawkins, 1996; Morrone, Denti, & Spinelli, 2002; Muller et al., 1998).

The external noise reduction hypothesis has two distinct formulations: noise exclusion and distractor suppression. These two varieties of noise reduction are not mutually exclusive, but they do suggest different kinds of underlying computations. Noise exclusion refers to the notion that attention can diminish the impact of external noise that is coextensive with the signal of interest. Specifically, attention can change the properties of perceptual filters, enhancing the signal portion of the stimulus and mitigating the noise (e.g., Doshier & Lu, 2000a, 2000b; Lu & Doshier, 1998; Lu, Lesmes, & Doshier, 2002). In this formulation, attention acts like a filter at a specific location, only letting specific information pass;

different filters process information outside that filter (i.e., distractors at other locations).

Under the distractor suppression formulation of external noise reduction, attention enables the observer to disregard information outside the focus of attention. That is, attention can help the observer utilize a specific filter, disregarding filters that provide unwanted information. Noise-limited models of distractor suppression incorporate internal noise arising from sources such as spatial and temporal uncertainty of targets and distractors, as well as external noise resulting from distractors and masks. Several studies have attributed attentional facilitation to reduction of external noise, either because a near-threshold target presented alone could be confused with empty locations (spatial uncertainty) or because a suprathreshold target could be confused with suprathreshold distractors. According to these models, performance decreases as spatial uncertainty and the number of distractors increase, because the noise they introduce can be confused with the target signal (Baldassi & Burr, 2000; Cameron, Tai, Eckstein, & Carrasco, 2004; Kinchla, 1992; Morgan, Ward, & Castet, 1998; Shiu & Pashler, 1994; Solomon, Lavie, & Morgan, 1997). Presumably, precues allow observers to monitor only the relevant location(s) instead of all possible ones. This reduction of statistical noise with respect to the target location is also known as reduction of spatial uncertainty (Davis, Kramer, & Graham, 1983; Eckstein et al., 2000; Kinchla, 1992; Nachmias, 2002; Palmer, 1994; Shiu & Pashler, 1994; Sperling & Doshier, 1986; Verghese, 2001). A recent and comprehensive study describes physiological measures and behavioral predictions distinguishing uncertainty vs. increased sensitivity models (Eckstein, Peterson, Pham, & Droll, 2009).

According to the distractor suppression formulation of external noise reduction, attention affects performance in a given area by actively suppressing the strength of representation for areas outside its locus. Some studies report that attentional effects emerge when distractors appear with the target (distractor exclusion), but not when the target is presented alone, and are more pronounced as the number of distractors increases (Cameron et al., 2004; Eckstein & Whiting, 1996; Foley, 1998; Palmer, 1994; Shiu & Pashler, 1994, 1995; Verghese, 2001). These studies argue that attention allows us to exclude distractors that differ along some relevant dimension from the signal by narrowing a filter that processes the stimulus (Baldassi & Burr, 2000; Davis et al., 1983; Foley, 1998; Morgan et al., 1998; Palmer, 1994; Solomon et al., 1997).

It is important to note that "suppressing the strength" of distractors can take the form of a change in decision criteria, which entails attention helping the observer to weight information from different sources (e.g., Kinchla, 1992; Shaw, 1984). In general, decision-based explanations of attention argue that selection allows observers to "listen" to useful filters and base choices upon those filters. In this sense, distractor suppression can be seen as an external noise reduction mechanism that operates via a decision template that is molded around the target attributes.

3.3. Methodological considerations when testing covert attention

As mentioned above, the Posner cueing paradigm (Posner, 1980) is a seminal procedure in the study of attention. This paradigm allows us to compare performance when attention is directed to either the target location (attended condition), away from that location (unattended condition) or distributed across the display (neutral or control condition). For endogenous attention, a central cue indicates the most likely location of the subsequent target with a given cue probability (e.g., 70%). Central or symbolic cues take about 300 ms to direct endogenous attention in a goal- or conceptually-driven fashion. Central cues are typically small lines presented at fixation that point to particular locations of the visual field (e.g., upper left quadrant; Fig. 2); symbolic cues include

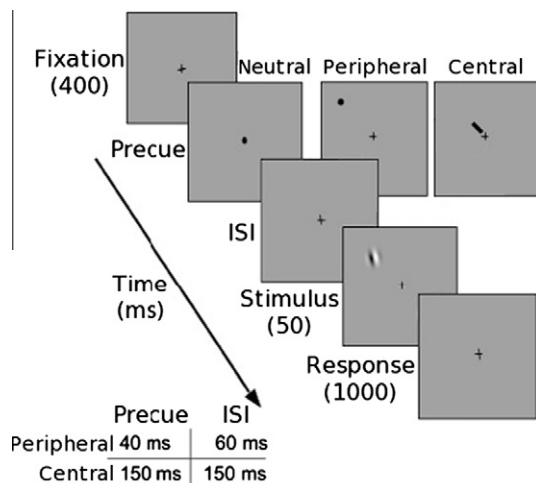


Fig. 2. Sequence of events in a trial (after the classic Posner paradigm). Observers perform a two-alternative forced-choice (2AFC) orientation discrimination task on a tilted target Gabor patch, which appears at one of four isoeccentric locations. The target is preceded by a central cue (instructing observers to deploy their endogenous attention to the upcoming target location), a peripheral cue (reflexively capturing attention to the upcoming target location), or a neutral cue (baseline). The cue in this example is valid. The timing (precue and interstimulus interval) for endogenous and exogenous conditions differs (along with their respective neutral conditions), in order to maximize the effectiveness of the cues.

different numbers or colored shapes that indicate different locations where the observer is to attend (e.g., number 1 or a red circle indicates upper left quadrant, number 3 or a blue circle indicates lower right quadrant). For exogenous attention, a brief peripheral cue, typically a dot or a small bar, is presented adjacent to one of the target locations, and is not always predictive of the subsequent target location. Peripheral cues attract spatial attention in an automatic, stimulus-driven manner within ~ 100 ms.

In the neutral trials, a small disk appears in the center of the display (central neutral cue) or several small bars appear at all possible target locations (distributed neutral cue), or a couple of long lines encompass the whole display (distributed neutral cue), indicating that the target is equally likely to occur at any possible location. Performance is comparable with these different types of neutral cues. The performance difference between a single peripheral cue and a distributed-neutral cue is comparable to the difference between a single peripheral cue and a central-neutral cue in a variety of tasks, e.g., acuity (Carrasco et al., 2002), texture segmentation (Yeshurun et al., 2008), letter identification (Talgar, Pelli, & Carrasco, 2004), and temporal resolution (Yeshurun, 2004). All cues indicate display onset, but only the transient or sustained cue provides information, with a given probability, about the location of the upcoming target. Many studies discussed in Sections 4 and 5 use the Posner paradigm or a variant of it.

The following are some critical methodological issues to be considered when using spatial cues to test for sensory effects of attention:

Given that ~ 200 – 250 ms are needed for goal-directed saccades to occur (e.g., Mayfrank, Kimmig, & Fischer, 1987), the stimulus-onset-asynchrony (SOA) for the endogenous cue may allow observers to make an eye movement towards the cued location. Thus, to verify that the outcome of this manipulation is due to covert attention, it is necessary to monitor the observers' eyes to ensure that central fixation is maintained throughout each trial.

Spatial cues should convey only information that is orthogonal to the task, e.g., in a discrimination task they could indicate probable target location but not the correct response (e.g., the orientation of a stimulus: left vs. right; Fig. 2). Many experiments manipulate sustained attention in detection tasks with cues indi-

cating that a certain location has a given probability of containing the target. Although a high probability encourages observers to direct their attention to a particular location, it is hard to determine whether the enhanced detection is due to facilitation of information coding at that location, to probability matching, or to a decision mechanism, i.e., the higher probability encourages observers to assign more weight to information extracted from that probability location (Kinchla, 1992). By using a two-alternative-forced-choice (2AFC) in which the observers discriminate stimuli preceded by a cue (e.g., the orientation of a stimulus: left vs. right), even when the cue is 100% valid in terms of location, it conveys no information as to the correct response. Thus, we can assess whether a cueing effect reflects changes in sensory (d'), rather than decisional (criterion), processes.

Another critical factor is that of spatial uncertainty. According to noise-limited models, performance decreases as spatial uncertainty increases, because the empty locations introduce noise that can be confused with the target signal. For instance, a spatial uncertainty effect is present for low contrast pedestals but not for high contrast pedestals (Foley, 1998). Uncertainty about the target location produces a more noticeable degradation at low than at high performance levels (Eckstein & Whiting, 1996; Pelli, 1985), and uncertainty is larger for less discriminable stimuli (Cohn, 1981; Nachmias & Kocher, 1970; Pelli, 1985). Thus, uncertainty models predict that the precueing effect would be greater for low contrast stimuli and when localization performance is poor (e.g., Carrasco et al., 2000, 2002; Cohn, 1981; Nachmias & Kocher, 1970; Pelli, 1985). Some studies have considered the effects of uncertainty reduction as a benchmark and have evaluated whether attention effects go beyond them (e.g., Carrasco et al., 2000, 2002; Eckstein, Shimozaaki, & Abbey, 2002; Morgan et al., 1998). As mentioned above, physiological measures and behavioral predictions can distinguish uncertainty vs. increased sensitivity models (Eckstein et al., 2009).

Many of the studies described in this review deal with discrimination tasks, because they depend on attention more than detection judgments do (e.g., Bashinski & Bacharach, 1980; Bonnel & Miller, 1994; Bonnel, Stein, & Bertucci, 1992; Downing, 1988; Muller & Findlay, 1987; Shaw, 1984). This difference may be due to the fact that the perceptual distinction between larger or smaller sensory signals (detection) poses a much simpler problem for the visual system than the distinction between sensory signals that are equally large but differ in qualitative ways (discrimination).

4. Covert attention can increase contrast sensitivity

4.1. Signal enhancement and external noise reduction

There are a number of mechanisms that have been proposed to explain how attention might affect perception, many of which can be subsumed within the perceptual template model (PTM). The PTM provides a theoretical and empirical framework to assess the mechanisms of attention by systematically manipulating the amount and/or characteristics of the external noise added to the stimuli and measuring modulation of perceptual discriminability.

According to the PTM, a signal is analyzed by a perceptual template. There are three characteristic mechanisms by which attention can interact with the perceptual template to improve performance: (1) Stimulus enhancement, which is mathematically equivalent to internal additive noise reduction, means that attention turns up the gain on the perceptual template, improving performance through amplification of the signal stimulus (Fig. 3a). Increased gain helps to overcome internal noise in low-noise displays, but has little effect in high external noise because the external noise and signal stimulus are amplified equally (Fig. 3b).

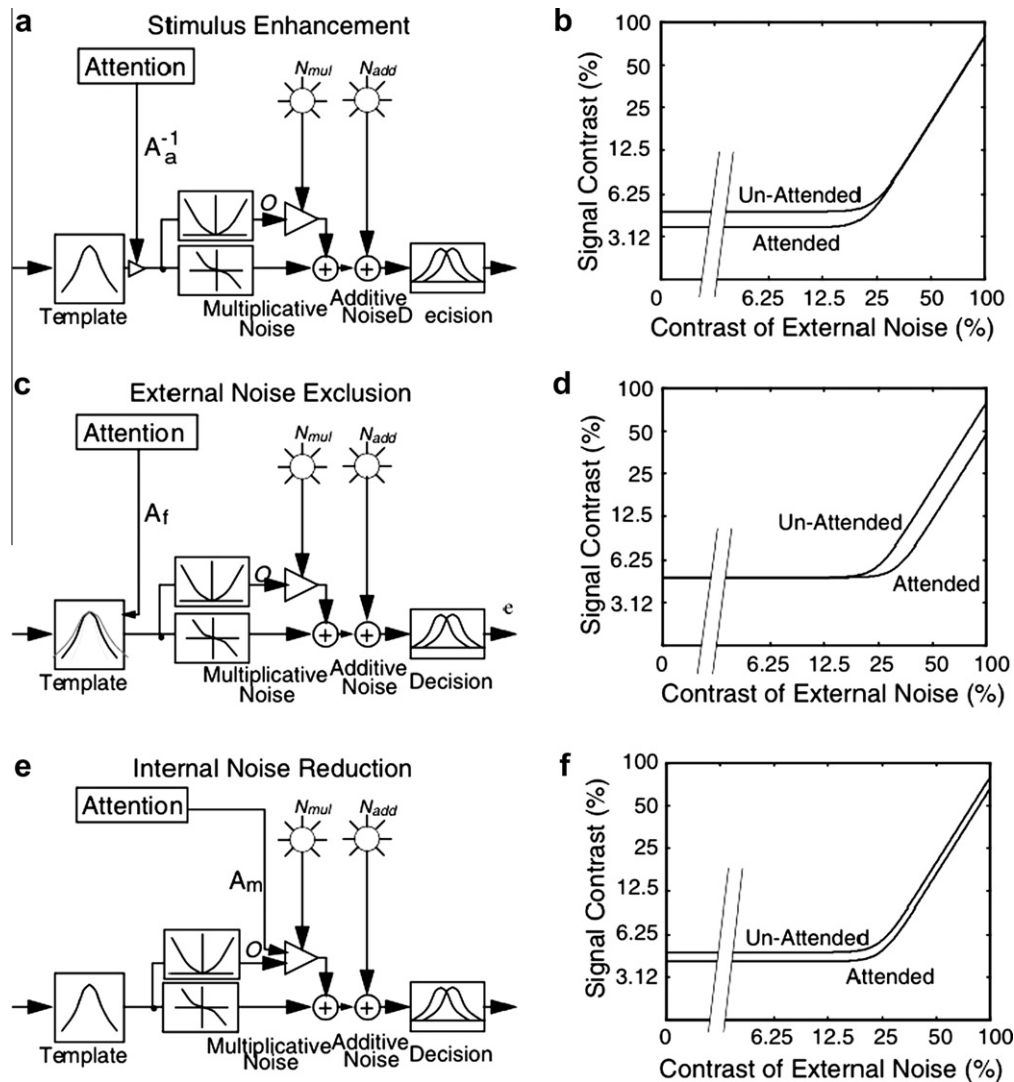


Fig. 3. (a) Stimulus enhancement affects both the signal and the external noise in the input stimulus in the same way; thus, there is no retuning of the perceptual template entering the decision. (b) Stimulus enhancement has an effect at low- but not high-levels of external noise. (c) External noise exclusion reduces the effects of external noise through filtering, or retuning of the perceptual template that enters in the decision. (d) External noise exclusion improves performance in the region of high external noise, where there is external noise to exclude. (e) Internal noise reduction. Multiplicative noise increases with increasing contrast in the stimulus display. (f) Performance improves across all levels of external noise. [Reprinted from Lu et al., 2009].

(2) External noise exclusion reduces the effects of external noise through filtering (Fig. 3c), resulting from focusing the perceptual template on the appropriate spatial region or content characteristics of the stimulus. Excluding external noise improves performance only where there is already significant external noise in the stimulus to filter out (Fig. 3d). (3) Multiplicative internal noise reduction (Fig. 3e) would impact performance across all levels of external noise with slightly larger effects in high external noise. This pattern is rarely observed. The magnitude of the attention effect is the same (on the log contrast axis) at different performance levels (e.g., 75% and 85% performance threshold) for signal enhancement (Fig. 3a) or external noise exclusion (Fig. 3b). But that is not the case for multiplicative noise reduction. Thus, were there an effect across all levels of external noise, testing at two performance levels would disambiguate a combination of both stimulus enhancement and external noise reduction from multiplicative noise reduction. In the first case, the effect would scale, whereas in the second case it would not.

The PTM is an extension of models of the human observer (Burgess, Wagner, Jennings, & Barlow, 1981; Pelli & Farell, 1999)

that incorporates known qualities of the visual system (for an integrative review see Lu & Doshier, 2008). Accuracy is constrained by internal limitations (receptor sampling errors, noise in neural responses, information loss during neural transmission) and external noise in the stimulus. Performance in d' (or % correct) for psychometric functions or contrast threshold from TvC (threshold vs. contrast) functions is measured as a function of task, attention, external noise and contrast. The parameters of the PTM model are estimated from psychometric functions (Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2008) or from TvC functions from two or three measured threshold levels (Doshier & Lu, 1998; Lu & Doshier, 1999).

Using an external noise paradigm, cueing attention to a spatial location has revealed external noise exclusion and signal enhancement as the primary and secondary mechanisms underlying spatial attention. Many studies have concluded that in the absence of uncertainty, one of the primary roles of spatial attention is to exclude external noise in the target region (Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2000; Lu et al., 2002). Transient attention increases contrast sensitivity in conditions of low noise, indicative of signal enhancement, and also improves performance in high noise

conditions, indicative of external noise reduction (Lu & Doshier, 1998, 2000). However, these authors have attributed sustained attention effects exclusively to external noise reduction (Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2000; Lu et al., 2002; but see Ling & Carrasco, 2006a). Fig. 4 illustrates a trial sequence to manipulate sustained attention via a central precue. In this example the precue is invalid, because it points to a different location than the one the observer is asked to respond to when the stimuli and the response cue appear simultaneously. The bottom panel shows that for this sample observer, the precue lowered the contrast threshold for high- but not low-levels of external noise; i.e. the signature of external noise reduction.

External noise paradigms have been widely used to probe different levels of visual processing and to examine properties of detection and discrimination mechanisms. These paradigms assume that signal processing is noise-invariant, i.e., external noise adds to the variance of a single perceptual template, but that that filter remains unperturbed with different levels of external noise. Some authors, however, have questioned this key assumption. For instance, the observed perceptual template, as indexed by the classification-image methodology, becomes tuned to progressively lower spatial frequencies as external noise increases. This finding suggests that the perceptual template changes as a function of external noise (Abbey & Eckstein, 2009). More recently, using a detection task in which crowding is usually not observed, it has been shown that some types of external noise result in crowding effects for high- but not for low-noise contrasts. This finding also questions the noise-invariance assumption (Allard & Cavanagh, 2011).

4.2. Exogenous/transient attention and contrast sensitivity

Many of the studies described in this section involve an orientation discrimination task, because this dimension has been well characterized both psychophysically and neurophysiologically, and a link between findings obtained with these two approaches has been well established (De Valois & De Valois, 1988; Graham, 1989; Regan

& Beverley, 1985; Ringach, Hawken, & Shapley, 1997). In addition, orientation discrimination is used to assess the effect of attention on stimulus contrast because performance on this task improves with increasing contrast (e.g., Nachmias, 1967; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987), and because fMRI response increases monotonically with stimulus contrast (Boynton, Demb, Glover, Heeger, 1999). Moreover, the shared nonlinearity between the contrast response function and the magnitude of the attentional modulation across different areas of the dorsal and ventral visual pathways indicate a close link between attentional mechanisms and the mechanisms responsible for contrast encoding (Martinez-Trujillo & Treue, 2005; Reynolds, 2005).

The effect of attention on contrast sensitivity has been well documented with studies employing an array of methods to manipulate attention (e.g., Carrasco et al., 2000; Doshier & Lu, 2000a, 2000b; Foley, 1998; Huang & Dobkins, 2005; Lee, Itti, Koch, & Braun, 1999; Lee, Koch, & Braun, 1997; Lu & Doshier, 1998, 2000; Morrone, Denti, & Spinelli, 2004; Smith, Wolfgang, & Sinclair, 2004; Solomon, 2004; Solomon et al., 1997). A number of psychophysical studies have shown that contrast sensitivity for the attended stimulus is enhanced in the presence of competing stimuli (e.g., Carrasco & McElree, 2001; Doshier & Lu, 2000a, 2000b; Foley, 1998; Huang & Dobkins, 2005; Lee et al., 1997; Lee, Itti et al., 1999; Lu & Doshier, 1998; Morrone et al., 2004; Solomon et al., 1997). In some studies, the target was displayed simultaneously with distractors and observers had to indicate whether the target had an increment or decrement in contrast. Performance deteriorated as number of stimuli increased. However, the cue improved performance (Solomon et al., 1997) and this effect increased with number of distractors (Foley, 1998). These authors interpreted these findings as resulting from uncertainty reduction, which assumes that valid spatial cueing of an upcoming target location improves performance simply by reducing the number of locations to be monitored from all possible target locations to one location (Eckstein et al., 2009; Foley, 1998; Kinchla, 1992; Palmer, 1994; Shaw, 1984; Solomon et al., 1997).

Other studies have shown that attentional benefits go beyond what is predicted by uncertainty reduction (e.g., Carrasco et al., 2000, 2002; Doshier & Lu, 2000a, 2000b; Lee et al., 1997; Ling & Carrasco, 2006a; Lu & Doshier, 1998; Morgan et al., 1998). For instance, Lee et al. (1997) measured contrast threshold and orientation thresholds, which are well characterized under normal viewing conditions (e.g., Rovamo & Virsu, 1979; Virsu & Rovamo, 1979), in the ‘near absence’ of attention. They asked observers to carry out two concurrent visual tasks, one of them highly demanding of attention (‘primary task’), in which optimal performance is reached only when attention is fully focused, and thus almost completely withdrawn from the other task (‘secondary task’). This paradigm ensures that less attention is devoted to the secondary task, thus the term near absence of attention (Braun, 1994; Braun & Julesz, 1998). Performing a concurrent task increased both orientation and contrast thresholds, and that the effect was more pronounced for the former than the latter (Lee et al., 1997).

In a subsequent study, thresholds were compared when observers performed various tasks with full transient attention and with attention focusing elsewhere on a concurrent, secondary task (Lee, Itti et al., 1999). The measurements included a dipper curve (contrast detection and contrast increment detection), contrast masking thresholds (for masks of different orientations and spatial frequencies), orientation discrimination thresholds, and spatial frequency discrimination thresholds. Based on this information, the authors fit a standard “linear-filter-population-interacting-through-divisive-normalization model”, which revealed how transient attention changes these filters and their interactions. The difference between the two attention conditions yielded results consistent with an intensified competition among linear filters, specifically larger gain

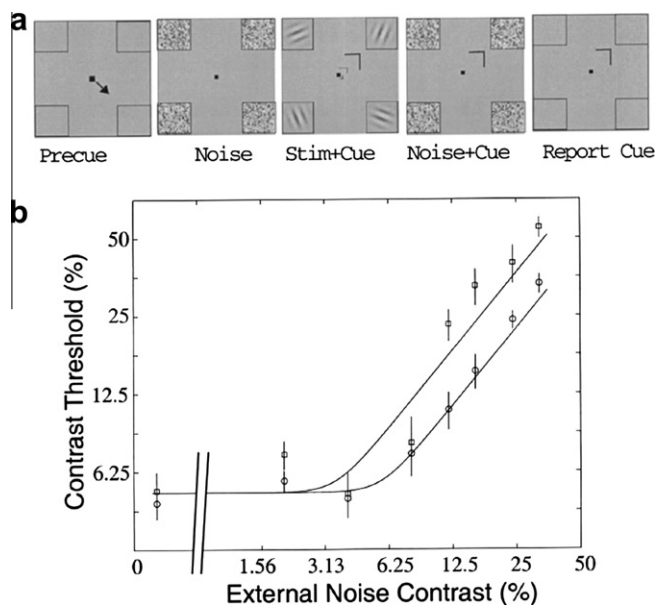


Fig. 4. (a) Trial sequence illustrating an invalid cue: a central cue indicates a location; the stimulus and the response cue appear simultaneously indicating to the observer the target location. (b) Contrast threshold vs. external noise contrast data from a sample observer. Endogenous attention reduces contrast thresholds at high noise levels but not at low noise levels, suggesting tuning of the perceptual template to exclude external noise. [Reprinted from Doshier & Lu, 2000a, 2000b].

exponents in both the numerator and the denominator of the normalization, which across the population resulted in higher response gain, higher response amplitude, and sharper orientation and spatial frequency tuning. Based on the psychophysical results and the modeling, the authors concluded that transient attention (a) has a generic rather than a task-specific effect, in that it (b) boosts both excitatory and suppressive inputs prior to the divisive normalization, and (c) that the final effect on the population response depends on stimulus configuration (i.e., the relative strength of target and distractor stimuli).

Another study evaluated whether the effect of attention on contrast sensitivity could be mediated by signal enhancement (Carrasco et al., 2000). To assess the conditions for which the effect of attention can be attributed to signal enhancement, it is necessary to ensure that a performance benefit occurs under conditions that exclude all variables that the external noise reduction models hold to be responsible for the attentional effect (e.g., Baldassi & Burr, 2000; Davis et al., 1983; Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2000; Morgan et al., 1998; Nachmias, 2002; Solomon et al., 1997). That is, the target should be suprathreshold (to reduce spatial uncertainty) and presented alone, without distractors and local or multiple masks (e.g., Cameron et al., 2002; Carrasco et al., 2000, 2002; Golla, Ignashchenkova, Haarmeier & Thier, 2004; Ling & Carrasco, 2006a).

For a wide range of spatial frequencies, contrast threshold decreased when the target location was preceded by a peripheral cue appearing adjacent to the target location, compared to when it was preceded by a neutral cue. A signal detection theory (SDT) model of external noise reduction could account for the cueing benefit in an easy discrimination task (vertical vs. horizontal Gabor patches). But that was not the case when location uncertainty was reduced by increasing overall performance level, increasing stimulus contrast to enable fine discriminations of slightly tilted suprathreshold stimuli, or presenting a local post-mask. An SDT model that incorporates intrinsic uncertainty (the observers' inability to perfectly use information about the elements' spatial or temporal positions, sizes, or spatial frequencies) revealed that the cueing effect exceeded the one predicted by uncertainty reduction. Given that the attentional benefits occurred under conditions that exclude all variables predicted by the external noise reduction model, the results support the signal enhancement model of attention (Carrasco et al., 2000). This finding is consistent with those of the low-noise conditions in the external noise plus attention paradigm (Lu & Doshier, 1998, 2000).

Another study showed that transient attention decreased the threshold of the psychometric function for contrast sensitivity in an orientation discrimination task across the contrast psychometric function (Cameron et al., 2002). Two control experiments were conducted to assess the role of spatial uncertainty. First, attention increased performance to the same extent in conditions with different uncertainty levels, even though observers required higher stimulus contrasts to perform the discrimination task with a small (4°) than with a large (15°) tilt. Second, for a 15° -tilted target, discrimination and localization performance were tightly coupled, but performance on the localization task was much better than on the discrimination task with a 4° -tilted target, and yet the attentional effect was comparable for both orientation conditions. Thus, given that there was no added external noise and the results of the control experiments show that spatial uncertainty cannot explain the cue effect on contrast threshold, the observed attentional benefit is consistent with a signal enhancement mechanism (Cameron et al., 2002).

There is consensus that attention improves performance at the attended location, but there is less agreement regarding the fate of information that is not directly attended, i.e. outside the focus of attention (Eriksen & Hoffman, 1974; Kinchla, 1992; Rock & Gut-

man, 1981). How sensitive to contrast are observers at the unattended locations? To understand how performance differs at attended and unattended locations, it is necessary to compare performance in both valid and invalid conditions with performance in a neutral condition (Carrasco & Yeshurun, 1998; Hawkins et al., 1990; Luck et al., 1994; Pestilli & Carrasco, 2005; Posner, 1980). A cue is considered valid when it indicates the target location, and it is considered invalid when it indicates another location (Posner, 1980; see Fig. 5).

Transient attention increases sensitivity at the cued location. However, when a peripheral cue indicates target location, in principle, some of its effect could be due to a conceptually-driven, voluntary component of attention. Even though, the timing between cue onset and stimulus onset is too brief for sustained attention to be deployed, to eliminate this possible contamination, a non-predictive cue was used. To assess contrast sensitivity at both cued and uncued locations, observers were asked to discriminate the orientation of one of two Gabor patches simultaneously presented left and right of fixation. Contrast sensitivity was measured at the cued (valid cue) and uncued (invalid cue) locations, and compared with the contrast sensitivity obtained at the same locations when the target was preceded by a cue presented at fixation (neutral cue). A response cue was presented after the Gabor stimuli, indicating to the observer for which Gabor stimulus the orientation was to be reported; in valid trials, the cue location and response cue match and in invalid trials, they do not match; Fig. 5b). The response cue equates location uncertainty across conditions (Eckstein et al., 2002; Ling & Carrasco, 2006b; Lu & Doshier, 2000; Pestilli & Carrasco, 2005; Pestilli et al., 2007). Observers were told that the peripheral cue was uninformative, i.e., it preceded the target or the distractor with the same probability.

Results from all observers indicate that despite the simplicity of the display, there is a performance trade-off: the cue increases sensitivity at the cued location (benefit) and impairs it at the uncued location (cost), as compared to the neutral condition (Pestilli & Carrasco, 2005; see also Pestilli et al., 2007). This is also the case for an intermediate stage of processing – second order contrast (Barbot et al., 2011). Given that for an ideal observer the uninformative cue would not reduce uncertainty, this finding supports sensitivity-based explanations, i.e. signal enhancement at the cued location and external noise reduction at the uncued location. This study provides evidence for the notion that exogenous attention directs observers' attention to the cued location in an automatic fashion (Cheal et al., 1991; Muller & Rabbitt, 1989a; Nakayama & Mackeben, 1989; Yantis & Jonides, 1996).

4.3. Endogenous attention and contrast sensitivity

Using an external noise procedure, Lu and Doshier reported that exogenous attention is mediated by signal enhancement (at low levels of external noise) and external noise reduction (at high levels of external noise), whereas endogenous attention is only mediated by external noise reduction (Doshier & Lu, 2000a, 2000b; Lu, Liu, & Doshier, 2000; Lu et al., 2002). This result is surprising given that electrophysiological studies have reported facilitation effects of attention in conditions of low noise. Ling and Carrasco (2006a, 2006b) compared these two types of covert attention using the same task, stimuli and observers. They evaluated whether a signal enhancement mechanism underlies both types of attention and investigated the neural model underlying signal enhancement by measuring the psychometric functions for both types of attention to assess whether they have similar or different effects on the contrast response function. Observers performed a 2AFC orientation discrimination task on a slightly tilted Gabor patch.

Results indicated that both endogenous and exogenous attention have a similar effect on performance; both types of attention

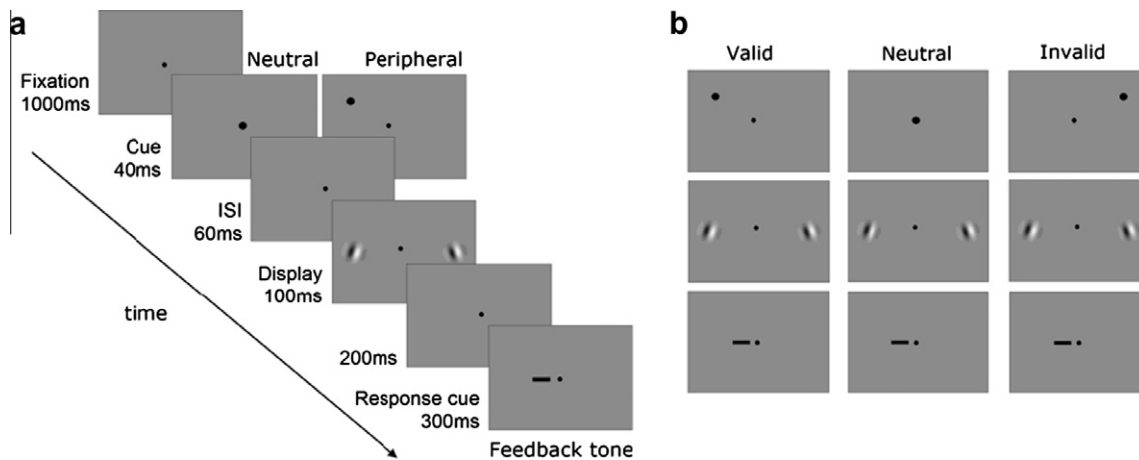


Fig. 5. (a) A trial sequence. Following a fixation point, a cue appears either above one of the two Gabor locations (peripheral cue) or at fixation (neutral cue). After an ISI, two Gabor stimuli are simultaneously presented (randomly oriented to the left or to the right) on the horizontal meridian. Then a response cue appeared at fixation to indicate the target Gabor for which the observer had to report the orientation. On one third of the trials the response cue points to a precued Gabor. On another third of the trials it points to the Gabor that was not precued. In the remaining trials the precue was presented in the center of the screen and the response cue was equally likely to indicate the Gabor to the right or to the left of fixation. (b) Examples of types of trials. In a valid trial the locations indicated by the peripheral cue and by the response cue match. In an invalid trial the locations indicated by the peripheral cue and by the response cue do not match. In a neutral trial the cue is presented at fixation and the response cue indicates the left Gabor in half of the trials and the right Gabor in the other half.

increase contrast sensitivity under zero-noise conditions (the display contained nothing to be suppressed, since there was no added external noise). Hence, both attentional systems can be mediated by a signal enhancement mechanism. However, they have different effects on the contrast response function: Endogenous attention seemed to operate via contrast gain, i.e. a shift in threshold, whereas exogenous attention seemed to operate via response gain, i.e. a shift in asymptote (see also Pestilli et al., 2007; Pestilli, Ling, & Carrasco, 2009). For a detailed discussion of contrast gain and response gain, see Section 4.6. These results cannot be explained by an uncertainty reduction model, which would predict that the attention effect should be most prominent with low contrast stimuli (Pelli, 1985), and that the effect would be the same for both types of attention. The findings of Carrasco and colleagues are in agreement with those of Lu and Doshier regarding exogenous attention: under low external noise conditions, it operates via signal enhancement. However, the results for endogenous attention are inconsistent with those reported previously by Doshier and Lu (2000a, 2000b). A difference that could help reconcile the discrepancy lies in the amount of time observers were given to deploy their sustained attention. The short 150 ms SOA may have precluded an emergence of the signal enhancement mechanism in the Doshier and Lu (2000a, 2000b) studies.

With a dual task paradigm, a sustained attention task was used to investigate the independence of the attentional resources on the processing of luminance- and chromatic-modulated stimuli. Observers' threshold vs. contrast (TVc) functions were measured under conditions of full- or poor-attention. Interestingly, the effect of attention was constant at pedestal contrasts above 0%, consistent with a response gain model (Morrone et al., 2004; Fig. 6). Similar results have been obtained with visually evoked potentials (Di Russo, Spinelli, & Morrone, 2001). Based on the findings that there was interference only when both stimuli involved luminance or color contrast, the authors concluded that the two attributes are processed separately and that they engage different attentive resources. However, this conclusion regarding independence of attentional resources is controversial. Some authors have pointed out that the attentional demand of the central task may have been higher for the same contrast than the different contrast conditions (Huang & Dobkins, 2005; Pastukhov, Fischer, & Braun, 2009).

Using a similar dual task paradigm, a subsequent study tested whether attention operates via contrast or response gain. Huang and Dobkins (2005) found evidence for both contrast gain and response gain, and proposed a hybrid model in which attention first undergoes contrast gain, followed by a later-stage response gain modulation. The authors attributed the differing findings to experimental parameters; they state that the contrasts they tested captured the entire response functions better, and that the dual task used by Morrone et al. may have not been demanding enough.

Whereas the dual task paradigm has some advantages, such as eliminating location uncertainty reduction as an alternative explanation, it has some disadvantages too. Dual task paradigms do not control the deployment of attention very well and make it hard to isolate the source of possible processing differences (e.g., Pashler & Johnston, 1998; Sperling & Doshier, 1986). Ling and Carrasco (2006a) speculate that the difference in results with those obtained by Huang and Dobkins (2005) and Morrone et al. (2002, 2004) may be due to the way in which attention was manipulated. First, in dual task paradigms, attention is not directed to a specific location, but the amount of resources being spread to all locations is manipulated. Second, to manipulate attention those authors withdrew attention from the target, whereas Ling and Carrasco (2006a, 2006b) directed attention towards the target. For an alternative explanation for these differences, see below (Section 4.6).

The consequences of endogenous attention on contrast sensitivity have also been investigated by employing a selective adaptation procedure to assess the spatiotemporal properties of the visual system. Prolonged exposure to one type of stimulus reduces sensitivity to that stimulus, and (to a somewhat lesser degree) other similar stimuli thus allowing for the selective adaptation of a particular feature, such as spatial frequency or orientation (Blakemore & Campbell, 1969; Graham, 1989; Movshon & Lennie, 1979; see Section 6.2.1). Capitalizing on this procedure, and on the finding that the magnitude of adaptation increases with the intensity of the adaptor stimulus (Langley, 2002), the time course of attention's effects on contrast sensitivity was assessed. Given that attention boosts the strength of a signal, it initially enhances contrast sensitivity, but over time sustaining endogenous attention to an adapting pattern actually impairs sensitivity because the adapting signal is stronger at the attended location. Conversely, contrast sensitivity

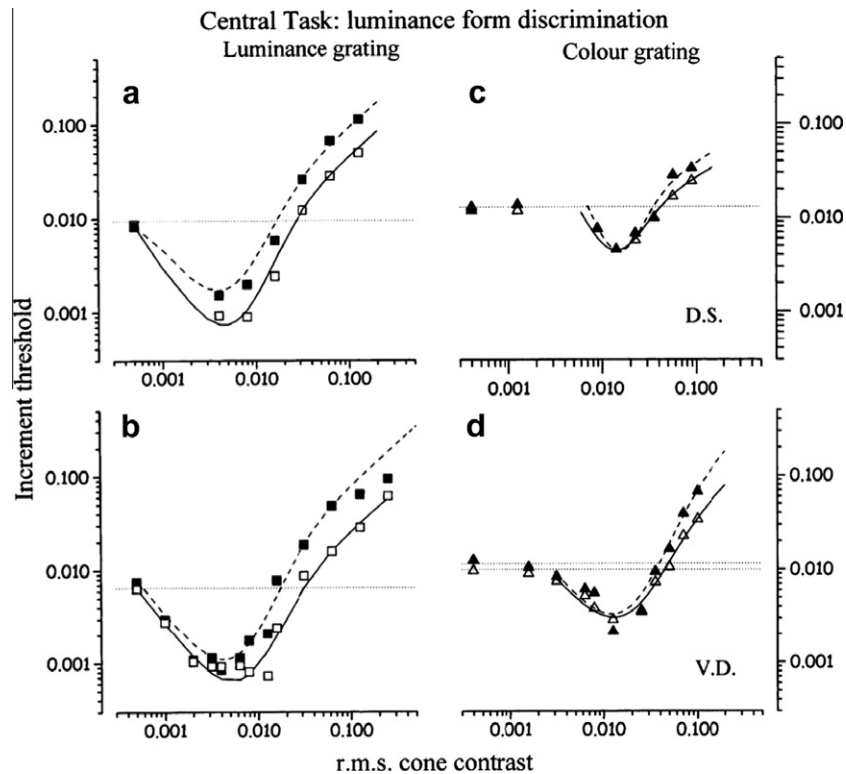


Fig. 6. Increment thresholds vs. pedestal contrast for two observers (rows). Filled symbols are data from the unattended condition; unfilled symbols are data from the attended condition. For judgments on luminance gratings (a and b) an attentional effect is visible from medium to high pedestal contrasts. For judgments on chromatic gratings (c and d), an attentional effect is visible only at high contrasts. These data are consistent with a response gain mechanism. [Reprinted from Morrone et al., 2004].

at an unattended location is impaired at short adapting times, but this effect gradually disappears and over time yields enhanced contrast sensitivity, because the adapting signal is weaker at the unattended than the attended location (Ling & Carrasco, 2006b).

4.4. Attention and perceived contrast

From psychophysical and neurophysiological evidence indicating that covert attention increases contrast sensitivity, one might infer that attention changes contrast appearance. But does attention alter appearance? Whether attention can actually affect the perceived intensity of a stimulus has been a matter of debate dating back to the founding fathers of experimental psychology and psychophysics—Helmholtz, James, and Fechner (Helmholtz, 1866/1911). Surprisingly, until the last decade, very little direct empirical evidence has been brought to bear on the issue (Prinzmetal, Amiri, Allen, & Edwards, 1998; Prinzmetal, Nwachuku, Bodanski, Blumenfeld, & Shimizu, 1997; Tsal, Shalev, Zakay, & Lubow, 1994) and some methodological issues questioned the results of these studies (see Carrasco, Ling, & Read, 2004; Treue, 2004). To investigate this issue further, Carrasco, Ling, et al. (2004) implemented a novel paradigm that enables to assess the effects of spatial cueing on appearance and to test subjective contrast, while circumventing methodological limitations of previous studies, making it possible to study subjective experience more objectively and rigorously (Luck, 2004; Treue, 2004).

Exogenous attention significantly increased perceived contrast. When a Gabor stimulus was peripherally cued, the point of subjective equality (PSE) was shifted – the apparent contrast of the stimulus for which transient attention had been drawn to was higher than when attention was not drawn there. That is to say, when observers attend to a stimulus, they perceive it to be of significantly higher contrast than when they perceive the same stimulus

without attention (Carrasco, Ling, et al. (2004)). An attentional effect consistent with these findings has been obtained using low-contrast sine-wave gratings (Hsieh, Caplovitz, & Tse, 2005). Multiple control experiments have ruled out alternative accounts of these findings based on cue bias or response bias with regard to perceived contrast (Carrasco, Fuller, & Ling, 2008; Carrasco, Ling, et al. (2004); Fuller, Rodriguez, & Carrasco, 2008; Ling & Carrasco, 2007), as well as with regard to the effects of exogenous attention on perceived spatial frequency (Gobell & Carrasco, 2005), saturation (Fuller & Carrasco, 2006) motion coherence (Liu, Fuller, & Carrasco, 2006), stimulus size of a moving object (Anton-Erxleben, Henrich, & Treue, 2007), flicker rate (Montagna & Carrasco, 2006), and speed (Fuller, Park, & Carrasco, 2009; Turatto, Vescovi, & Valsecchi, 2007). However, alternative explanations have been proposed for the effects of exogenous attention on perceived contrast (Schneider, 2006) and reply by (Ling & Carrasco, 2007; Prinzmetal, Long, & Leonhardt, 2008) and reply (Carrasco et al., 2008; Schneider & Komlos, 2008) and reply by (Anton-Erxleben, Abrams, & Carrasco, 2010).

The appearance paradigm has been adapted to investigate the effect of endogenous attention, which also increases perceived contrast (Liu, Abrams, & Carrasco, 2009). Another study has shown that endogenous attention can also modulate perceived brightness (Tse, 2005). This author concludes that bottom-up models of neuronal processing cannot account for this finding. Moreover, he proposes that understanding this phenomenon may require new models that include higher-level mechanisms than gain control, such as surface, boundary formation, and inhibition among higher level surfaces or objects.

A recent study investigated the effect of exogenous attention on contrast appearance with concurrent electrophysiological and behavioral measures (Stormer, McDonald, & Hillyard, 2009). The authors reported that cross-modal spatial cueing of attention

increased perceived contrast of the stimulus at the attended location concurrent with an amplified neural response in the contralateral visual cortex. Specifically, cueing attention to one of two identical stimuli boosted early processing (100–140 ms) of the attended stimulus in the ventral occipitotemporal visual cortex. Moreover, the amplitude of the enhanced neural response correlated positively with the perceived contrast of the cued stimulus, which provides converging evidence that contrast appearance arises from early cortical processing of visual stimuli. Crucially, the cueing of attention enhanced neural processing in the same ventral regions of the visual cortex that are responsive to physical differences in contrast. These results contradict the hypothesis that the effect of attention is due to a decisional bias (Schneider & Komlos, 2008). By providing converging evidence from human electrophysiology and behavior (Stormer et al., 2009) these authors demonstrate that the enhanced perceived contrast at the cued location is attributable to an effect of attention on early visual processing. These studies provide evidence for a contrast gain model (Reynolds & Desimone, 1999; Reynolds, Pasternak, & Desimone, 2000) in which attention increases perceived contrast by boosting early sensory processing in visual cortex, thus enhancing the effective contrast of the stimulus.

The visual system operates on the retinal image so as to maximize its usefulness to the perceiver, often producing nonveridical percepts. The visual system does not provide an internal one-to-one copy of the external visual world; rather, it optimizes processing resources. Attention is a pervasive example of this perceptual optimization: attention augments perception by optimizing our representation of sensory input and by emphasizing relevant details at the expense of a faithful representation (e.g., Carrasco et al., 2008; Fuller et al., 2008; Treue, 2004). The biophysical machinery of the brain engenders our phenomenological experience of the world: attention, both intra-modal and cross-modal, affects not only how we perform in a visual task but also what we see and experience (Carrasco, 2009).

4.5. Neurophysiological studies: attentional facilitation and selection

There has been a long-standing debate with regard to the neural computations underlying selective visual attention (e.g., Boynton, 2009; Carrasco, 2006; Desimone & Duncan, 1995; Pestilli, Ling, & Carrasco, 2009; Reynolds & Chelazzi, 2004; Reynolds & Heeger, 2009). Single-unit monkey physiology (Chen et al., 2008; Cohen & Maunsell, 2009; Martinez-Trujillo & Treue, 2002; McAdams & Maunsell, 1999; Mitchell, Sundberg, & Reynolds, 2009; Reynolds et al., 2000; Thiele, Pooresmaeli, Delicato, Herrero, & Roelfsema, 2009; Williford & Maunsell, 2006) and human neuroimaging (Buracas & Boynton, 2007; Li, Lu, Tjan, Doshier, & Chu, 2008; Murray, 2008) studies have reported various effects of attention on neural response. Attention increases the amplitude of neuronal responses and reduces their variability. Attention also increases synchronization of neuronal activity that correlates with enhanced neuronal and behavioral responses to changes in attended stimuli (e.g., Fries, Reynolds, Rorie, & Desimone, 2001).

Experiments examining how covert attention modulates visual performance and neuronal activity in visual cortex have documented a variety of empirical phenomena, some of which appear to be mutually contradictory. Central to this debate are studies of the interactions between attention and stimulus contrast both in terms of behavior and neural populations (Boynton, 2009; Pestilli et al., 2009; Reynolds & Heeger, 2009). Two types of gain control mechanisms have been considered in neural responses to luminance-modulated stimuli: contrast gain and response gain (Sclar, Lennie, & DePriest, 1989; Fig. 7). How do attentional changes at the neural level affect the psychophysical contrast response function? Fig. 7A shows the signature of contrast gain – a shift in the

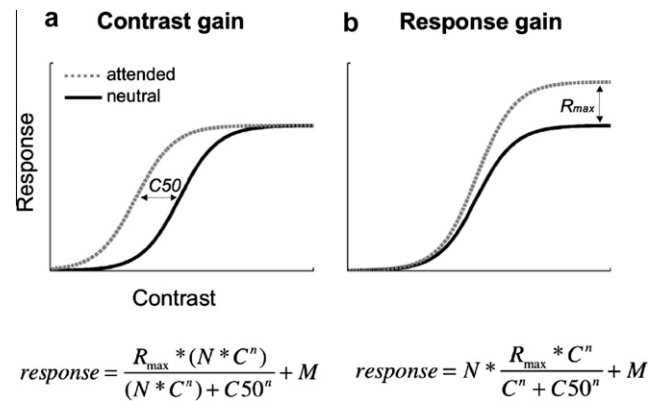


Fig. 7. Possible effects of attention on the contrast response function. (a) The left panel depicts a contrast gain model for attention. Contrast gain predicts an increase in sensitivity that is a function of stimulus intensity, and is characterized by a leftward threshold (C_{50}) shift in the contrast response function. The dashed curve represents the signature curve shift brought about by attentional contrast gain; the shape of the function does not change but rather shifts leftward – boosting the effective contrast of the stimulus. (b) In the right panel, the dashed curve (attended) represents the effects of attention according to response gain models. Response gain predicts an increase in firing rate, which is characterized by a change in the shape of the curve – in slope and asymptote (R_{max}). C_{50} , threshold; R_{max} , asymptote; n , slope; C , contrast level; N , attentional modulation; and M , response at lowest stimulus intensity.

contrast response function to the left. In the case of attention, this reflects a decrease in the contrast required for the neuron to respond at the same level as in a neutral condition. The maximal attentional modulation is at the dynamic range of the contrast response function. Some neurophysiological and behavioral experiments have shown a change in contrast gain, i.e., a leftward shift of the contrast-response (Li et al., 2008; Martinez-Trujillo & Treue, 2002; Reynolds & Chelazzi, 2004; Reynolds et al., 2000) and psychometric functions (Ling & Carrasco, 2006a; Pestilli et al., 2009).

Fig. 7b shows the signature of a response gain – an increase in firing rate proportional with stimulus intensity. Response gain predicts that attentional modulation increases monotonically as a function of contrast. The results of some experiments suggest that attention increases neuronal responses by a multiplicative response gain factor (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999) and similarly improves performance via upward-scaling of the psychometric function (Barbot et al., 2011; Ling & Carrasco, 2006a; Morrone et al., 2002, 2004; Palmer & Moore, 2009; Pestilli & Carrasco, 2005; Pestilli et al., 2007). Other results suggest an additive effect of attention across the entire contrast range or a combination of both response gain and contrast gain changes (Buracas & Albright, 2009; Huang & Dobkins, 2005; Williford & Maunsell, 2006). And still other results show additive offsets dependent on visibility (Thiele et al., 2009). These ostensibly contradictory findings have been taken to represent alternative models of attention (Boynton, 2009; Lee & Maunsell, 2009; Martinez-Trujillo & Treue, 2002; McAdams & Maunsell, 1999; Pestilli et al., 2009; Reynolds & Chelazzi, 2004; Reynolds et al., 2000).

A number of neurophysiological studies have shown that directing sustained attention to a stimulus increases neuronal sensitivity, so that neurons respond to an attended stimulus much as they would were its luminance increased. It is possible to relate these findings to studies in anesthetized cats and monkeys documenting how luminance contrast affects neuronal responses. The same models explaining contrast-dependent changes in neuronal response can account for contrast-dependent modulation of the competitive interactions observed when multiple stimuli appear within a neuron's receptive field (for reviews see Martinez-Trujillo & Treue, 2005; Reynolds, 2005; Reynolds & Chelazzi, 2004).

With regard to attentional facilitation, single-unit recording studies have found that spatial attention can enhance responses evoked by a single stimulus appearing alone in a neuron's receptive field (e.g., Ito & Gilbert, 1999; McAdams & Maunsell, 1999; Motter, 1993; Reynolds et al., 2000). Reynolds et al. (2000) assessed the effects of sustained attention on contrast sensitivity when a single stimulus appeared in a neuron's receptive field. The monkey's task was to detect a target grating that could appear at an unpredictable time at the cued location. The target's luminance contrast was randomly selected to ensure that the monkey had to attend continually to the target location. Consistent with a contrast gain, in V4, an extrastriate visual area at an intermediate stage of the ventral processing stream, attention shifts the contrast response function horizontally with the most pronounced changes occurring at its dynamic range (steepest region). When the grating stimulus appearing in the neuron's receptive field was below the contrast response threshold (5% and 10% contrast; Fig. 8a), it failed to elicit a response, when unattended. However, when the monkey attended to its location in the RF the same 10% contrast elicited the neuron to respond. Attention did not alter the neuronal response when the stimulus was above saturated contrast. Across a population of V4 neurons, the highest increments in firing rate were observed at contrasts in the dynamic range of each neuron's CRF (Fig. 8b). For a cell to reliably detect an unattended stimulus, its contrast needed to be 50% higher than that of the attended stimulus; i.e., attention was equivalent to about 50% increase in contrast (Reynolds et al., 2000); similar estimates have been obtained in MT (Martinez-Trujillo & Treue, 2002) and in V4 (Reynolds & Desimone, 2003).

Given our limited ability to process information, it is also crucial to understand how attentional selection of behaviorally relevant stimuli from among competing distractors may be instantiated at a neural level. Neuronal recordings within the extrastriate cortex have revealed a direct neural correlate of attentional selection. Moran and Desimone (1985) were the first to show that the firing rate is determined primarily by the task-relevant stimulus. This seminal study showed that when two stimuli are presented within the receptive field, the neuron's response to the pair is greater when the monkey is asked to identify the stimulus corresponding to the neuron's preferred color and orientation than when asked to identify the non-preferred stimulus. Several studies have shown that the attentional modulation depends on the similarity between the attended stimulus properties and the sensory preferences of the neuron, both in the ventral stream (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993, 2001; Reynolds & Desimone, 2003; Reynolds et al., 1999; Sheinberg & Logothetis, 2001) and in the dorsal stream (Treue & Martinez-Trujillo, 1999; Treue & Maunsell, 1996).

Reynolds et al. (1999) found that in V4 the response to a pair of stimuli lies between the responses elicited by either stimulus alone, the preferred and the non-preferred (e.g., vertical or horizontal lines). When the monkey attends to the preferred stimulus, the response to the pair increases so that it approaches the high response level elicited when it is presented by itself; conversely, when the monkey attends to the non-preferred stimulus, the response is reduced so that it approaches the low response elicited when it is presented by itself. In short, attending to the preferred stimulus increases the response evoked by the pair, but attending to the poor stimulus reduces such response. These effects result in increased saliency of the attended stimulus representation and a corresponding suppression of the neuronal representation of unattended stimuli.

Similar results have been obtained for a variety of stimuli. For instance, Martinez-Trujillo and Treue (2002) presented two pairs of random dot patterns, one inside the RF and one outside the RF in area MT, and Chelazzi, Miller, Duncan, and Desimone (2001) obtained a

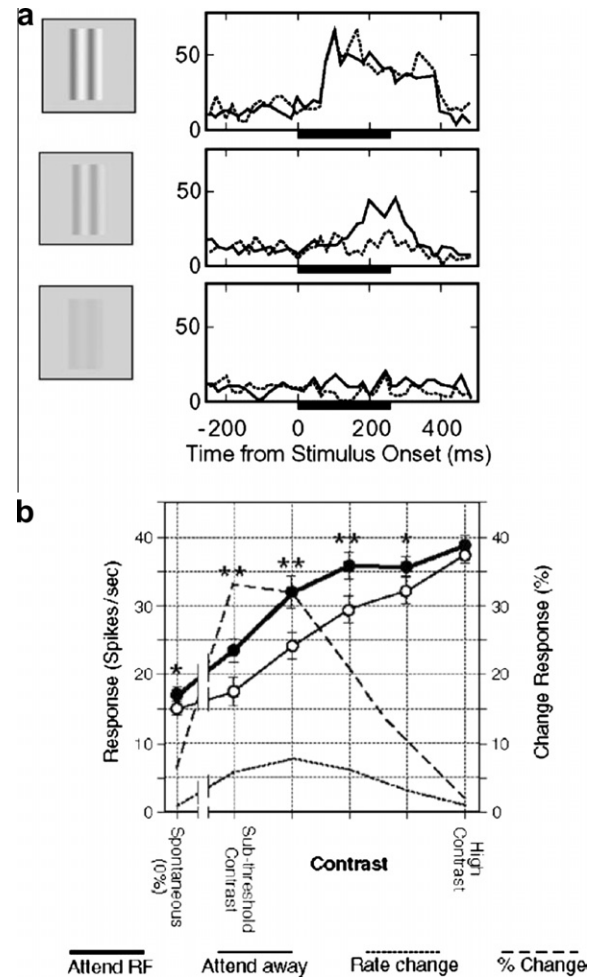


Fig. 8. Response of a sample neuron from area V4 as a function of attention and stimulus contrast. (a) The contrast of the stimulus in the receptive field increased from 5% (bottom panel) to 10% (middle panel) to 80% (top panel). The monkey had to detect a grating at the attended location. On each trial, attention was directed to either the location of the stimulus inside of the receptive field (solid line) or a location far away from the receptive field (dotted line). Attention reduced the contrast threshold to elicit a response (middle panel), but did not affect the response at saturation contrast (top panel). (b) Averages responses of V4 neurons while the monkey attends to the location (thick line) or away (thin line) of the receptive field (thin line). The horizontal line depicts the five different contrast values of the gratings presented inside the RF, which spanned the dynamic range of the neuron. The dashed and dotted lines show percentage and absolute difference in firing rate, respectively, across the two attention conditions, as a function of contrast. [Adapted from Reynolds et al., 2000].

similar pattern of results when recording in area V4 of monkeys performing a visual search task involving objects (faces and houses). The findings that attending to the preferred stimulus increases the response to the pair but attending to the poor stimulus reduces the response evoked by the pair, provide support for attentional models positing that response suppression mediates the selection of one stimulus and the inhibition of the other (e.g., Desimone & Duncan, 1995; Ferrera & Lisberger, 1995; Lee, Itti et al., 1999).

Based on these findings that facilitation is observed when attention is directed to a single stimulus appearing alone within the receptive field, and that when two stimuli appear within a neuron's receptive field, the neuronal response is dominated by the stimulus that is task relevant, Reynolds et al. (1999) have proposed the contrast gain model of attention. The linking hypothesis is that attention operates by multiplying the effective contrast of the behaviorally relevant stimulus or, equivalently, increases the neuron's contrast sensitivity. As would occur with an increase in the

stimulus contrast attention is assumed to lead to increases in the strength of the excitatory and inhibitory inputs activated by the attended stimulus (Reynolds et al., 1999). This effect results in a shift of the contrast response function to the left, just as in some electrophysiological (Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000) and psychophysical (Cameron et al., 2002; Carrasco, Ling, et al., 2004; Doshier & Lu, 2000b; Ling & Carrasco, 2006a) studies. Also, as attention shifts contrast, its effect on the tuning curve is predicted to be the same as an increase in contrast: to cause a multiplicative increase in the tuning curve (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999). Moreover, as attention shifts contrast, its effect on the neuronal response depends on whether attention is directed towards the preferred or the non-preferred stimulus (Chelazzi et al., 2001; Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000). However, neurophysiological and psychophysical studies have shown that attention also alters response either via response gain (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999) or a combination of both response gain and contrast gain changes (Buracas & Albright, 2009; Huang & Dobkins, 2005; Williford & Maunsell, 2006).

4.6. Models of enhanced contrast

The normalization model of attention (Reynolds & Heeger, 2009) was proposed to attempt to reconcile the seemingly conflicting, empirical findings of the effects of attention on sensory responses in visual cortex just discussed – contrast gain vs. response gain. This computational theory identifies two critical factors that determine the effect of attention on contrast response functions and, consequently, on behavioral psychometric functions: the size of the stimulus and the spatial spread of attention, known as the attention field. Changing the relative sizes of these two factors allows the model to reveal response gain changes, contrast gain changes, and various combinations of response gain and

contrast gain changes. Specifically, the model predicts that attention increases response gain when the stimulus is large and the attention field small, and that it increases contrast gain when the stimulus is small and the attention field is large (Fig. 9). The core idea is that the attention field reshapes the distribution of activity across the population of neurons, shifting the balance between excitation and suppression, yielding either a change in response gain, contrast gain or a combination of the two (see Reynolds & Heeger, 2009 for mathematical derivation).

The architecture of the model predicts a shift between response gain changes and contrast gain changes, because the effect of attention is to multiply the stimulus-evoked activity before divisive normalization (Reynolds & Heeger, 2009). Alternatively, if attention modulated activity after normalization then it would always yield response gain changes, regardless of the size or shape of the attention field. Other computational models of attention, although ostensibly similar to the normalization model of attention, do not predict the shift from response to contrast gain changes. Some of these models presume that spatial attention always has the same effect on the excitation and suppression (that is, the numerator and the denominator of the normalization equation), always yielding a contrast gain change (Boynton, 2009; Reynolds & Chelazzi, 2004; Reynolds & Desimone, 1999). In another model, attention affects only the strength of the normalization, always yielding a response gain change (Lee & Maunsell, 2009). Particular to the normalization model of attention is the idea that the effects of attention on the numerator and denominator can differ depending on the relative sizes of the stimulus and the attention field, altering the balance between excitation and suppression.

A key prediction of the Normalization Model of Attention is that the effect of attention can systematically shift from a change in response gain to contrast gain with smaller stimuli and a broader attention field. This prediction was tested recently and confirmed, by using spatial uncertainty to manipulate attention field size

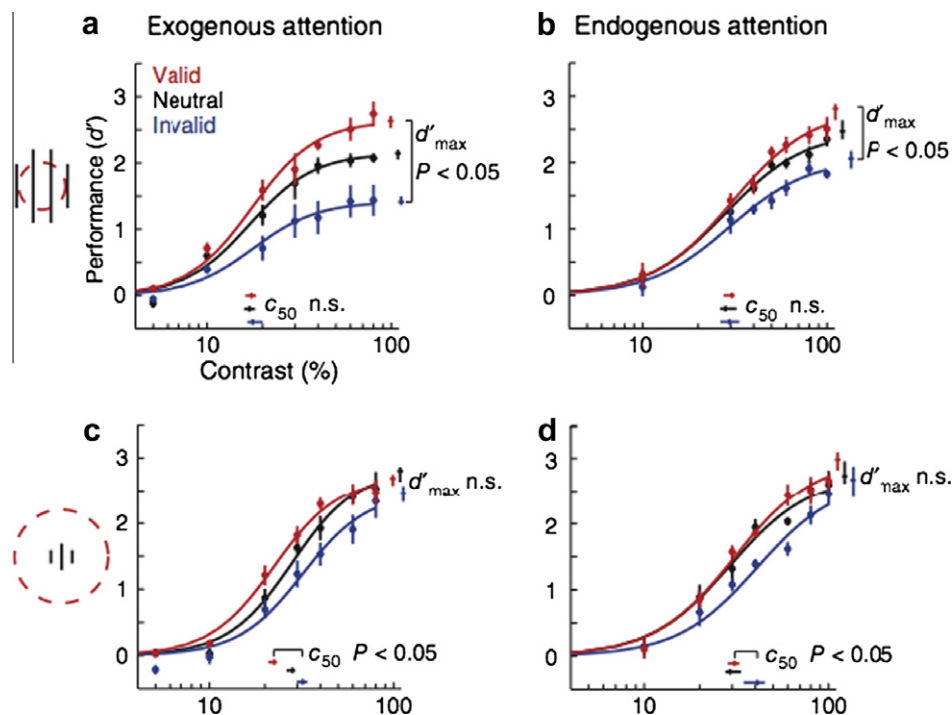


Fig. 9. Effects of exogenous and endogenous attention on performance (d') as a function of contrast. (a and b) Large stimulus with small attention field. (c and d) Small stimulus with large attention field. Exogenous attention is shown in (a and c). Endogenous attention is shown in (b and d). Shown are plots of psychometric functions for each attentional condition (valid, neutral and invalid pre-cues) and parameter estimates (c_{50} , contrast yielding half-maximum performance; d'_{max} , asymptotic performance at high contrast). Each data point represents the mean across 4 observers. Error bars on data points are $\pm$ 1.e. Error bars on parameter estimates are confidence intervals obtained by bootstrapping. [Reprinted from Herrmann et al., 2010].

(Herrmann et al., 2010). Fig. 9 shows that when the stimuli are large and the size of the window is small, both exogenous (Fig. 9a) and endogenous (Fig. 9b) attention yielded response gain. However, when the stimuli are small and the size of the window is large, both exogenous (Fig. 9c) and endogenous (Fig. 9d) attention yielded contrast gain. An fMRI experiment confirmed that the attention field was larger with spatial uncertainty than without it. The authors conclude that, as predicted by the Normalization Model of Attention, attention modulates activity in visual cortex in a manner that can resemble either a change in response gain or contrast gain, depending on stimulus size and attention field size. They suggest that such differences in the experimental protocols may also explain previous discrepancies among psychophysical studies (Ling & Carrasco, 2006a; Morrone et al., 2002, 2004; Pestilli & Carrasco, 2005; Pestilli et al., 2007; Pestilli et al., 2009). With constant stimulus size, some studies have found that exogenous attention alters performance via a response gain change, whereas endogenous attention does so via a contrast gain change (Huang & Dobkins, 2005; Ling & Carrasco, 2006a; Pestilli & Carrasco, 2005; Pestilli et al., 2007, 2009). A response gain change could have been elicited by brief peripheral cues nearby the stimulus, whereas a contrast gain change could have resulted from endogenous cues at fixation, rather than cues adjacent to the stimulus, which may have encouraged a narrower or larger attention field, respectively. Moreover, the different results seem to be related to differences in stimulus size; for endogenous attention, response gain changes were reported with the largest stimuli (Morrone et al., 2002, 2004), a combination of contrast and response gain changes was observed with intermediate stimulus sizes (Huang & Dobkins, 2005) and contrast gain changes were reported with smaller stimuli (Ling & Carrasco, 2006a).

4.7. Attention increases fMRI BOLD response in human visual cortex

Neuroimaging studies yield a measure of population neural activity, which may prove even more relevant for behavior than the response of single units. Due to the inherently noisy nature of individual neurons, it is likely that our brain analyzes neural responses by recruiting activity across large cell populations to guide perception and behavior, rather than only relying on the activity of few cells (Abbott & Dayan, 1999; Parker & Newsome, 1998; Pouget, Dayan, & Zemel, 2000, 2003). fMRI studies of spatial attention have often demonstrated large signal increases in V1 to a stimulus that is attended vs. unattended (e.g., Brefczynski & DeYoe, 1999; Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999). However, there is debate as to whether these changes are due to baseline shifts, differences in the stimulus-evoked response, or some combination of both. fMRI blood oxygen level-dependent (BOLD) responses to stimuli of varying contrast, i.e., contrast response functions (CRFs), measured in human visual cortex are closely predicted by CRFs averaged across a population of single neurons of macaque visual cortex (Heeger, Huk, Geisler, & Albrecht, 2000). Moreover, visual evoked potentials (VEPs) in human visual cortex have revealed that CRFs are modulated by attention multiplicatively (Di Russo et al., 2001).

Based on these findings, it was predicted that attentional modulation of CRFs in human visual cortex assessed with fMRI would reflect similar changes to those found in macaques' electrophysiology (Buracas & Boynton, 2007). To the authors' surprise, spatial attention had an additive effect across stimulus contrasts on the fMRI in V1, and showed a trend in favor of an additive model in V2, V3, and MT, but the effect did not statistically differ from the predictions of the multiplicative/contrast-gain model. The authors consider three possible explanations for these findings: (a) fMRI may be dominated by an additive change in baseline activity and responses to non-optimal stimulus; (b) attention could have an

additive effect on the subthreshold synaptic activity that is considered to mediate the BOLD signal (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001); (c) attention modulation of fMRI signals, in addition to reflecting underlying neuronal activity, may reflect a direct modulation of vasculature by vasoactive agents. Whatever the underlying reason, their results showing similar effects across stimulus contrasts are consistent with attention increasing a baseline mechanism. Another study used event-related fMRI to separately measure the contribution of baseline-shifts and stimulus-evoked changes with spatial attention (Murray, 2008). He showed that the effect of spatial attention on the CRF in areas V1 to V3 could be accounted by a baseline shift. These results, as well as those of Buracas and Boynton's, are consistent with fMRI studies showing that spatial attention significantly increases the BOLD signal in the absence of a stimulus (Kastner & Ungerleider, 2000; Ress, Backus, & Heeger, 2000; Silver, Ress, & Heeger, 2007). The anticipatory "biasing" of V1 activity could in principle serve as a mechanism that allows attention to influence the initial feed-forward sweep of processing (Hopf et al., 2009).

By measuring the magnitude of the effect of attention over a wider range of stimulus contrasts, in both event-related and mixed designs, two separate effects of attention were identified in areas V1 to V4: An increase in baseline activity, which is unlikely to improve functional discrimination, and a contrast gain effect that could serve a functional role in stimulus processing (Li et al., 2008). Increasing the contrast gain of the visual system shifts the most sensitive operating range of the system toward lower contrasts, thus improving the visual system's ability to identify these stimuli. The results indicated that the magnitude of the attentional modulations was similar for all areas tested. The authors hypothesize that the differences with previous studies, in which attention's effect increased in higher cortical areas, could be due to the fact that they tested a wide range of stimulus contrasts whereas previous studies (e.g., Kastner et al., 1999; Maunsell & Cook, 2002) had tested only a single, intermediate contrast. The authors remain agnostic regarding whether feed-forward or feedback activity underlies the similar modulation across areas.

Less is known about the neural mechanism for exogenous attention and its effects on stimulus processing. Psychophysical findings demonstrating that exogenous attention increases contrast sensitivity suggest that it should also enhance neural activity in early stages of visual processing. This hypothesis was tested by measuring brain activity in early visual areas using rapid event-related fMRI in conjunction with a peripheral cueing paradigm to manipulate exogenous attention (Liu et al., 2005). Participants discriminated the orientation of one of two gratings preceded or followed by a non-predictive peripheral cue. Precueing the target location improved performance and produced a larger fMRI response in corresponding retinotopic areas. This enhancement progressively increased from striate to extrastriate areas. Thus, exogenous attention increases both perceptual performance and the concomitant stimulus-evoked activity in early visual areas. These results provide evidence regarding the retinotopically specific neural correlate for the effects of exogenous attention on early vision.

Larger attentional effects in higher visual areas have also been found in studies of endogenous attention (e.g., Kastner et al., 1999; Maunsell & Cook, 2002). Such a pattern is consistent with top-down modulation from frontal and parietal areas feeding back to the visual cortex, with diminishing effects in earlier visual areas. However, the attentional gradient could also be due to a feed-forward mechanism in which attentional modulation accumulates across sequential levels of processing. Whereas it has been established that endogenous (conceptually-driven) attention is mediated by a feedback mechanism (Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Kanwisher & Wojciulik, 2000; Kastner

& Ungerleider, 2000; Schroeder, Mehta, & Foxe, 2001), a feed-forward mechanism seems more likely in the case of transient (stimulus-driven) attention. The attentional effect increases along the hierarchy of visual areas, from V1 to V4. Because attention can boost the signal, its effect would be more pronounced in extrastriate than striate areas, where the contrast response functions get steeper, due to areal summation across progressively larger receptive fields in higher areas (Sclar, Maunsell, & Lennie, 1990). Thus, a feed-forward mechanism in which attentional modulation accumulates across sequential levels of processing could underlie the attention gradient (Liu et al., 2005).

5. Covert attention can increase spatial resolution

Spatial resolution, our ability to discriminate fine patterns, is not uniform across locations in the visual field. It decreases with eccentricity. Correspondingly, signals from the central parts of the visual field are processed with greater accuracy and faster reaction times (e.g., Cannon, 1985; Carrasco, Evert, Chang, & Katz, 1995; Rijdsdijk, Kroon, & van der Wildt, 1980). In many tasks, these performance differences are eliminated when stimulus size is enlarged according to the cortical magnification factor which equates the size of the cortical representation for stimuli presented at different eccentricities (e.g., Rovamo & Virsu, 1979). However, there are also qualitative differences in neural processing between central and peripheral vision. Thus, compensating for cortical magnification does not eliminate all differences (for a review see Kitterle, 1986). Moreover, spatial resolution is not uniform across isoeccentric locations. It is better along the horizontal meridian than the vertical one, and better in the lower region than in the upper region of the vertical meridian (Fuller et al., 2008; Montaser-Kouh-sari & Carrasco, 2009; Talgar & Carrasco, 2002).

There are several factors contributing to differences in spatial resolution across eccentricities. A greater proportion of cortex is devoted to processing input from the central part of the visual field than from the periphery (cortical magnification) in many cortical visual areas. In area V1, approximately 25% of cortex is devoted to processing the central 2.5° of visual angle (De Valois & De Valois, 1988). Neuronal RF sizes increase with eccentricity, as the RF density decreases. Thus, as eccentricity increases, information is pooled over a larger area, diminishing sensitivity to fine patterns. Moreover, the visual system's peak sensitivity to spatial frequencies decreases with eccentricity (Kitterle, 1986).

In this Section 1 review a series of psychophysical studies that provide evidence for the 'resolution hypothesis', which states that attention can enhance spatial resolution, and that the magnitude of such an effect increases with eccentricity (Carrasco & Yeshurun, 2009; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 1999; Yeshurun & Carrasco, 2000). These studies show that when spatial attention is directed to a given location, performance improves in visual search, acuity, texture segmentation (unless resolution is already too high for the task at hand, see below), and crowding tasks, which are mediated by spatial resolution. In general, observers can discriminate finer details when attending to the target location than when attending to another location. I discuss mechanisms and models that are consistent with the findings that attention enhances spatial resolution.

5.1. Attention and visual search

In a visual search task, observers are typically required to detect the presence of a predefined target appearing among other irrelevant items; for instance, a red vertical line appearing among red tilted lines in a feature search, or a red vertical line appearing among red tilted and blue vertical lines in a conjunction search (e.g., Treis-

man, 1985). Performance in visual search tasks deteriorates as the target is presented at farther peripheral locations (Carrasco & Chang, 1995; Carrasco et al., 1995). This reduction in performance is attributed to the poorer spatial resolution at the periphery because performance is constant across eccentricity when stimulus size is enlarged according to the cortical magnification factor (Carrasco & Frieder, 1997; Carrasco, McLean, Katz, & Frieder, 1998; but see Wolfe, O'Neill, & Bennett, 1998). Similarly, a study in which attention was manipulated (rather than inferred, like in many visual search studies) showed that attention (induced by a peripheral cue) eliminates the eccentricity effect for both features and conjunctions (Carrasco & Yeshurun, 1998). The ability of the peripheral cue to ameliorate this performance decrement supports the resolution hypothesis because it implies that by improving performance more at peripheral than at central locations, attention can minimize resolution differences between the fovea and the periphery.

Additional evidence for the idea that attention enhances spatial resolution in visual search was provided by a study in which orientation thresholds were assessed in a visual search task (Morgan et al., 1998). A Gabor patch was presented in one of two possible orientations, with or without distractors, and it was found that thresholds increased in the presence of distractors. Based on the steepness of the set-size effects and the weak summation effects for multiple targets of the same tilt, the authors attributed this effect to a central limiting noise source at the level of the integrator. Interestingly, they found that when distractors were present, indicating the target location with a peripheral cue reduced orientation thresholds to the level found when the target was presented alone. The authors suggested that focusing attention on the target location reduced thresholds because attention reduces the scale over which an image is analyzed (Morgan et al., 1998). Similar findings were obtained measuring orientation discrimination of a tilted target in the presence of distractors: discrimination thresholds increased with set size but cueing the target location eliminated this effect (Baldassi & Burr, 2000). The authors attributed the set size effect to perceptual summation of targets and distractors and suggest that such summation is under rapid attentional control so that the visual system increases performance over a limited area. These results are also consistent with a reduction of spatial scale of processing and distractor exclusion.

5.2. Attention and acuity tasks

Acuity tasks are designed to measure the observer's ability to resolve fine details. Performance in some of these tasks, like the detection of a small gap in a Landolt-square, is limited by the retinal mosaic, whereas in other tasks, like identification of offset direction with Vernier targets, performance is hyperacute and limited by cortical processes (e.g., Levi, Klein, & Aitsebaomo, 1985; Thomas & Olzak, 1986). Directing transient attention to the target location improves performance in both acuity and hyperacuity tasks. To investigate whether covert attention can enhance spatial resolution via signal enhancement in a visual acuity task, observers were asked to indicate which side of a supra-threshold Landolt-square had a gap. Performance decreased with eccentricity. A peripheral cue, however, improved observers' performance in terms of both speed and accuracy, and the magnitude of this improvement increased with eccentricity. Similarly, directing attention to the location of a Vernier target allowed observers to identify smaller horizontal offsets in a hyperacuity task (Yeshurun & Carrasco, 1999). The same pattern of results emerged when all sources of added external noise were eliminated from the display; i.e., local masks, global masks, and distractors (Carrasco et al., 2002). Consistent findings emerged from a comparative study that evaluated the effects of covert attention on Landolt acuity in humans and non-human

primates (Golla et al., 2004). The findings for both species demonstrate consistently enhanced acuity when the target location was precued as compared to a no-cue condition. Also in line with the human psychophysical studies, the attentional effect increased with eccentricity in both human and non-human primates. Moreover, cueing the location of a line that sometimes contains a small gap enables observers to better detect whether the gap was present and to localize its location (Shalev & Tsal, 2002). All these findings further support the idea that attention enhances spatial resolution.

Furthermore, increased spatial acuity brought about by exogenous and endogenous attention is coupled with decreased acuity at unattended locations (Montagna et al., 2009). Gap-size thresholds for Landolt-squares were measured for each attention type (exogenous, endogenous) and three cueing conditions (cued, neutral, uncued). For exogenous attention, observers were explicitly told that the peripheral cue was uninformative, i.e., not predictive of target location or gap side. For endogenous attention, observers were informed that the cue would indicate the target location, but not the gap side, on 70% of the central-cue trials. For both exogenous and endogenous attention, acuity thresholds were lower in the cued and higher in the uncued condition compared to the neutral baseline condition (Fig. 10). The fact that acuity trade-offs emerge for very simple, non-cluttered displays, in which only two stimuli (one target and one distractor) are competing for processing, challenges the idea that perceptual processes are of unlimited capacity (e.g., Palmer et al., 2000). On the contrary, this finding suggests that trade-offs are an inherent characteristic of attentional allocation, and that such a mechanism has a general effect across different stimulus and task conditions, thus supporting the idea that covert spatial attention helps regulate the expenditure of cortical computation.

As mentioned above (Section 3.2), there are alternative hypotheses regarding attentional mechanisms, such as shifts in the decisional criterion, location uncertainty reduction, or reduction of external noise (e.g., Doshier & Lu, 2000a, 2000b; Eckstein et al., 2002; Kinchla, Chen, & Evert, 1995; Lu & Doshier, 2004; Shiu & Pashler, 1994). Note that the attention effects on acuity measures discussed in this section (Carrasco et al., 2002; Golla et al., 2004; Montagna et al., 2009; Yeshurun & Carrasco, 1999) could not be accounted for by any of these hypotheses for the following reasons: (a) the peripheral cue did not convey information regarding the correct response but only indicated the target location, or conveyed no information regarding either the correct response or the target location; (b) the peripheral cue did not associate a higher probability with one of the responses and observers could not rely on its presence to reach a discrimination decision; (c) a suprathreshold target could not be confused with the blank at the other locations and was presented alone, without other items to introduce external noise; (d) similar results were obtained when two suprathreshold targets were presented at fixed locations, which could not be confused with the blank at other locations; and (e) similar results were found with and without a local post-mask. Therefore, the improved performance in acuity tasks could only be accounted for by the resolution hypothesis; i.e., attention enhances spatial resolution at attended locations.

5.3. Attention and texture segmentation

Improved resolution is advantageous because many everyday tasks (e.g., reading or searching for small objects) benefit from heightened resolution. However, in certain situations resolution enhancement is not beneficial; for example, when a global assessment of a scene is required (e.g., viewing an impressionist

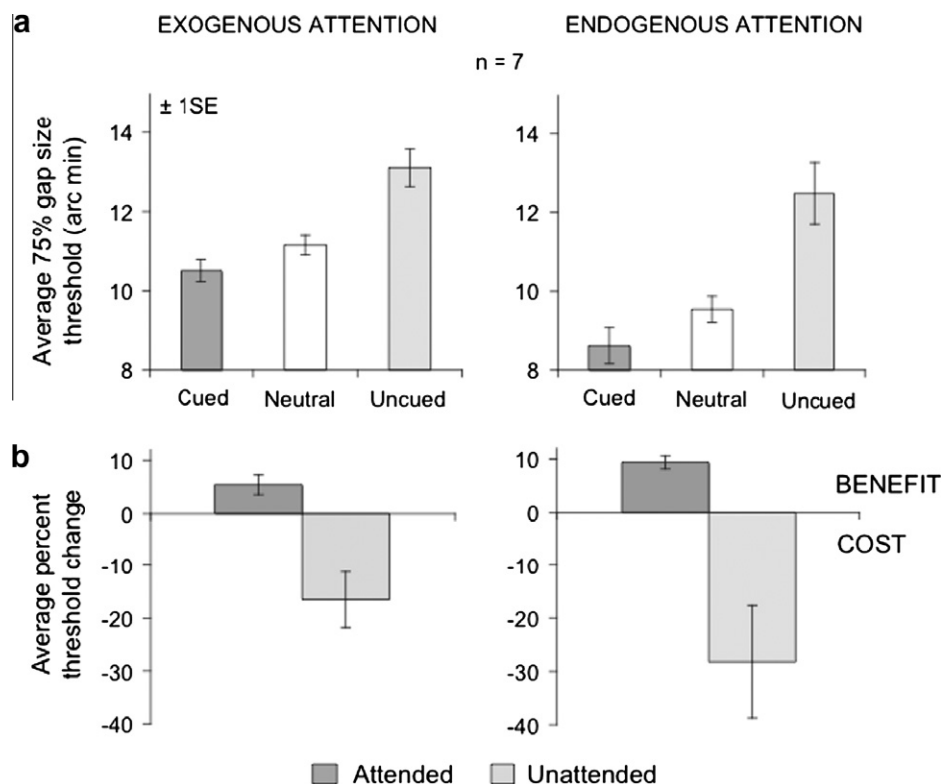


Fig. 10. (a) Average gap-size thresholds (75% localization accuracy) for both exogenous (top-left panel) and endogenous (top-right panel) attention for the cued, neutral, and uncued conditions. (b) The bottom panels depict the average percent change in acuity thresholds at cued and uncued locations as compared to the neutral condition for exogenous (left) and endogenous (right) attention. Negative values indicate a cost in acuity, whereas positive values indicate a benefit. Error bars show ± 1 SE. [Reprinted from Montagna et al., 2009].

painting; when we want to see a whole tree rather than its individual leaves) or when navigating through the world under poor atmospheric conditions (e.g., fog or haze). The fact that increasing spatial resolution can be detrimental (e.g., in tasks where performance is diminished by heightened resolution) enabled a crucial test of the resolution hypothesis. If attention indeed enhanced resolution, performance at the attended location should be impaired rather than improved in such a task (Yeshurun & Carrasco, 1998). To address this, a basic texture segmentation task was used in which a to-be-detected texture target was embedded in a background of an orthogonal orientation. Without attentional manipulation, observers' performance in this task is highest at mid-peripheral locations, and drops as the target appears at more central or farther peripheral locations. This 'central performance drop' (CPD) is attributed to a mismatch between the average size of spatial filters at the fovea and the scale of the texture (Gurnsey, Pearson, & Day, 1996; Kehr, 1997). The size of these filters at the fovea is too small for the scale of the texture. Thus, spatial resolution at the fovea would be too high for the task. The filters' average size increases gradually with eccentricity, and is presumably optimal around the performance peak. At farther locations, performance decreases because the filters are too big and the resolution is too low for the task. Thus, enlarging the scale of the texture shifts the peak of performance to farther locations, whereas decreasing this scale shifts the peak of performance towards the center (Gurnsey et al., 1996; Joffe & Scialfa, 1995; Kehr, 1997).

If attention enhances spatial resolution, attending to the target location should improve performance at the periphery where the resolution is too low, but should impair performance at the fovea where the resolution is already too high for the task (Yeshurun & Carrasco, 1998). To test these predictions peripheral cues were presented with this texture segmentation task. Accuracy was higher for the cued than the neutral trials at the more peripheral locations, but was lower at central locations (Fig. 11a). The spatial extent of the CPD increases with the size of the scale of the texture, which was manipulated by viewing distance (Gurnsey et al.,

1996; Joffe & Scialfa, 1995); compare neutral functions in Fig. 11a–c). Consistent with this finding, attention impaired performance in a larger range of eccentricities with a larger than with a medium scale of the texture (compare Fig. 11b and a). Conversely, with a smaller texture scale, performance was impaired at a smaller range of eccentricities than with a medium texture (compare Fig. 11c and a). This study demonstrated that transient attention improves performance when it is limited by resolution that is too low, but hinders performance when it is limited by resolution that is too high for the task. Thus, the scale of the texture and the average size of the filters at a given eccentricity determine whether attention helps or hinders performance. The finding that transient attention affects performance even at the fovea is in accord with a study that demonstrated that targets that occur unexpectedly at fixation capture attention in a stimulus-driven manner similar to attentional capture in the periphery (Coull, Frith, Buchel, & Nobre, 2000). The impairment at central locations is predicted by the resolution hypothesis. The spatial resolution model is the only model that can predict impairments of this nature (Yeshurun & Carrasco, 1998).

A possible mechanism by which covert attention enhances spatial resolution is by increasing sensitivity to high spatial frequencies. To test this hypothesis, a peripheral cueing procedure was employed in conjunction with selective adaptation to spatial frequency (Carrasco, Loula, et al., 2006). As mentioned above, the selective adaptation procedure is used to assess the spatiotemporal properties of the visual system (Blakemore & Campbell, 1969; Graham, 1989; Movshon & Lennie, 1979). While keeping the stimulus content identical, the availability of spatial frequency information was thus manipulated by reducing observers' sensitivity to a range of frequencies. Hence, by adapting to high spatial frequencies, the non-optimal filters would be removed from the normalization process and the magnitude of the CPD would be diminished. Furthermore, were the central attentional impairment (Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998) due to an increased sensitivity to high frequencies and a reduced sensitivity to lower frequencies,

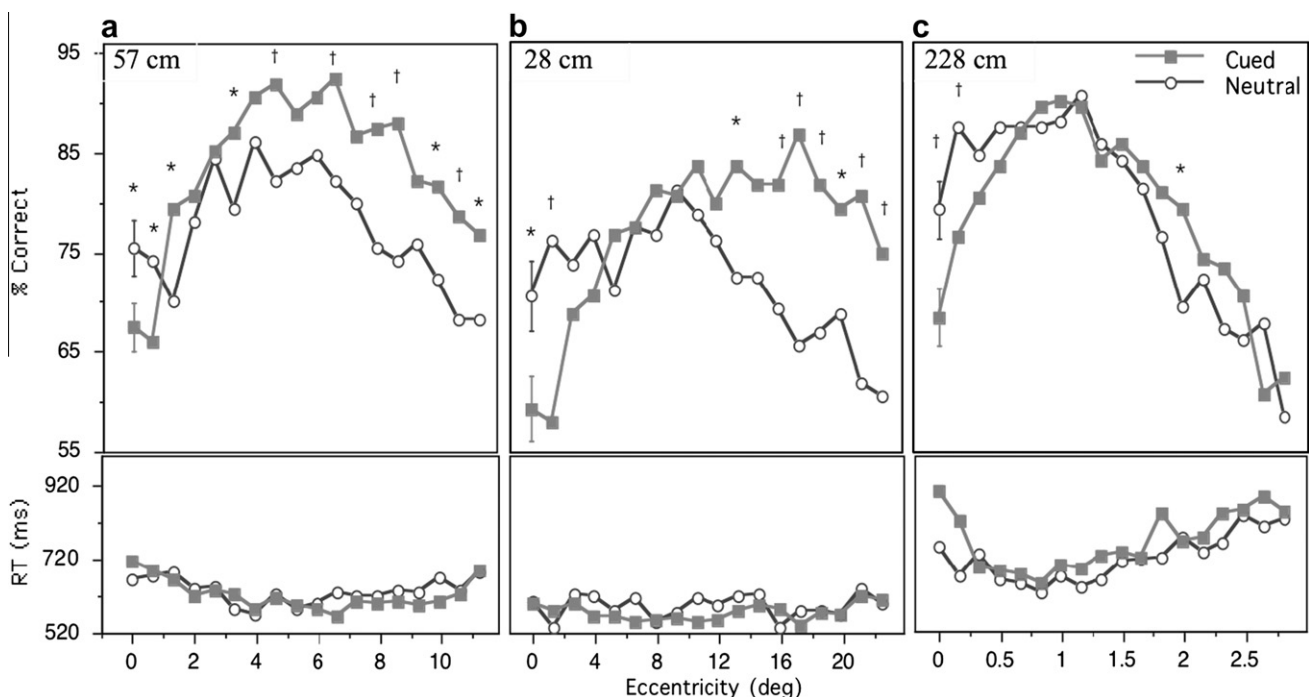


Fig. 11. Observers' performance as a function of target eccentricity and cueing condition for the three viewing distances. Viewing distance is indicated at the top of each panel. Because viewing distance varied, the eccentricity values (abscissa) differ in the three panels [Adapted from Yeshurun & Carrasco, 1998].

adapting to high spatial frequencies should eliminate the attentional impairment at central locations and diminish the benefit in the peripheral locations. The results of Carrasco, Giordano, et al.'s (2006); Carrasco, Loula, et al.'s (2006) study confirmed these predictions, indicating that the CPD is primarily due to the predominance of high spatial frequency responses, and that covert attention enhances spatial resolution by increasing sensitivity to higher spatial frequencies.

Based on the vertical meridian asymmetry for spatial resolution, i.e., higher acuity for the lower than upper vertical meridian at iso-eccentric locations (Carrasco et al., 2002), another study investigated whether the location of the performance peak differed as a function of hemifield along the vertical meridian. Performance peaked at farther eccentricities in the lower than in the upper vertical meridian, consistent with the resolution being higher in the lower meridian (Montaser-Kouhsari & Carrasco, 2009). Furthermore, the degree of enhanced resolution brought about by transient attention was constant along the vertical meridian (Talgar & Carrasco, 2002). These findings indicate that the vertical meridian asymmetry is limited by visual rather than attentional factors, and lend strong support to the hypothesis that attention enhances spatial resolution at the attended location.

To assess the level of processing at which transient attention affects spatial resolution, textures composed of narrow-band stimuli were used. Such stimuli ensure that first- or second-order filters of various specific scales will be differentially stimulated (Yeshurun & Carrasco, 2000). At the level of the visual cortex, texture segmentation theoretically involves passage of visual input through two layers of spatial linear filters, separated by a point-wise non-linearity. The first-order linear filters are assumed to perform a more local analysis of spatial frequency and orientation, and are thought to reflect the activity of simple cortical cells in area V1. The second-order linear filters are considered to be of a larger scale and assumed to perform a more global analysis on the output of the first-order filters plus the intermediate non-linearity (e.g., Bergen & Landy, 1991; Graham, Beck, & Sutter, 1992; Sutter, Beck, & Graham, 1989). In a two-interval forced-choice task, observers had to indicate the interval containing a target composed of patches with orthogonal orientation to the background elements. On the cued trials, a peripheral cue indicated the display onset and the target location. This cue always indicated the location where the target would appear but conveyed no information regarding whether the target would be present in the first or the second interval. On the remaining trials, a neutral cue indicated the display onset but not the target location; it could appear in a number of locations. For both first-order low- and high-frequency conditions, accuracy was higher for cued than neutral trials at more peripheral eccentricities, but it was lower at central locations. In contrast, the attentional effect differed as a function of the second-order spatial frequency content: attention impaired performance in a greater range of eccentricities for the low than the high frequency condition, and an attentional benefit emerged only for the high frequency condition. These findings suggest that attention operates at the second stage of filtering, possibly by reducing the size of the second-order filters (Yeshurun & Carrasco, 2000).

Again, the alternative mechanisms of attention mentioned above, such as shifts in the decisional criterion, location uncertainty reduction, or reduction of external noise (e.g., Doshier & Lu, 2000a, 2000b; Eckstein et al., 2002; Kinchla et al., 1995; Lu & Doshier, 2004; Shiu & Pashler, 1994) fail to account for the effects of transient attention on texture segmentation, because all these alternative hypotheses would predict a benefit on performance throughout all eccentricities. Only the resolution hypothesis predicts the attentional impairment of performance at central locations. Therefore, the findings of the texture segmentation studies lend strong support to the resolution hypothesis.

The texture segmentation studies described thus far show that transient attention increases spatial resolution even when it is detrimental to the task at hand. As mentioned above, improved resolution is advantageous for many everyday tasks, but in certain situations resolution enhancement is not beneficial. Would the pattern of results be the same with endogenous/sustained attention, which is considered to be more flexible and capable of adapting to task demands? A central cue was used to test whether the effect of attention effect would be similar to that found with peripheral cues (Yeshurun et al., 2008). In some of the experiments conducted during this study the texture segmentation task was the same as the one employed with transient attention in previous studies (Carrasco, Loula, et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 2008). In other experiments the texture was modified from a homogeneous to a heterogeneous background to preclude the need for a post-mask and thus ensure that performance is limited only by spatial factors (Yeshurun, Montagna & Carrasco's Fig. 5; originally introduced by Potechin & Gurnsey, 2003). The average orientation of line elements in the texture display was diagonal, the actual orientation of each line element was chosen at random from a uniform distribution of orientations. As the range of sampled orientations around the mean increases, the target patch becomes harder to detect. The central cue was composed of a digit indicating the eccentricity at which the target may appear and a line indicating the quadrant in which the target may appear.

Interestingly, unlike transient attention (Fig. 11), sustained attention improves performance in texture segmentation tasks at all eccentricities; there is no attentional impairment at foveal or perifoveal locations. The finding that performance improves at fovea is in agreement with behavioral and neurophysiological enhancements at the fovea for focused vs. distributed attention (Miniussi, Rao, & Nobre, 2002). Moreover, the improvement at all eccentricities is consistent with the idea that sustained attention is more flexible than transient attention, and suggests that sustained attention can also decrease the resolution at central locations where an increase in resolution would be detrimental (Yeshurun & Carrasco, 1998). The finding that sustained attention affects texture segmentation in a different manner than transient attention is consistent with studies demonstrating differential effects for both kinds of attention on a variety of visual tasks (Briand, 1998; Briand & Klein, 1987; Doshier & Lu, 2000a, 2000b; Giordano et al., 2009; Hein et al., 2006; Ling & Carrasco, 2006a; Ling, Liu, & Carrasco, 2009; Lu & Doshier, 1998, 2000; Yeshurun & Carrasco, 1998).

To assess the contribution of location uncertainty at the decisional level to the effect of sustained attention on texture segmentation, Yeshurun et al. (2008) compared the benefit yielded by pre-cues and post-cues. The results showed that the benefit of the central pre-cue went well beyond the mere effect of location uncertainty at the decisional stage; it improved the quality of the texture representation. The effects of sustained attention on texture segmentation could be accounted for by an attentional mechanism that is capable of either enhancement (at peripheral locations) or decrement (at central locations) of spatial resolution to optimize performance. This view of sustained attention portrays a highly adaptive mechanism that can adjust its operation on a trial-by-trial basis. Note, however, that the eccentricity-independent effect of sustained attention could also be attributed to an attentional mechanism that affects texture segmentation by improving the signal-to-noise ratio at all eccentricities through means other than resolution modification, such as the reduction of external noise at early levels of processing (e.g., Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2004), possibly via distractor suppression (e.g., Shiu & Pashler, 1994).

5.4. Attention and crowding

Crowding is the impaired recognition or identification of a stimulus that is caused by the presence of nearby distractor stimuli. Of the several proposed theories of crowding, two dominate the literature. The first of these theories centers on the idea of an “integration field,” and argues that crowding occurs due to excessive feature integration. When observers identify a target, they have to pool information from several feature detectors over some area, known as the integration field (Pelli, Palomares, & Majaj, 2004). Integration fields increase in size as one moves further into the periphery, which in turn increases the probability that the integration process will incorporate flankers into the target signal. When the integration field includes flankers, the target signal is no longer sufficient for identification (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli et al., 2004; Solomon & Morgan, 2001). Hence, crowding occurs when the visual system uses inappropriately large integration fields. Following this reasoning, crowding depends exclusively on the target-flanker distance and its ratio with eccentricity, and, correspondingly, the critical distance between target and flanker reflects the size of the integration field.

The second dominant explanation of crowding is the attention resolution theory. This theory suggests that crowding reflects the limitation of the spatial resolution of attention; observers are unable to attend to or select only the target due to the coarse spatial resolution of attentional acuity, despite visual acuity being sufficient for the target's identification. According to this theory, critical spacing remains proportional to eccentricity, but it is the minimal selection region of attention that determines the extent of crowding (e.g., Chakravarthi & Cavanagh, 2007; He, Cavanagh, & Intriligator, 1996, 1997; Intriligator & Cavanagh, 2001; Tripathy & Cavanagh, 2002). Stimulus features further determine crowding in this model, with interference assumed to occur only when flankers share the defining dimension of the target (e.g., color or spatial frequency). Thus, when two or more items are within the smallest possible selection region of attention and share a defining feature, they are selected as a group and the identification of an individual item is not possible.

There is a debate regarding the role of attention in crowding (Intriligator & Cavanagh, 2001; Pelli et al., 2004; Petrov & Popple, 2007; Reddy & VanRullen, 2007; Scolar, Kohnen, Barton, & Awh, 2007). However, some have hypothesized that if attention enhances spatial resolution, it could also reduce interference. Indeed, many studies have reported that directing attention to the target location via peripheral cues leads to better overall performance in crowded displays (Felisberti & Zanker, 2005; Huckauf & Heller, 2002; Scolar et al., 2007; Strasburger, 2005; Van der Lubbe & Keuss, 2001; Yeshurun & Rashal, 2010). However, whereas some studies have found that exogenous attention reduces the critical target – flankers distance at which the flankers no longer interfere with target identification (Yeshurun & Rashal, 2010), others have reported such an effect only at some eccentricities ($\sim 1\text{--}2^\circ$; Strasburger, 2005; $\sim 4^\circ$, Van der Lubbe & Keuss, 2001); yet others have failed altogether to find such an effect (Scolar et al., 2007). It is possible that this attentional effect on the critical distance was not found in previous studies (e.g., Huckauf & Heller, 2002; Strasburger, 2005) due to forward masking effects between the attentional cue and the target (Yeshurun & Rashal, 2010).

In Yeshurun and Rashal's (2010) study, the attentional reduction of the critical distance between target and flankers was found at three different eccentricities (3° , 5° and 9°). The critical distance was defined as the target-flanker distance at which accuracy reached 90% of the asymptotic value. Fig. 12 shows that the critical distance for the cued condition was significantly smaller than for the neutral condition. The vertical lines indicate the critical distance for cued and neutral conditions. The pattern of results was

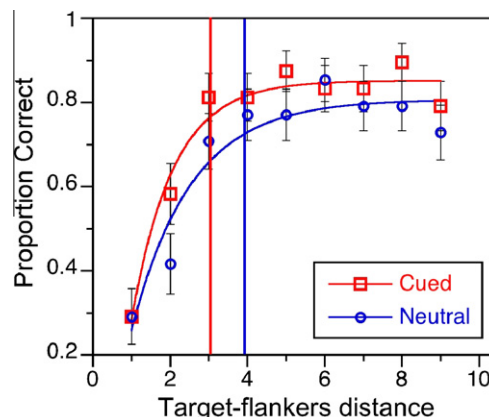


Fig. 12. Proportion correct as a function of the target-flankers distance. The vertical lines indicate the critical distance (90% of asymptotic value) for cued and neutral conditions [Adapted from Yeshurun & Rashal, 2010].

the same whether or not a backward mask was presented. Thus, the authors conclude that the decreased critical distance in the cued condition does not reflect a mere reduction in interference between the mask and the target. Whereas such a possibility is consistent with attention accelerating information accrual (Carrasco, Giordano, & McElree, 2004, 2006; Carrasco & McElree, 2001; Smith, 2000), and is plausible when there was a backward mask, it is not plausible in the absence of such a backward mask (Carrasco et al., 2002). In addition, precueing reduced the critical distance even when the peripheral cue was uninformative indicating that the reduction in critical distance brought about by attention does not depend on voluntary allocation of attention. The authors conclude that exogenous attention reduces the area over which the presence of flankers interferes with target identification, and suggest that the reduction of the critical distance may reflect a reduction in the size of the integration fields at the attended location.

5.5. Attention, spatial resolution and appearance

The studies discussed above show that spatial resolution is enhanced by exogenous/transient attention, regardless of whether this helps or hinders performance, and by endogenous/sustained attention if such an enhancement results in improved performance, but not if it would be detrimental for the task. Does attention also affect appearance of the types of stimuli used to assess spatial resolution?

Using the paradigm developed to assess the effects of attention on contrast appearance (Carrasco, Ling, et al., 2004), it has been shown that exogenous attention increases both perceived spatial frequency and Landolt square gap size (Gobell & Carrasco, 2005). In line with this study, it has been found that exogenous attention also increases the perceived size of moving visual patterns (Anton-Erxleben et al., 2007).

Similarly, a rapid serial visual presentation (RSVP) paradigm developed to assess endogenous attention on perceived contrast (Liu, Abrams, & Carrasco, 2009) was adapted to investigate the effects of endogenous attention on spatial resolution, particularly on perceived spatial frequency. Just like exogenous attention, endogenous attention increased perceived frequency (Abrams, Barbot, & Carrasco, 2010). These three studies (Abrams et al., 2010; Anton-Erxleben et al., 2007; Gobell & Carrasco, 2005) included a number of control experiments that rule out possible alternative interpretations of the findings of increased perceived spatial resolution, such as cue bias or response bias.

A previous study had reported that sustained attention did not shift the mean apparent spatial frequency, but merely reduced the

variance of the estimates (Prinzmetal et al., 1998). The discrepancy between this study and the studies reporting that attention increases perceived spatial frequency may result from methodological differences. In the Prinzmetal et al. (1998) study the location of spatial attention was not manipulated; instead, a dual-task procedure was used, and the difficulty of the primary letter identification task (simultaneous vs. sequential presentation) was varied to manipulate attentional deployment in the secondary appearance task. Furthermore, given that there was no independent measurement ensuring that attention had been deployed to the correct location, which is necessary to confirm the successful allocation of attention, the results of this study are inconclusive.

Another line of studies supporting the view that attention affects perceived attributes of stimuli has shown that cueing the target location with a peripheral cue reduces perceived line length (Tsal & Shalev, 1996). These authors proposed that the visual field consists of a grid of attentional receptive fields (ARFs), a hypothetical construct that operates as a functional receptive field, whose operation follows an all-or-none principle. Thus, when a stimulus appears within its boundaries this unit signals its entire length to the central processor (Tsal, Meiran, & Lamy, 1995). Moreover, because the ARFs are smaller at the attended than the unattended field, the attended line is systematically perceived as shorter than the unattended one (Tsal & Shalev, 1996). In a subsequent study, the authors strengthened their conclusion that smaller receptive fields mediate the effect of involuntary attention, thus increasing spatial resolution, by ruling out cue salience and spatial interactions between the cue and the target as factors that could interact with line-length judgments (Tsal, Shalev, & Zakay, 2005). Differences in the manipulation of attention and cueing parameters may explain the discrepancy with the results reported by Anton-Erxleben et al. (2007).

Both endogenous attention and exogenous attention also affect perceived position by repelling briefly presented vernier stimuli away from its focus. Consistent with the known temporal dynamics of these systems discussed in the Introduction, the effect of exogenous attention in this study was transient whereas the effect of endogenous attention was sustained. This repulsion effect illustrates that attention can distort the encoding of nearby positions and suggests an overrepresentation of space around the attended area (Suzuki & Cavanagh, 1997; see also Wardak, Deneve, & Ben Hamed, 2010).

Spatial attention is also critical for observers' ability to report accurately the relative position of two stimuli. When attention is

prevented from shifting to a target location by a concurrent task, performance on reporting relative position of two features (e.g., of two colored stimuli) falls to chance (Lee, Koch, Braun, 1999; Li, VanRullen, Koch, & Perona, 2002; Pastukhov et al., 2009). The performance drops are large and fit well with the hypothesis that attention enhances spatial resolution, as well with the enhanced resolution models and the single-unit studies on attention and resolution presented below.

Adapting the paradigm developed by Carrasco and colleagues to study effects of attention on appearance (Carrasco, Ling, et al., 2004), a recent study has shown that attention also distorts perceived shape. Depending on cue placement inside or outside the contour of an oval, the aligned dimension (height or width) was perceived longer or shorter, respectively. Visual cues alter perceived shape so that the oval contours were repelled (Fortenbaugh, Prinzmetal, & Robertson, 2011). These results are consistent with those of Anton-Erxleben et al. (2007) and with the explanation they proposed to account for effects of attention on the size of an object.

5.6. Mechanisms and models of enhanced resolution

Recent neurophysiological studies in macaques have offered insight into the potential mechanisms by which attention enhances resolution. These findings have indicated that endogenous attention shifts and shrinks RFs in areas V4, MT and LIP (Anton-Erxleben, Stephan, & Treue, 2009; Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Kusunoki & Goldberg, 2003; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). Specifically, if both a preferred and a non-preferred stimulus are present in a neuron's RF, that cell's responsiveness depends on attentional state. Attending to the preferred stimulus increases the cell's firing rate, whereas attending to the non-preferred stimulus attenuates it. This finding illustrates that attention shifts and/or constricts the RF of the cell at the attended location (as was suggested by Moran and Desimone (1985), shown by Anton-Erxleben et al. (2009) and Womelsdorf et al. (2006); and modeled by Womelsdorf, Anton-Erxleben, and Treue (2008)). Thus, attention helps overcome the apparent limit to its spatial resolution imposed by the large RF in higher areas of visual cortex.

Fig. 13a shows the receptive fields of a single MT cell while a monkey was either performing a fixation task or while attention was directed into the RF. The shrinkage of the RF is clearly visible when attention is switched into the RF. Fig. 13b plots the distribu-

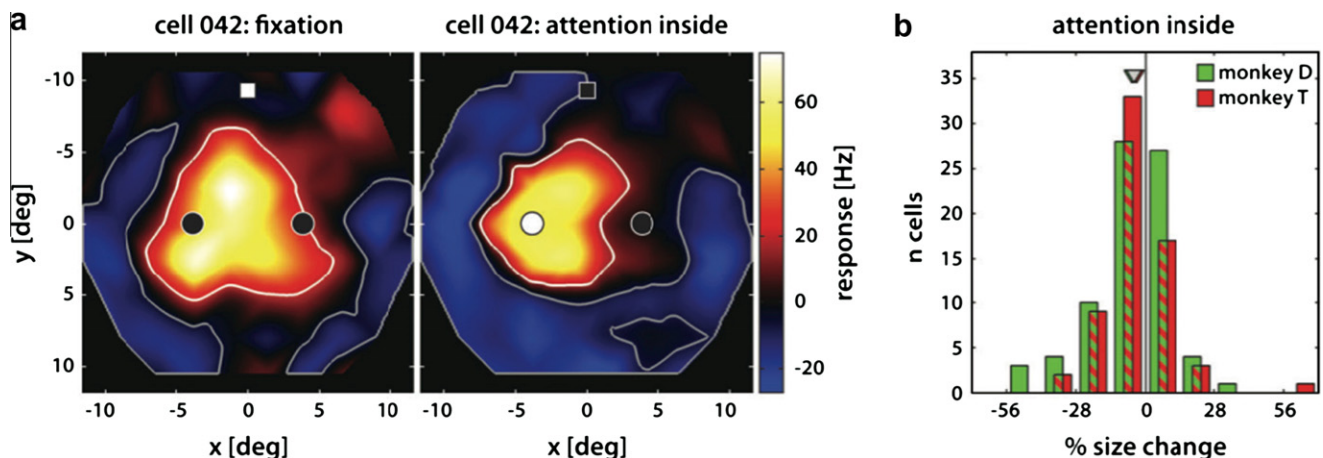


Fig. 13. Size changes of the receptive field center with attention. (a) Receptive field maps of a representative cell when a task was done at the fixation point (left graph; fixation is indicated by the white square) and when a position inside the RF was attended (right graph; the attended location is indicated by the white circle). The RF area, outlined in white, is clearly reduced with attention inside the RF. Colors represent spiking activity in Hz. (b) Plots the distribution of RF size changes (in% of the RF diameter in the fixation condition) for all 142 cases in which attention was directed into the RF [Adapted from Anton-Erxleben et al., 2009].

tions of size changes for the whole sample of cells studied. There was a significant, ~5% mean shrinkage of diameter for a group of 142 cells (from 2 monkeys). The authors ruled out the possibility that the change in RF size could be an effect of the attentional modulation of the surround. They compared the RF size changes for the group of cells with surround suppression and those without it and found no significant difference between them. The authors interpret this finding to suggest that attentional modulation of the surround and effects on RF size result from independent mechanisms (Anton-Erxleben et al., 2009). Such shifting and shrinking provide a possible neural mechanism for the enhancement of spatial resolution that has been reported in the behavioral literature. These findings suggest that voluntary attention could allow for a more fine-grained analysis of the attended area.

A recent neuroimaging study has also suggested that endogenous attention can modulate spatial resolution by both boosting signal gain, which improves the signal-to-noise ratio, and by narrowing position tuning at the neural population level, which produces more spatially distinct activity for adjacent stimuli (Fischer & Whitney, 2009). The spatial spread of the fMRI BOLD response from V1 through V4 produced by adjacent stimuli showed less overlap when observers were attending at stimulus locations vs. attending to fixation, regardless of the increased peak response associated with attention. These results indicate both boosting signal gain and narrowing position tuning at the neural population level. Such a dual mechanism could allow the visual system to effectively maximize the flexibility and dynamic range of spatial resolution. The authors mention their findings are consistent with a computational model of attentional gain fields, which postulates that attention can modulate spatial resolution by adjusting position tuning at the neural population level, even if signal gain is held constant (Salinas & Abbott, 1997).

Reducing receptive field size, however, would not necessarily lead to the percept of higher spatial frequency, and it is not the only way to enhance spatial resolution. Attention could also enhance spatial resolution by reweighting the population response in favor of higher spatial frequency receptors (Balz & Hock, 1997; Carrasco, Loula, et al., 2006). This sort of mechanism will produce a particular pattern of differential activity in the population of distinct receptors sensitive to spatial frequency. By shifting sensitivity to channels tuned to higher spatial frequencies, attention causes an activity pattern similar to that which would be observed in response to a stimulus of higher spatial frequency in the absence of attention (Balz & Hock, 1997; Carrasco, Loula, et al., 2006; Yeshurun & Carrasco, 2000). Consequently, deploying attention could give rise to the phenomenological experience of a stimulus of higher spatial frequency (Abrams et al., 2010; Gobell & Carrasco, 2005).

Along similar lines, Tsal and colleagues have suggested that stimuli at attended locations are analyzed with a finer grain than stimuli at unattended locations. They propose that an attentional receptive field (ARF) has no resolution within its area, so its size determines the resolution with which a scene can be analyzed. Changes in spatial resolution and localization judgments with attention have been used to argue that such ARFs exist (Shalev & Tsal, 2002; Tsal & Bareket, 1999, 2005; Tsal & Shalev, 1996). Fig. 14 illustrates how an ARF could interact with a broken line stimulus in such a way that would predict a decrease in gap-thresholds when the stimulus is attended (Shalev & Tsal, 2002).

Psychophysical and electrophysiological studies of attention have inspired models that explicitly assign visual attention a role in object recognition. For instance, Deco and colleagues (Deco & Schurmann, 2000; Deneve, Latham, & Pouget, 1999; Shalev & Tsal, 2002) extended the standard interpretation of selective attention as a spotlight that gates a local region of the visual field to a higher level of processing, while inhibiting the unattended regions. They

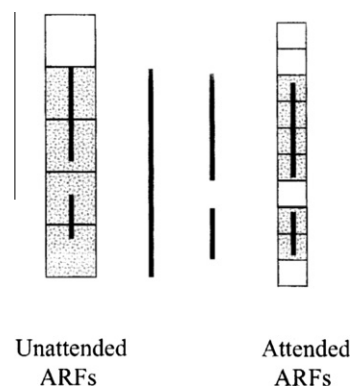


Fig. 14. Predictions of the ARF model. A broken line may be perceived as solid when unattended (large ARFs—left panel), but as broken when attended (small ARFs—right panel). [Reprinted from Shalev & Tsal, 2002].

assumed that attention also enhances the spatial resolution within the spotlight for further processing. An extension of this model enables the competitive dynamics to operate on different spatial-frequency channels in parallel to search through hierarchical patterns (Deco & Heinke, 2007). Other computational models also postulate that interactions among visual filters result in both increased gain and sharpened tuning (Lee, Itti et al., 1999; Salinas & Abbott, 1997).

A question related to how attention enhances spatial resolution deals with the spatial scale over which attention exerts its effects. Studies with humans have provided direct neurophysiological evidence for spatial suppression surrounding the focus of attention in several areas of visual cortex (Hopf et al., 2006; Muller & Kleinschmidt, 2004). Based on their finding that while observers attended to a location, responses in early visual areas were higher for stimuli farther from the attended location than relatively close to it, Muller and Kleinschmidt (2004) suggested a Mexican hat-like distribution of attentional modulation within early visual cortex. Although there is agreement on the crucial role of the frontoparietal network in attentional control (e.g., Green & McDonald, 2008; Hopfinger et al., 2000; Lauritzen, D'Esposito, Heeger, & Silver, 2009), it is possible that the surround inhibition may be partly due to long range horizontal connections and lateral inhibition in early visual cortex itself (Angelucci et al., 2002) a mechanism that facilitates contrast enhancement (Muller, Mollenhauer, Rosler, & Kleinschmidt, 2005).

This hypothesis of the Mexican hat-like distribution of attentional modulation was supported by a study utilizing magnetoencephalographic (MEG) recording. To investigate the spatial profile of cortical activity surrounding the focus of attention, observers were presented with a target surrounded by distractors. Observers were asked to attend to a color pop-out target while probe stimuli (task-irrelevant luminance increments) appeared at varying distances from the target. High-density MEG recordings revealed that the profile of responses to these probes was shaped like a "Mexican hat"; i.e., the electromagnetic response to the probe was enhanced when the probe was presented at the location of the target, but was suppressed in a narrow zone surrounding the target and then recovered at more distant locations (Hopf et al., 2006). Fig. 15a shows that the waveform was largest when the target location was probed (PD0), smallest when the location adjacent to the target was probed (PD1), and intermediate when the non-adjacent locations to the target were probed (PD2–PD4). This pattern of responses indicates an enhancement at the target location and suppression at the adjacent location, compared with the more distant locations. This demonstrates that a narrow zone of attenuated cortical responsiveness surrounds the attended item. Fig. 15b shows the magnitude of the average ERMF effect, using the difference between each observer's individual efflux and influx maxima. Again, attending to the location adjacent to the probe's location led

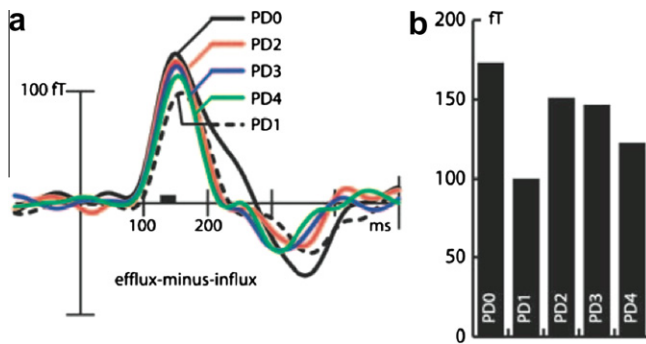


Fig. 15. (a) Time course of the event-related magnetic field (ERMF, difference between corresponding efflux- and influx-field maxima) response for each probe distance; PD0: location was probed; PD1: location adjacent to the target was probed; PD2-PD4: non-adjacent locations to the target were probed (b) Mean size of the probe-related response between 130 and 150 ms, collapsed across corresponding probe-distance conditions. The size of the effect represents the average of the ERMF difference between the observers' individual field maxima and minima. [Adapted from Hopf et al., 2006].

to a smaller probe response than attending to the probe's location or attending one location farther from the probe.

Consistent with other psychophysical studies (Bahcall & Kowler, 1999; Cave & Zimmerman, 1997; Cutzu & Tsotsos, 2003; Muller et al., 2005), the center-surround profile suggests that attending to a stimulus places a ring of inhibition around it. This spatial structure would be optimal to attenuate the most harmful noise during target identification, such as the one exerted by the flankers crowding the target. These findings are consistent with the selective tuning model proposed by Tsotsos and colleagues (Tsotsos, Culhane, & Cutzu, 2001; Tsotsos et al., 1995).

According to the selective tuning model proposed by Tsotsos and colleagues (Tsotsos et al., 1995, 2001) attention optimizes the search procedure by selectively tuning the visual processing network. They propose an architecture of attentional selection that explicitly predicts a suppressive zone surrounding the focus of attention. This model provides an account of attentional selection in the visual cortex based on hierarchical winner-take-all (WTA) processes that propagate in top-down directions through visual cortex. Connections representing input from irrelevant locations are pruned away from level to level in a pyramid of visual computations, yielding a pass zone of enhanced activity for connections representing the attended input. Connections immediately surrounding the pass zone become suppressed, leading to a profile of cortical responsiveness with an excitatory center and an inhibitory surround.

5.7. Conclusion

Psychophysical and neuroimaging studies with humans and electrophysiological studies with monkeys have lent support to the resolution hypothesis, which states that attention can enhance spatial resolution at the attended location. Hence, the observer can resolve finer details at the attended locations. Computational models have implemented possible architectures via increased gain and sharpened tuning, which could be responsible for the enhanced resolution brought about by covert attention. Attention helps overcome limits of spatial resolution imposed by the large RF in higher areas of visual cortex.

6. Feature-based attention

Most studies of attention have examined the effects of selectively attending at particular locations in the visual field. However, attention can also be selectively deployed to visual features, such

as particular orientations, colors or directions of motion, regardless of their locations (e.g., Boynton, 2009; Haenny, Maunsell, & Schiller, 1988; Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Treue & Martinez-Trujillo, 1999; Yantis, 2000). Feature-based attention (FBA) enhances particular features within a dimension at the expense of unattended or behaviorally irrelevant features. Thus, it is an important component for a visual system that needs to devote limited processing resources on the most relevant sensory inputs regardless of where in the visual field they are located. FBA enhances the representation of image components that share a particular feature throughout the visual field. FBA is important because we often know a defining feature of an object without knowing its location – e.g., the Perception textbook is blue and it is somewhere on the bookshelf; my friend is somewhere in the cafeteria and he often wears an orange jacket; cabs in New York are yellow.

Psychophysical, electrophysiological and neuroimaging studies have demonstrated that attention can select feature values within a dimension (e.g., vertical vs. horizontal orientation, upward vs. downward motion; Baldassi & Verghese, 2005; Haenny et al., 1988; Lankheet & Verstraten, 1995; Ling, Liu, & Carrasco, 2009; Liu, Larsson, et al., 2007; Liu, Stevens, et al., 2007; Martinez-Trujillo & Treue, 2004; Maunsell, Sclar, Nealey, & DePriest, 1991; Muller et al., 2006; Saenz, Buracas, & Boynton, 2003; Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999). Some authors have also used the term FBA to refer to attention to one feature dimension or another (e.g., motion vs. orientation), and several neuroimaging studies show that attending to different feature dimensions (e.g., motion, color) modulates activity in cortical areas specialized for processing those dimensions (e.g., MT+, V4/V8) (e.g., Chawla, Rees, & Friston, 1999; Liu, Slotnick, Serences, & Yantis, 2003; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Wojciulik, Kanwisher, & Driver, 1998). In this Section 1 will focus on the former case, i.e., the selection of features within a dimension, and specify otherwise when I refer to selective attention to feature dimensions.

Using a variety of approaches, it has also been confirmed that FBA operates both within (e.g., Ling et al., 2009; Liu, Larsson, et al., 2007; Liu, Stevens et al., 2007; Muller et al., 2006) and outside the spatial locus of attention, which enables the effects of FBA to spread across space. In fact, psychophysical (Boynton, Ciaramitaro, & Arman, 2006; Felisberti & Zanker, 2005; Liu & Mance, 2011; Rossi & Paradiso, 1995; Saenz et al., 2003) and neurophysiological (Hayden & Gallant, 2005; McAdams & Maunsell, 2000; Motter, 1994a; Saenz, Buracas, & Boynton, 2002; Seidemann & Newsome, 1999; Treue, 2001; Treue & Martinez-Trujillo, 1999) studies reveal that FBA is deployed simultaneously throughout the visual field, independent of the locus of spatial attention. It therefore modulates visual processing even in locations that are irrelevant to the observer's current task (e.g., Arman, Ciaramitaro, & Boynton, 2006; Serences & Yantis, 2007; Zhang & Luck, 2009).

In this Section 1 first review a number of psychophysical and neurophysiological studies that illustrate the role of FBA in visual search. Then I explain how FBA affects processing at the attended location and outside the attended location, and how FBA affects spatial interactions. I end this section by summarizing some of the contributions of computational models of FBA.

6.1. FBA and visual search

The selective representation afforded by FBA is particularly useful in visual search; i.e., when searching for a target stimulus that has known features but whose location amidst distracters with different features is unknown. Visual search is a popular paradigm, which, starting with the research of Treisman and Gelade (1980), has been used to study our ability to detect, discriminate or localize a target among distracters [see Nakayama & Martini, 2011

review on visual search]. In a 'feature search' (e.g., an observer is instructed to detect a red tilted target amongst red vertical distractors), it would be useful for the observer to grant priority in processing tilted features, or to enhance their representation. In the case of conjunction search, an observer may be instructed to detect a red tilted target, or to discriminate its tilt (left vs. right), amidst blue tilted and red vertical distractors. In this case, it would be useful for the observer to prioritize the processing of red and/or tilted items. Indeed, some authors have proposed that an early stage of the search process is to select the subset of stimuli that contain at least one of the target's features (e.g., Egeth, Virzi, & Garbart, 1984; McElree & Carrasco, 1999; Wolfe & Horowitz, 2004). Support for this proposal comes from studies in which cueing relevant features (either size or color) aided performance in visual search tasks, under some conditions, by prioritizing processing of those stimuli and guiding spatial attention to them before others (Moore & Egeth, 1998; Shih & Sperling, 1996). Although these two studies conclude that FBA does not enhance the signal, other behavioral and neurophysiological studies have provided evidence of enhancement. Also relevant to the role of FBA in visual search is the finding that the effect of feature guidance increases when a selection bias can build over successive trials because the target feature remains the same from trial to trial (Carrasco, Ponte, Rechea, & Sampedro, 1998; Muller, Heller, & Ziegler, 1995; Wolfe, Butcher, Lee, & Hyle, 2003; Wolfe & Horowitz, 2004).

Single-unit recordings have provided direct evidence for feature selection during visual search: the responses of individual neurons are enhanced when attention is deployed to the feature value they are selective for (e.g., vertical orientation, upward motion direction or red color). Many studies have examined area V4, which is critically involved in intermediate stages of visual processing, and implicated in figure-ground segmentation, grouping, form recognition, shape perception, visual search and color (Gallant, Shoup, & Mazer, 2000; Pasupathy & Connor, 1999; Schiller, 1995; Schiller & Lee, 1991). Dynamic tuning shifts in V4 play a critical role in these processes. For instance, an early study suggested that FBA might change color selectivity, resulting in increased sensitivity to behaviorally relevant features (Motter, 1994a, 1994b). Monkeys viewed arrays of mixed stimuli and had to attend to a subset of stimuli with a color or luminance that matched a cue stimulus. V4 responses were stronger when the stimulus in their receptive fields matched the cue. Note that in this task both FBA and spatial attention may have played a role because it is possible that changes in neuronal activity reflected a mechanism that targeted spatial locations identified by the animal as behaviorally relevant based on color or luminance.

In a subsequent study, monkeys searched for a target defined by its color or shape (or a combination of both) among many objects of various colors and shapes. The response of V4 neurons was stronger to objects in their receptive fields that had the neurons' preferred features when the objects were the search targets than when they were distractors (Bichot, Rossi, & Desimone, 2005). Similar results were obtained in area MT when monkeys searched for targets defined by conjunctions of color and motion direction (Buracas & Albright, 2009). Neurons in the frontal eye fields also responded most strongly to targets in conjunction search, and more strongly to distractors that shared one target feature than to distractors that shared none (Bichot & Schall, 1999).

Neurophysiological studies have also shown that shifting attention between different feature *dimensions* (e.g., color or orientation) modulates activity in cortical areas specialized for processing those dimensions. For instance, in one study using delayed match to sample the responses of most V4 neurons were affected by whether the monkey was attending to the orientation or color of a stimulus distant from the receptive field (McAdams & Maunsell, 2000). This result supports the idea that FBA changes

activity throughout the visual-field representation in a useful way for visual search.

6.2. Feature-based effects at attended locations

Notwithstanding advances in electrophysiological studies of visual search, this paradigm is not ideal to assess whether and how attention affects sensory representations. In most human studies of visual search the role of attention has been inferred rather than directly manipulated, and only a few studies have taken into account basic visual and stimulus factors (e.g., Carrasco & Frieder, 1997; Carrasco et al., 1995; Carrasco, McLean, et al., 1998; Geisler & Chou, 1995; Palmer, 1995; Palmer et al., 2000; Vergheze, 2001; Vergheze & Nakayama, 1994). Furthermore, search tasks always involve spatial attention (either covert or overt) thus complicating the assessment of FBA per se in these tasks.

Because a visual stimulus always occupies a certain spatial location, it is important to control spatial selection when studying feature-based selection. Thus, studies of FBA generally use compound stimuli that contain multiple features superimposed over the same spatial location, and observers are required to attend to one of those features. This section reviews studies that investigate FBA at the attended location, i.e. at the local level. The next section reviews the consequences of these manipulations, whereby feature-related activity spreads to locations other than the attended one.

6.2.1. Behavioral studies

6.2.1.1. Adaptation aftereffects. The effects of selectively attending to a relevant feature presented simultaneously with other features have been investigated in behavioral studies of aftereffects following selective adaptation. This strategy allows researchers to address whether attending to a feature enhances selective responses to that feature. Selective adaptation is defined as decreased sensitivity following prolonged exposure to a stimulus, and similar stimuli, resulting in aftereffects (Carrasco, Figueroa, & Willen, 1986; Kohn, 2007; Movshon & Blakemore, 1973; Ohzawa, Sclar, & Freeman, 1982; Pantle & Sekuler, 1968). Neurophysiologically, this reduced sensitivity has been attributed to a contrast gain control mechanism, whereby adaptation decreases the gain of detectors tuned to the adapter stimulus (Ohzawa et al., 1982). Neural adaptation tends to increase with stronger neuronal response to the adapting stimulus (Gardner et al., 2005; Sclar et al., 1989). Correspondingly, the magnitude of adaptation increases with the intensity of the adapter stimulus. For instance, adapting to higher contrast gratings results in greater threshold elevation (Langley, 2002) and longer recovery time (Greenlee, Georgeson, Magnussen, & Harris, 1991).

When observers are asked to selectively attend to one of two spatially superimposed dot fields that differ in motion direction, the contribution of the attended field to the resulting motion aftereffect is stronger than if it were not attended (Lankheet & Verstraten, 1995). Another study dealing with motion aftereffects showed that when observers adapt continuously to motion in a particular direction, over which brief motion pulses of another direction are superimposed, the direction of the subsequent motion after-effect changes if observers are required to monitor for the pulses (Alais & Blake, 1999). Depending on which of the 8 'attentional' motion directions was combined with the adapting motion, small systematic deviations in the direction of the motion aftereffect should follow a sinusoidal pattern oscillating around 180°. The authors hypothesized that if attention boosted the neuronal response to an attended motion, then active conditions would yield a larger-amplitude sinusoid than passive conditions. Fig. 16 shows the direction and magnitude of the motion aftereffect plotted as a function of the direction of attended motion. As predicted, attention enhanced the deviations in the motion aftereffect in the

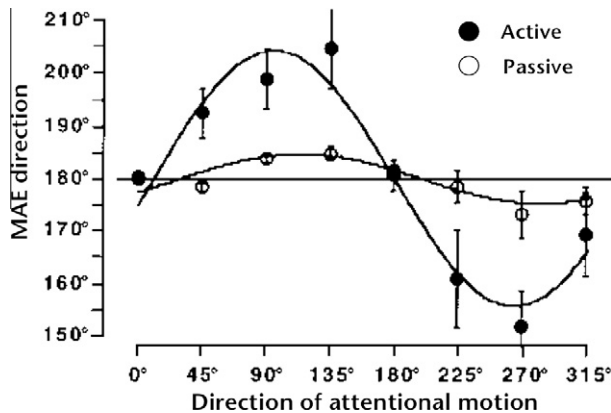


Fig. 16. Motion aftereffect directions obtained from pairing eight attentional motion directions with the adapting motion. Data from active (attended) and passive trials are plotted separately. The amplitudes of the best-fitting sinusoids are 24.27° and 4.63° , respectively. Data points show the averages for four observers; error bars indicate ± 1 SEM [Adapted from Alais & Blake, 1999].

direction opposite to the adapting motion. Taken together, these results imply that FBA selectively increases responses to the attended direction. Similar results have been shown for superimposed gratings of different orientations. Selectively attending to a given color or orientation increases the extent of the corresponding aftereffects (Liu, Larsson, et al., 2007; Spivey & Spirn, 2000). These studies suggest that attending to a feature can result in a stronger response of a neural population tuned to that feature.

6.2.1.2. Perceptual performance. Many psychophysical studies have demonstrated that FBA improves detection and enhances performance. Early studies showing that foreknowledge about spatial frequency (Davis & Graham, 1981; Davis et al., 1983) and direction of motion (Ball & Sekuler, 1981) enhance task performance support the notion that attention reduces uncertainty about stimulus features. Later work has shown that feature-based cues can affect low-level visual sensitivity. For instance, attending selectively to dots moving in a particular direction improves detection of speed increments, relative to when observers simultaneously monitor the superimposed dots moving in the opposite direction (Liu, Stevens et al., 2007). In addition, advance knowledge of a stimulus's feature improves perception even in the absence of simultaneous distractors. For example, a critical-band masking paradigm has shown that precueing the orientation of a stimulus improves its detection (Baldassi & Verghese, 2005), and an equivalent-noise paradigm has revealed that precueing the approximate direction of moving dots improves direction discrimination (Ling et al., 2009). These studies are consistent with the hypothesis that attention boosts sensitivity in the psychophysical channels that best represent the target stimulus, and indicate differences in the way spatial attention and FBA affect orientation-tuning curves (see below, Section 6.3.2, comparing effects and mechanisms of spatial attention and FBA).

6.2.2. Neurophysiological studies

Measurements of activity in visual cortex have provided the neural correlates of FBA. FBA selectively modifies the neural representations of elements within visual scenes that match the currently attended feature. An early study of FBA in area V4 illustrates this modification. Monkeys were trained to view a rapid sequence of gratings and to respond when they saw a grating that matched the orientation of a cue grating. The responses of most recorded neurons varied depending on which orientation the animal

was looking for (Haenny et al., 1988; see also Hayden & Gallant, 2005; Maunsell et al., 1991).

The neural signatures of FBA have also been investigated using neuroimaging techniques. Early PET and fMRI (Beauchamp, Cox, & DeYoe, 1997; Shulman et al., 1999; Watanabe et al., 1998) studies indicate that FBA modulates activity in several visual areas (e.g., V1 and MT+/V5) in response to expectations regarding the task-relevant feature dimension. Paying attention to stimulus features across the entire visual field enhances neural activity in the cortical areas specialized to process those features (Liu et al., 2003; O'Craven et al., 1997; Schoenfeld et al., 2007). For example, a study combining fMRI and neuromagnetic recordings found that a moving stimulus elicited a larger neural response in the motion-sensitive area MT when movement was relevant than when color was relevant, whereas a color-change stimulus produced greater activity in the color-selective area V4/V8 when color was attended than when movement was relevant (Schoenfeld et al., 2007).

Neuroimaging studies have also shown FBA modulation of targets that are spatially coextensive with distractors of different feature values. For instance, attending to one color in a display containing intermingled colored moving dots increases the amplitude of SSVEPs to that color compared to when that color is not attended (Muller et al., 2006). Studies using voxel-based multivariate pattern classification overcome the spatial resolution limitations of fMRI, thus enabling the assessment of featural attentional effects in specific retinotopic visual areas. When participants attended to one of two superimposed grid patterns, a classifier based on voxels from V1 to V4 could reliably predict the attended orientation (Kamitani & Tong, 2005). Attention increases the BOLD response in voxels tuned for the attended orientation (or near it), relative to voxels tuned for the unattended orientation. Consistent with the feature-similarity gain model, this pattern of responses suggests that attending to one orientation biased the population activity toward the attended orientation, the behaviorally relevant stimuli, at the expense of behaviorally irrelevant stimuli (see also Serences & Boynton, 2007; Serences, Saproo, Scolari, Ho, & Muftuler, 2009).

Another useful technique to investigate FBA across multiple areas in human visual cortex is fMRI response adaptation. Measurements of adaptation with fMRI allow scientists to make inferences about neural activity at the subpopulation level beyond the resolution of a single image voxel (Grill-Spector & Malach, 2001; Krekelberg, Boynton, & van Wezel, 2006). The fMRI adaptation technique was used in combination with psychophysics to investigate the selective power, perceptual consequences and neural basis of FBA at the location of spatial attention (Liu, Stevens et al., 2007). Observers were adapted to two super-imposed oblique gratings while attending to one grating only. The magnitude of attention-induced orientation-selective adaptation was measured psychophysically and physiologically, by the behavioral tilt aftereffect and fMRI response adaptation, respectively. Selective attention strengthened both the tilt aftereffect and orientation-specific BOLD neural adaptation in several visual areas (from V1 to V7). The finding that the attention adaptation effect was constant from V1 to V7 may reflect a passive feed-forward relay of attentional effects in V1. This scenario is consistent with the finding of a constant level of adaptation across visual areas, which has been interpreted as an adaptation effect in V1 propagating across extrastriate areas without additional adaptation occurring in those areas (Larsson, Landy, & Heeger, 2006). Furthermore, the adaptation technique enables a quantitative link between neural responses (measured by fMRI) and behavior. The magnitude of the tilt aftereffect significantly correlated with the BOLD response to the attended orientation in V1, the earliest site of orientation coding. This indicates that FBA strengthened the neural encoding of the attended orientation component and consequently affected the tilt aftereffect. These results

show that FBA can selectively increase the response of neuronal subpopulations that prefer the attended feature, even when the attended and unattended features are coded in the same visual areas and share the same retinotopic location.

A steady-state visual evoked potentials (SSVEP) study of visual search provided evidence in humans that the features of an attended stimulus are selected and facilitated in a parallel, additive fashion. Observers viewed a display containing red bars and blue bars, with half of the bars of each color oriented horizontally and half vertically. All bars were randomly intermixed and moving unpredictably. Observers attended to one of these four types of bars, each of which flickered at a different rate and thus elicited its own frequency-tagged SSVEP. SSVEP amplitudes were largest in response to the bars with both the attended color and orientation, intermediate to the bars having one of the two attended features, and smallest to the bars having none of the attended features. Moreover, the SSVEP amplitude to the attended conjunction stimulus was equal to the sum of the amplitudes for the individual feature enhancements (Andersen, Hillyard, & Muller, 2008). This finding is consistent with the parallel guidance mechanism proposed by “guided search” theories (Wolfe, O’Neill, & Bennett, 1998) to account for the rapid identification of conjunction targets.

A recent SSVEP study, focusing on temporal dynamics, has also shown results consistent with the idea of attention as a limited resource mechanism. Observers viewed superimposed patches of red and blue dots and monitored the set of dots of a cued color to detect brief intervals of coherent motion while ignoring such intervals in the unattended set of dots. The SSVEP signals showed enhancement of the attended and a suppression of the unattended dots. However, the tradeoff did not occur simultaneously; the time course of the transient facilitation for the attended features was earlier than that for the sustained suppression of the unattended features during cued shifts of feature-selective attention (Andersen & Muller, 2010). Moreover, observers’ performance correlated with a measure of attentional modulation of the SSVEP signal (the facilitation of the attended minus the suppression of the unattended conditions).

6.3. Feature-based attention outside the attended location

FBA has the remarkable property that its effects are not constrained to the location of the stimuli that are voluntarily attended; they spread across space. In this Section 1 review first neurophysi-

ological investigations of this phenomenon and then the psychophysical studies, because findings from the former have inspired the latter. For example, FBA can enhance the neural responses to a particular color regardless of the locations where stimuli with that color appear in the scene.

6.3.1. Neurophysiological studies

The seminal demonstration of the global spread of FBA stems from the research of Treue and Martinez-Trujillo (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999) in the dorsal pathway, specifically in MT neurons. MT is important in the processing of motion, a fundamental visual dimension mediated by directionally tuned cortical neurons (Britten, Shadlen, Newsome, & Movshon, 1993; Movshon & Newsome, 1996; Rust, Mante, Simoncelli, & Movshon, 2006). Treue and Martinez-Trujillo trained macaque monkeys to detect speed and direction changes in a field of moving dots presented on one side of fixation while a second field of moving dots was presented in the opposite hemifield (Fig. 17a). Both patches always moved in the same direction but different directions of motion were presented on different trials. On some trials (top), an attention cue instructed the animal to detect a change in the motion of the patch outside the receptive field, which had either a preferred or null direction. On other trials (bottom) the attention of the animal was directed to the fixation spot to detect a change in luminance. Recording the activity of MT neurons with receptive fields covering the irrelevant stimulus revealed that firing rates were modulated by the direction of the attended stimulus. Neurons responding to the irrelevant stimulus that preferred the direction of the attended stimulus increased their firing rate whereas those that preferred the opposite direction decreased their firing rate (Fig. 17b). Thus, attention to a particular direction of motion does not increase responses across all neurons. Rather, it has a push–pull effect that increases responses only for neurons that prefer motion close to the attended direction (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999).

Treue and Martinez-Trujillo developed the ‘feature-similarity gain model’ to explain these and other previous findings. Top-down attentional modulations change the gain of individual sensory neurons in a multiplicative fashion, to a degree that is proportional to the similarity between the currently attended feature value and the cell’s tuning preference. Responses of cells tuned to similar features are enhanced, but responses of cells that prefer

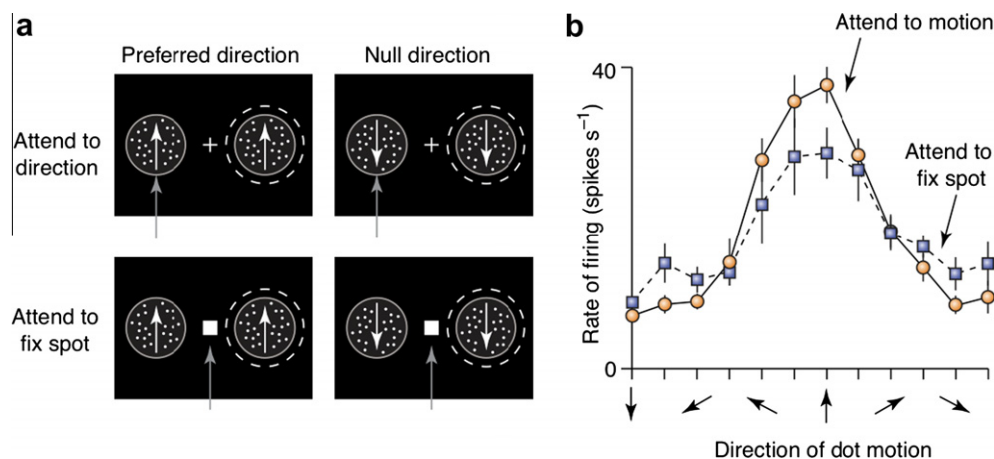


Fig. 17. Feature-based attention in MT. (a) Schematic representation of tasks used to assess the effects of attention to direction of motion. Two patches of random dots were presented, one within the RF of the neurons being record (broken white line). On some trials (top), a cue at the beginning instructed the animal to pay attention to the motion of the patch outside the receptive field to detect a change in that motion. On other trials (bottom) the attention of the animal (gray arrows) was directed to the fixation spot to detect a change in luminance. (b) Responses of a representative MT neuron to different directions of motion during the two attentional conditions. Attention to the preferred direction of motion increased the response of the neuron, but attention to the null direction of motion decreased its response. [Reproduced from Martinez-Trujillo & Treue, 2004, as printed in Maunsell & Treue, 2006].

very different features are suppressed. At the level of the neuronal population, these gain changes create a non-multiplicative modulation of the selectivity of the population response (Martinez-Trujillo & Treue, 2004). The outcome is that stimuli sharing features similar to those of the target are represented more strongly in visual cortex.

Maunsell and Treue (2006) have interpreted the finding that MT modulation was similar in size to that seen in V4 (McAdams & Maunsell, 2000) to suggest that the same FBA system acts in both the dorsal and ventral visual pathways. Note that although the magnitude of the effect is suggestive, it is not sufficient in order to infer the FBA is a unitary mechanism. Regardless of whether or not FBA is a unitary mechanism, the feature similarity gain model has provided a useful framework to explain all the findings from FBA electrophysiological studies, and has inspired neuroimaging and psychophysical studies of FBA.

A different take on the global spread of FBA is suggested by a study in which macaque monkeys were trained to track one of two superimposed fields of rotating and translating dots (Wannig, Rodriguez, & Freiwald, 2007). The monkeys were cued by the color of a fixation spot to attend to one of two transparent random-dot surfaces, one red and one green, which occupied the same region of space. Recording from single-units in area MT showed enhanced responses of neurons stimulated by the target field compared to those stimulated by the distractor field. Note that a rotating field stimulates neurons of different directional preference at each of its locations. Surface-based effects of attention were still present, although less pronounced, without differential surface coloring. These results show that attention can select surface representations and modulate visual processing in area MT. A parsimonious account is that the response enhancement in this case pertained not to a single attended feature (direction of motion) but to an attended “surface” comprising a range of different features. Thus, the global spread of FBA may actually be guided by surface segmentation (Treue & Katzner, 2007).

Neuroimaging studies requiring participants to attend to specific features of stimuli have revealed patterns of neural activity in human visual cortex that parallel the electrophysiological evidence for the spread of FBA to task-irrelevant locations. Feature-specific modulation has even been observed at spatial locations where no stimuli were present (McMains, Fehd, Emmanouil, & Kastner, 2007; Serences & Yantis, 2007). These studies suggest that FBA is applied across the visual field.

Studies comparing two conditions in which the physical stimulus is unchanged and only the attended feature value varies have yielded results consistent with the feature-similarity gain model. For instance, in one experiment human observers were cued to selectively attend to one of two superimposed dot fields moving in opposite directions, and to detect changes in its speed while ignoring a single group of moving dots presented in the opposite hemifield. BOLD responses in many visual areas (V1, V2, V3, V3A and MT+) to these ignored dots were higher when their motion direction matched that of the attended dots than when it matched the direction of the unattended moving dots (Saenz et al., 2002). A similar effect emerged within the color dimension; the fMRI response to an unattended stimulus was modulated by the color of a subset of stationary dots that observers attended to in the opposite visual hemifield.

In a subsequent study, two moving stimuli were placed to the left and right of a fixation point. Each stimulus was created by the superposition of two random dot patterns, so that observers perceived two surfaces sliding transparently across each other. When observers allocated attention to one of the two superimposed surfaces within one compound stimulus, a pattern classification algorithm could recover the attended motion direction for cortical regions representing the attended and the unattended

locations (Fig. 18a). Remarkably, the attended motion direction could be recovered in the unattended hemifield (Fig. 18b) even during trials when the unattended stimulus was not presented (Fig. 18c; Serences & Boynton, 2007). These results show that attending to a particular direction in one location of the visual field specifically modulates direction-selective units across the visual field, and that in addition to altering the stimulus representation, FBA biases baseline activity levels across the visual field.

Attentional modulations in the absence of direct visual stimulation might be mediated by a purely endogenous (or top-down) gain control mechanism, similar to the baseline modulation in neural activity induced by spatial attention (e.g., Chawla et al., 1999; Hayden & Gallant, 2005; Kastner et al., 1999; Luck, Girelli, McDermott, & Ford, 1997; McMains et al., 2007; Ress et al., 2000). Baseline shifts have been observed during the time elapsed between a cue instructing the observer where or what to attend and the stimulus onset. However, given that the baseline shift in the above study emerged while observers were monitoring a stimulus on the other side of the visual field, the FBA spread could result from hard-wired cross-hemispheric connections between similarly tuned neurons in corresponding visual areas (Serences & Boynton, 2007).

In addition to modulating the attended feature outside the focus of attention, FBA also affects the processing of task-irrelevant features that are associated with the attended feature. This was demonstrated by a study in which observers were asked to attend to dots of one color superimposed with dots of another color, all moving randomly. Simultaneously, in the other hemifield there were two groups of dots; those of one color were flickering while those of the other color were moving coherently. When the coherently moving dots had the same color as the observers attended in the other hemifield, their associated BOLD response in MT was higher than when they had the ignored color (Sohn, Chong, Papathomas, & Vidnyanszky, 2005).

The global spread of FBA has also been shown with other neuroimaging techniques. For instance, recordings of event-related potentials (ERP) have shown that FBA modulates feed-forward visual processing, as reflected by the P1 wave, when there is simultaneous competition between attended and ignored feature values. Observers were instructed to attend to dots of a given color (red), which were intermixed with dots of another color (green), and to detect occasional luminance decrements in the attended subgroup. Color-based attention altered the feed-forward flow of information within 100 ms of stimulus onset, even for stimuli presented at spatially unattended locations (Zhang & Luck, 2009).

6.3.2. Behavioral studies

6.3.2.1. Adaptation and other aftereffects. Recall that adaptation studies using superimposed features have provided a useful tool to study FBA at the attended location (Alais & Blake, 1999; Lankheet & Verstraten, 1995; Liu, Larsson, et al., 2007; Spivey & Spirn, 2000). Other studies have extended those results by measuring aftereffects following adaptation to an additional ignored stimulus in the other hemifield and provided further evidence that FBA spreads across locations.

A similar paradigm to that used in the fMRI experiment of Saenz et al. (2002) revealed that attending to one of two superimposed motion stimuli on one side of the visual field modulated the motion aftereffect from a single motion stimulus presented in the opposite visual field (Arman et al., 2006). Attention to the first stimulus also induced a motion aftereffect when there had been no adaptor at the test location. This may be a behavioral consequence of the finding that FBA alters baseline activity at the ignored locations (Serences & Boynton, 2007), and suggests that FBA modulates the firing rates of direction-selective neurons with spatial receptive fields in non-stimulated regions of the visual field.

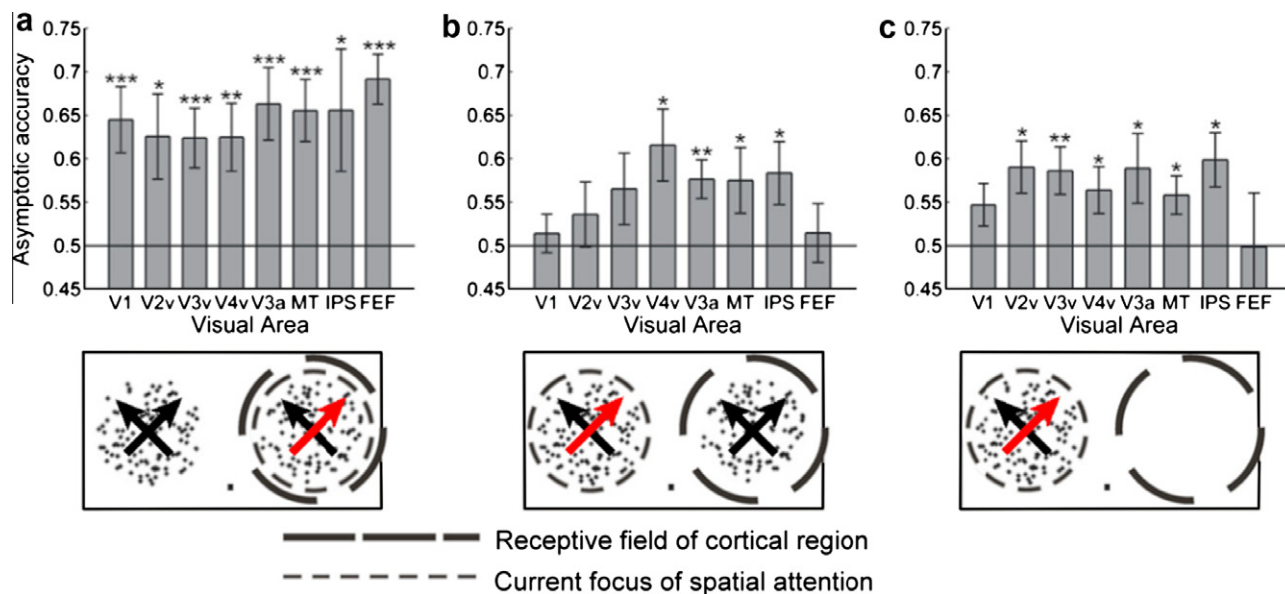


Fig. 18. (a) Classification accuracy based on responses in regions-of-interest (ROIs) contralateral to the focus of spatial attention (spatial attention *inside* RF). (b) Classification accuracy based on responses to an ignored stimulus (spatial attention *outside* RF). (c) Classification accuracy based on the responses to an unstimulated region of space (baseline activity). [Adapted from Serences & Boynton, 2007].

This ‘remote adaptation’ effect was recently used to test the assumption that the magnitude of FBA modulation is independent of distance from the attended location, which is present in some computational models of attention (Boynton, 2005; Reynolds & Heeger, 2009). Assessing the motion aftereffect at different distances from the adaptor both when it appeared at foveal and at peripheral locations revealed that the spread of FBA seems to be constant across space, regardless of distance and hemifield (Liu & Mance, 2011; Fig. 19). This result is consistent with the finding that FBA increases baseline activity across neuronal subpopulations that prefer the attended feature (e.g., Chawla et al., 1999; Hayden & Gallant, 2005; McMains et al., 2007; Serences & Boynton, 2007).

Attention can also modulate adaptation to static stimuli in an orientation-specific manner. The tilt after-effect caused by exposure to an adaptor grating is strengthened when the adaptor has the same orientation of an attended Gabor patch at a distant location, even when the adaptor itself is rendered invisible by interocular suppression (Kanai, Tsuchiya, & Verstraten, 2006).

FBA may do more than just enhance the process of adaptation to stimuli with attended features. It may also shift the population response to the adaptor, and thus change the encoded feature value

and the perceived aftereffect. Consistent with this notion, a recent study found that the motion direction of a distant stimulus attended during adaptation changes the perceived direction of the motion aftereffect (Zirnsak & Hamker, 2010).

Along the same line, motion priming, a different kind of perceptual aftereffect, has revealed that subthreshold primes at an ignored location have a greater effect on subsequent test stimuli if they move in the same direction as another stimulus attended by the same color (Melcher, Papathomas, & Vidnyanszky, 2005). This ‘cross-feature’ spread was also supported by a study showing that attentional spread from color to motion affects both the strength of the motion aftereffect and the magnitude of the fMRI responses in human area MT+ (Sohn et al., 2005). Recent electrophysiological results are consistent with the cross-feature aftereffect in which direction similarity between different stimuli matter even when the monkey’s task was to detect a color change rather than a direction change (Katzner, Busse, & Treue, 2009).

All these aftereffect studies are consistent with neurophysiological studies in demonstrating that the encoding of an ignored stimulus is strengthened (and perhaps distorted) when its features match a distant attended target.

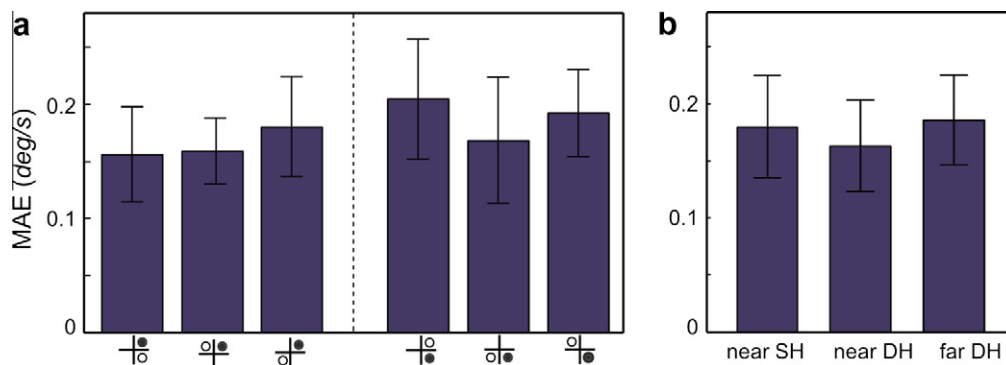


Fig. 19. (a) Attention induced MAE magnitude for each adapter-test pair. The icons below the x-axis depict the locations of the adaptor and test stimuli (solid circles: adaptor, empty circles: test). There were 4 possible locations on the intercardinal axes at 10 deg of eccentricity. Dashed vertical line separates results when the adaptor was in the upper right quadrant and in the lower right quadrant. (b) Attention induced MAE magnitude averaged across adapter locations, near SH: near location, same hemifield (1st and 4th columns in a), near DH: near location, different hemifield (2nd and 5th columns in a), far DH: far location, different hemifield (3rd and 6th columns in a). [Adapted from Liu & Mance, 2011].

6.3.2.2. Perceptual performance. In an early behavioral study on FBA, observers made two-interval forced choice discriminations of either the orientation or spatial frequency of centrally presented Gabor patches, which were followed on a minority of trials by a low-contrast grating that filled the entire screen except the location of the target Gabor. When the observers discriminated the stimulus orientation, hit rates for detecting the full-screen grating decreased with increasing difference between the target Gabor and the full-screen grating orientations. Analogous findings emerged for the corresponding spatial frequency stimuli (Rossi & Paradiso, 1995). These data are consistent with a spatial spread of increased sensitivity to the feature values attended at fixation. However, it is possible that the changes in hit rates were caused by changes in the observers' criteria rather than sensitivity because false alarm rates for each orientation and spatial frequency were not measured.

Studies measuring performance in simultaneous discriminations of spatially separated stimuli have shown effects of global FBA on visual performance in dual discrimination tasks. In these studies, two spatially separated stimuli are displayed simultaneously and observers are asked to judge some feature of both of them. Observers perform better when the two stimuli have similar feature values within the relevant dimension than when they have very different values. For instance, when observers are presented stimuli in two apertures, each containing two overlapping fields of dots moving in opposite directions, performance on a discrimination task is significantly better when the attended dot fields move in the same direction than when they move in opposite directions. In these kinds of experiments, spatial attention is kept constant because participants attend to both locations. These results, which are consistent with the global spread of FBA, have been shown for the dimensions of color, motion direction, speed and orientation (Lu & Itti, 2005; Saenz et al., 2003; Sally, Vidnyansky, & Papathomas, 2009; White & Carrasco, in press).

However, shared features do not always improve performance by rendering spatially distinct attributes easier to report. Typically, dual-task studies find no performance benefit when two tasks involve similar rather than dissimilar feature dimensions (Lee, Koch, et al., 1999; Pastukhov et al., 2009; but see Morrone et al., 2004). A recent study evaluated the effect of similar and dissimilar feature values, and measured dual-task costs with respect to motion flows (e.g., translation, rotation, expansion) presented to the left and right of fixation. Surprisingly, similarity between the two motion flows failed to benefit dual-task performance, but when both flows conformed to a common global flow (expansion or rotation) performance improved (Festman & Braun, 2010). Thus, the global spread of FBA may sometimes be guided by surface segmentation rather than by strict feature similarity.

6.4. Spatial interactions

FBA also has been shown to affect spatial interactions. Human observers can extract a given motion direction from fields of random dots moving simultaneously in two or more directions in the same region of the visual field, a phenomenon known as motion transparency [see review by Burr & Thompson, 2011 on motion processing]. The visual system can separate several overlapping noisy distributions of motion signal to perceive transparent motion. Capitalizing on this fact, some studies modulate have shown that FBA modulates perception of transparent motion with transparent surfaces containing superimposed direction of motion. For instance, observers are more likely to detect the presence of a given motion direction in a display with multiple directions when they are precued with that direction than when they are not. This finding suggests that attention can reliably improve the separability of directional signals in transparent motion processing by

affecting low level encoding mechanisms (Felisberti & Zanker, 2005).

FBA studies have also used motion repulsion; this term was introduced by Marshak and Sekuler (1979) to refer to the overestimation of the angle between two stimuli moving in different directions. When observers are presented with a foveal stimulus containing two superimposed motion directions with an angular deviation of 45°, and attend to one direction to detect a speed change, the motion repulsion effect for this direction is reduced. This finding suggests that FBA selectively changes the relative influence of motion signals moving across each other (Chen, Meng, Matthews, & Qian, 2005).

Another study has shown that FBA affects perceived direction in a motion repulsion paradigm by biasing spatial center-surround interactions in motion processing. Motion stimuli presented in the surround influence motion processing in the center at the neural and behavioral level (e.g., Braddick, Wishart, & Curran, 2002; Hiris & Blake, 1996; Kim & Wilson, 1997). Based on this finding, the authors instructed observers to attend to one of two superimposed motion directions in the spatial surround. The results indicate that the attended motion direction increases its influence on the center (Tzvetanov, Womelsdorf, Niebergall, & Treue, 2006).

Thus, the effect of FBA on motion repulsion depends on where the selectively attended motion component is. Whereas in the Chen et al. (2005) study FBA reduces motion repulsion, in the Tzvetanov et al. (2006) study, FBA enhanced motion repulsion. Both studies show that FBA to a particular transparent surface modulates the processing of motion components, altering motion repulsion and perception of direction.

6.5. Computational models

Most theories of attention rely on the idea that in a visual search situation, attention boosts the activity of neurons tuned for the target features. A computational model related to the feature-similarity gain model (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999) integrates single unit and fMRI data and explains global FBA through biased competition of neurons in area IT (Braddick et al., 2002; Corchs & Deco, 2002, 2004; Hiris & Blake, 1996; Kim & Wilson, 1997). This model is a neurodynamical system consisting of many interconnected modules that can be related to the dorsal and ventral pathways of visual cortex. The model is used to numerically compute the neural activity of area V4 and successfully simulates FBA effects reported in the literature.

However, both theoretical models and psychophysical evidence indicate that boosting the activity of neurons exactly tuned for the target features is not always optimal. It is suboptimal when performing a difficult discrimination between two very similar stimuli. In this case, gain should be applied to neurons tuned slightly away from the target because they are more sensitive to small changes in the relevant feature value (Jazayeri & Movshon, 2006, 2007; Navalpakkam & Itti, 2007; Purushothaman & Bradley, 2005; Regan & Beverley, 1985). For instance, the optimal feature gain modulation theory proposed by Navalpakkam and Itti (2007) combines information from both the target and distracting clutter to maximize the relative salience of the target. Simulations of several search conditions led to the prediction that sometimes it is optimal to enhance nontarget features. When searching for a target among distractors with very different features, the optimal strategy is to enhance the target feature, but when searching for a target among distractors with similar features, the optimal strategy is to enhance values slightly away from both targets and distractors. For instance, when trying to detect a vertical grating the most important neurons are those tuned to vertical. However, when trying to discriminate between two similar orientations, vertical (0°) and slightly tilted ($\pm 5^\circ$), the most important neurons are

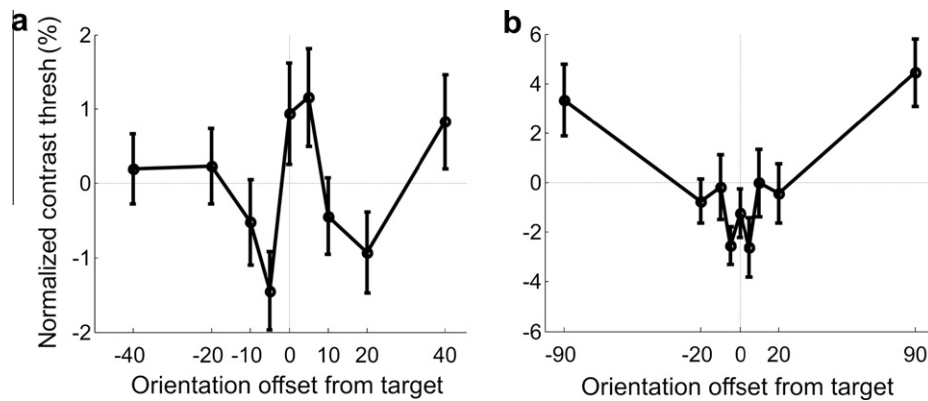


Fig. 20. Psychophysical data revealing how subjects deploy attentional gain (a) Normalized contrast detection thresholds when observers were engaged in a fine discrimination task. The x-axis labels refer to orientation offset of the to-be-detected Gabor from the target orientation. Positive values along the x-axis refer to rotation in the direction indicated by the color of the cue, and negative values refer to rotation in the direction opposite of that indicated by the cue. For example, if a red cue indicated that targets were rotated clockwise with respect to distractors, then all distractors rotated clockwise from the target would be denoted with a positive value and all distractors rotated counterclockwise would be denoted with a negative value. Note that since there is only one distractor orientation, positive rotational offsets denote exaggerated target features and negative offsets denote the distractor feature (-5° from the target) and exaggerated distractor features. (b) Normalized contrast detection thresholds when observers were engaged in a coarse discrimination task. All error bars are ± 1 SEM. [Adapted from Scolari & Serences, 2009].

those preferring $+15^\circ$ and -15° , because they have the largest change of activity between 0° and $\pm 5^\circ$ (Regan & Beverley, 1985). Psychophysical experiments using a visual search paradigm on human observers supported this prediction, thus suggesting that humans deploy the optimal gain modulation strategy. This is a consequence of population codes (Pouget & Bavelier, 2007), which play different roles depending on the nature of the task (Regan & Beverley, 1985).

However, the extent to which human observers are capable of adaptively engaging such a computationally optimal strategy has only recently begun to be explored. Scolari and Serences (2009) showed that when observers were faced with a very fine discrimination, contrast detection thresholds were lower for flanking orientations around the target (Fig. 20a); however, when observers performed a coarse discrimination task, contrast detection thresholds were lowest around the target orientation and highest at the distractor orientation (Fig. 20b). Thus, attention maximizes the differential response associated with targets and distractors during a difficult perceptual discrimination, regardless of the sign of this difference. The emerging view is that attention does not simply amplify the response of sensory neurons that are tuned to the target. Instead, attention optimizes the gain of sensory neurons in a flexible and adaptive manner for performing a perceptual task that is relevant to the observer. These results are consistent with the flexibility exhibited by sustained attention, but not by transient attention, in meeting the demands of texture segmentation tasks.

7. Comparison of spatial and feature-based attention

Psychophysical and electrophysiological studies have compared the effects of spatial attention and FBA to characterize their effects on performance and investigate whether and how the mechanisms underlying these two types of attention interact.

7.1. Psychophysical studies

Some studies have compared the efficacy of spatial- and FBA (e.g., Baldassi & Verghese, 2005; Liu, Stevens et al., 2007; Ling et al., 2009; Shih & Sperling, 1996; Theeuwes, 1989). Such a comparison is not always straightforward because different stimuli have almost always been used in the location and feature cue conditions. In the few cases when the same target and distracter stimuli have been used in both conditions, sometimes the cue stimuli

were physically different (e.g., Baldassi & Verghese, 2005; Theeuwes, 1989). Furthermore, each study has used only a single timing condition (except Liu, Stevens et al., 2007), which differs across studies, making it hard to compare across studies and to generalize the results.

To ensure that any observed effect would reflect differences in the attentional mechanisms, a study comparing the time course of FBA and spatial attention used identical physical stimuli for the cue and target and timing between them, and only varied the instructions associated with the cues to manipulate either FBA or spatial attention. Observers detected a speed increment in one or two compound motion stimuli preceded by a cue that indicated either the target location or direction. The cue-target stimulus-onset-asynchrony (SOA) was varied to assess the time course of the attentional effect. Results indicated that spatial attention was deployed earlier than FBA, but both types of attention improved performance to a similar extent at the 500-ms SOA (Liu, Stevens et al., 2007).

Is location itself a feature – perhaps a ‘special’ feature – in selecting information? Some propose that all stimulus attributes, including location, can be equally utilized for attentional selection (e.g., Bundesen, 1990; Duncan, 1981, 1984; Martinez-Trujillo & Treue, 2004; Patzwahl & Treue, 2009). Others contend that location information assumes priority in selection (e.g., Cave & Wolfe, 1990; Posner, Snyder, & Davidson, 1980; Treisman, 1988) and that it is the ‘default’ mode of selective attention, as suggested by studies that manipulated task relevance of spatial and feature information (Lamy & Tsal, 2000; Tsal & Lavie, 1993). However, the debate on the status of location in selective attention concerns multiple related, yet distinct, sub-topics (Lamy & Tsal, 2001). The finding that spatial (endogenous) attention is effective at ~ 300 ms whereas FBA is effective at ~ 500 ms (Liu, Stevens et al., 2007) argues against claims of location superiority, which are based on studies reporting null results of feature cueing in some conditions (Moore & Egeth, 1998; Shih & Sperling, 1996; Theeuwes, 1989). However, they suggest that location is special in the sense that spatial attention is activated earlier than FBA.

Do the same neural mechanisms underlie spatial attention and FBA? Space is represented topographically in the extrastriate cortex, whereas other features – e.g. orientation and spatial frequency – are not (Gattass, Sousa, & Gross, 1988). Thus spatial attention may operate by a different mechanism and have different effects on neuronal tuning than does attention for other features (David, Hayden, Mazer, & Gallant, 2008; Hayden & Gallant, 2005; Maunsell

& Treue, 2006). Moreover, it is likely that our percept does not arise from a single neuron, but rather from the activity of a population of neurons (Deneve et al., 1999; Jazayeri & Movshon, 2006; Pouget, Dayan, & Zemel, 2003; Pouget et al., 2000). Therefore, some studies, which I describe below, have asked what influence spatial attention and FBA may have on the population response (Baldassi & Verghese, 2005; Ling et al., 2009).

Recall that there are two prominent proposals for neural mechanisms with which attention might affect neural responses: gain modulation and changes in tuning (Baldassi & Verghese, 2005; Ling et al., 2009; Martinez-Trujillo & Treue, 2002, 2004; McAdams & Maunsell, 1999; Reynolds & Chelazzi, 2004; Williford & Maunsell, 2006). A gain model predicts that the overall population response to a stimulus is increased by a multiplicative factor across all feature detectors, as if the effective signal strength was “turned up” (Fig. 21a, left panel) or that it increases the response corresponding to the attended features without changing the response to other features in the same dimension. A tuning model predicts that attention does not increase the response to attended stimuli, but rather it suppresses the response to irrelevant noise, leading to a narrower population response profile (Fig. 21b, left panel). Note that these possibilities are not mutually exclusive, and attention may act by combining both mechanisms.

The attentional mechanisms of gain and tuning have also been characterized using the equivalent-noise paradigm (Ling et al., 2009). This paradigm measures sensitivity for a signal embedded in external noise as a function of increasing levels of external noise (Dakin, Mareschal, & Bex, 2005; Doshier & Lu, 2000a, 2000b; Lu & Doshier, 2000; Pelli & Farell, 1999). Gain and tuning models make distinct predictions regarding how attention will affect threshold vs. noise (TvN) functions. On the one hand, gain causes an overall multiplicative increase in the population response, and would thus increase discriminability only when the external noise is low (Fig. 21a, left panel). According to a gain model, as more external noise is added to the stimulus, the gain of the irrelevant external noise is increased as well. Because the signal-to-noise ratio does not improve with boosted gain, once the external noise outweighs the system's internal noise, any benefit of a gain modulation is precluded

with high external noise. Thus, an attention gain model yields a benefit (decreased threshold) only at low noise levels (Fig. 21a, middle panel). On the other hand, tuning suppresses the population response to irrelevant external noise. This increases discriminability only when there is sufficient external noise present for the system to suppress (Fig. 21b, left panel), which in turn precludes any benefit of a tuning modulation with low external noise. Thus, the signature of an attentional tuning model is a decreased threshold only at high noise levels (Fig. 21b, middle panel).

In the study by Ling et al. (2009), observers performed a 4-alternative forced-choice (4AFC) motion discrimination task with either spatial attention or FBA. The results indicate that in this motion task spatial attention effects are mediated by gain (Fig. 21a, right panel), whereas FBA effects are mediated by both gain and tuning mechanisms (Fig. 21b, right panel). Spatial attention and FBA may differ in their underlying mechanisms because they optimize our visual system based on different types of information: Whereas spatial attention guides an observer to a particular location, FBA guides an observer to a particular feature of the stimulus. Both spatial attention and FBA benefit from a gain increase of the population responses, which scales the overall response by a multiplicative factor. FBA also benefits from a tuning mechanism, which necessarily requires the observer's knowledge of the feature, around which to sharpen the population response by selectively suppressing irrelevant detector responses.

Using the method of noise masking, in which noise that is spatio-temporally coincident with a signal impairs detection or discrimination of that signal (Legge & Foley, 1980), a psychophysical study has suggested that spatial attention and FBA affect orientation-selective tuning curves differently (Baldassi & Verghese, 2005). The authors reported a reduction in threshold across the orientation-tuning curve with spatial attention, and a dip at the peak of the orientation-tuning curve with FBA. They interpreted the spatial attention results as a reweighting of detectors similar to a gain change, whereas FBA was proposed to affect orientation selectivity through tuning, by a boost of the detector corresponding to the attended feature, with no change in any other detectors.

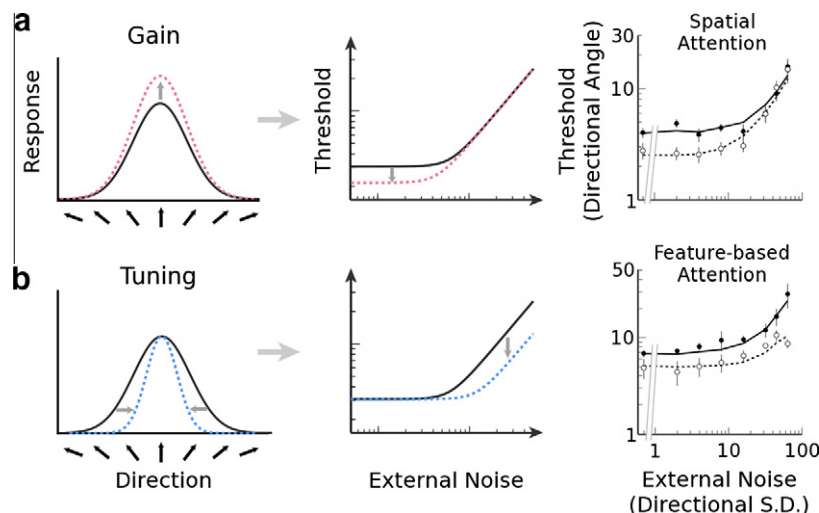


Fig. 21. The effect of gain and tuning on neural population responses and equivalent-noise curves. (a) A hypothetical population response to an attended upwards-moving stimulus. Dotted lines correspond to changes with attention. A gain model proposes an overall multiplicative increase in the population response to a stimulus (left panel). This amplified response would only lead to a benefit in discriminability at low levels of external noise (middle panel). This is the pattern of responses obtained for spatial attention (right panel). (b) A tuning model proposes a sharpening of the population response around the attended stimulus feature (left panel). This narrowed response would only lead to a benefit in discriminability at high levels of external noise, when there is noise to suppress (middle panel). Feature based attention leads to noise reduction across all external noise levels. Indicating both gain and tuning [Adapted from Ling et al., 2009].

Both studies (Baldassi & Verghese, 2005; Ling et al., 2009) conclude that endogenous spatial attention is mediated by a gain mechanism that increases the overall strength of the population response, and not by tuning. Consistent with these findings, other studies have shown that spatial attention increases the amplitude of the response but does not alter the perceptual tuning. This has been found using both noise image classification (in which observers' perceptual judgments are analyzed to determine the properties of the relevant perceptual filter; Eckstein et al., 2002; Murray, Sekuler, & Bennett, 2003; Neri, 2004) and critical-band masking (band-pass filtered noise to examine threshold elevation as a function of noise bandwidth; Lu & Dosher, 2004; Talgar et al., 2004).

With respect to FBA, both studies (Baldassi & Verghese, 2005 and Ling et al., 2009) conclude that it is mediated by a tuning mechanism at the population level. Ling et al. (2009) report that FBA also operates by increasing the overall strength of the population response, a gain mechanism, whereas Baldassi and Verghese (2005) do not. This discrepancy could be due to the difference in visual dimensions being studied (orientation vs. direction), or perhaps due to the different methods used to obtain the tuning curves (critical-band masking vs. equivalent noise). In any case, linking psychophysical performance with neurophysiological responses via biologically-plausible models based on population responses, both studies have concluded that at the population level, FBA is mediated by a tuning mechanism.

However, in other studies in which FBA had been manipulated, no tuning was observed. For instance, this was the finding in an investigation of the effects of FBA on perceptual tuning curves for direction of motion which used spatially overlapping target and distractor dots defined by contrast polarity, in which a few signal dots moved coherently. Observers attended to the dots of one contrast polarity and indicated their global motion direction. Perceptual tuning curves indicated that attention increased the perceptual weight allocated to target compared to distractor dot displacements, but that attention did not alter the selectivity for direction of motion (Murray et al., 2003). Similarly, a study manipulating both spatial attention and FBA and using a motion reverse correlation technique (by presenting very brief, fully coherent motion impulses in one of several different directions in a random sequence) to analyze motion tuning at high temporal resolution, revealed that attention increases the amplitude of direction of motion tuning curves but does not alter tuning width. These findings suggest that attention exerts a multiplicative effect on human perceptual tuning curves for motion direction (Busse et al., 2008).

7.2. Electrophysiological studies

In early electrophysiological studies, monkeys viewed arrays of mixed stimuli and had to attend to a subset of stimuli with a color or luminance that matched a cue stimulus. V4 responses were stronger when the stimulus in their RF matched the cue (Motter, 1994a). These studies suggested that FBA might change color selectivity, resulting in increased sensitivity to behaviorally relevant features. However, an alternative interpretation of these results has been offered (David et al., 2008). It is possible that monkeys may have deployed both spatial attention and FBA to perform the task; i.e., that the change in neuronal activity depended on a mechanism that targeted spatial locations identified by the animal as behaviorally relevant based on color or luminance. Thus, gain changes caused by attention may have caused apparent shifts in color selectivity. In contrast to Motter et al.'s studies, subsequent studies of FBA in area V4 (McAdams & Maunsell, 2000) and MT (Martinez-Trujillo & Treue, 2004) have reported only changes in response gain.

To avoid a potential confound of spatial attention on FBA, a recent study independently varied both types of attention to evaluate whether attention shifts the tuning of individual V4 spectral receptive fields (SRFs), using a match-to-sample task with natural images spanning the tuning space encoded by V4 neurons (David et al., 2008). The SRF is a two-dimensional tuning profile that describes the joint orientation-spatial frequency tuning of a neuron (Mazer, Vinje, McDermott, Schiller, & Gallant, 2002). Consistent with previous findings (McAdams & Maunsell, 2000; Reynolds et al., 2000; Williford & Maunsell, 2006), recordings revealed that spatial attention modulated baseline and gain and had little effect on spectral tuning. FBA also modulated the baseline and gain of about half the neurons, but in addition, FBA also shifted the spectral tuning of about one third of the neurons toward the attended spectral feature (David et al., 2008). These results provide evidence for the idea that the tuning properties of V4 neurons change dynamically to meet behavioral demands, i.e., the neural representation of shape in extrastriate visual cortex is dynamic and context-dependent (Gilbert & Sigman, 2007). Thus, in addition to representing visual objects by decomposing them into different dimensions, individual V4 neurons also partake in attentional selection by modulating their tuning along those dimensions (David et al., 2008).

In David et al.'s study, FBA and spatial attention tended to affect the same neurons. However, the finding that the spectral tuning shifts occur, regardless of whether spatial attention is directed into or away from the receptive field, suggests that at least some of the shifts are mediated by a global feature-based mechanism, and that the top-down influences of these two attentional systems arise from separate networks that feed back into V4. If separate networks implemented the two forms of attention, then their effects on neuronal responses should be additive and independent. Indeed, there is evidence that the effects of spatial attention and FBA may be additive. Treue and Martinez-Trujillo (1999) measured attentional modulation in macaque area MT, and found that spatial and feature-based effects are similar in magnitude, and that the sum of their effects was equivalent to a condition where attention was directed to both the feature and spatial location of a stimulus (inside and outside the receptive fields of MT neurons), which led them to conclude that their effects are additive. Analogous results have been shown in human fMRI, where the effects of spatial attention and FBA were shown to be additive across V1, V2, V3a, V4, and MT+ (Saenz, Boynton, & Koch, 2006).

A recent study isolated the effect of attention to a particular motion direction when two directions overlap (transparent motion) and compared the magnitude of this feature-based effect (alone) with that found when spatial attention was also manipulated within the receptive fields of MT neurons (Patzwahl & Treue, 2009). There were pronounced attentional effects based on the attended direction when target and distractor shared the same spatial location, and the magnitude of modulation was about double when target and distractor were both inside the receptive field but spatially separated. Moreover, the magnitude of spatial and FBA attentional effects in a given cell are correlated. The authors interpret this correlation to suggest that the modulations may reflect a unified attentional system in which location is simply another feature for which the cell is tuned to.

Additive effects have also been reported in the ventral system. Recordings in V4 using a task that controls both types of attention simultaneously (Hayden & Gallant, 2005), revealed that spatial attention and FBA can be described as additive processes with a small super-additive interaction term (Hayden & Gallant, 2009). The authors consider this additivity effect on responses of single visual neurons to be consistent with the idea that separate neural systems and different cognitive processes controlled both types of attention (Doherty, Rao, Mesulam, & Nobre, 2005).

8. Conclusion

As remarkable as the human visual and cognitive systems may be, inevitably we are still limited by both bandwidth and processing power. There is a fixed amount of overall energy available to the brain, and the cost of cortical computation is high. Attention is crucial in optimizing the system's limited resources. As a selective process, attention provides an organism with an optimized representation of the sensory input that emphasizes relevant details, at times even at the expense of a faithful representation of the sensory input.

This review has focused on advances in the study of visual attention in the last 25–30 years, during which the interest in this topic has been growing steadily. In the last decades, the field has shifted from focusing on determining whether a visual process is pre-attentive or attentive to systematically investigating the mechanisms of visual attention and the effects of such mechanisms on perception. The field has developed a consensus that attention is not a unitary construct, and that it is necessary to explicitly define and manipulate attention while keeping the task and stimuli constant, rather than to infer its presence. With close to 2500 articles on visual attention published since 1980, and more than half of them since 2005, it seems very likely that investigating the role of attention will continue to be a central enterprise in studying vision and cognition.

This review includes some studies of attention affecting early vision that illustrate how psychophysical studies allow us to probe the human visual system, and how evaluating the results in terms of theoretical models and relating them to possible neural correlates advances our understanding of the mechanisms underlying attentional modulation. I have explained how attentional effects exceed what is predicted by reduction of location uncertainty alone, a benchmark against which attention effects should be measured. I have focused on describing the effects of spatial and feature-based attention on perceptual effects mediated by early vision, for which the best mechanistic understanding has been achieved by the confluence of psychophysical, electrophysiological, neuroimaging, and computational studies. I have shown that trade-offs in processing result in increased performance at the attended location or feature and decreased performance at unattended locations or features, consistent with a selective representation of the world.

Our understanding of visual attention has been advanced by the integration of different levels of analysis and methodologies. In this review I illustrate how combining knowledge gathered from psychophysics, single-unit neurophysiology, neuroimaging, and computational techniques proves useful to understanding how attention affects perception. Yet, despite this progress, many unanswered questions remain. Each reader is likely to have his or her own list. While addressing those questions we should take into account that comparisons between psychophysical and neurophysiological results need to be made with caution, and that there are several ways in which their links can be strengthened, among them: (1) full characterization of the behavioral task in imaging studies designed to narrow the gap between psychophysical and electrophysiological studies; (2) systematic investigations of behavioral effects while characterizing single-unit activity, not a common practice in the past; (3) inclusion of biological constraints in the modeling of attention and in the generation of psychophysical experiments; (4) paradigms that directly measure the differences and interactions between endogenous and exogenous attention in humans; (5) paradigms that directly measure the differences and interactions between endogenous and exogenous attention in awake behaving monkey to develop systems models of both types of atten-

tion; (6) comparison of the mechanisms and temporal dynamics of voluntary attention to different visual features (e.g., color, orientation and direction of motion); (7) comparison of the patterns of neural activity evoked by attending to different features in visual areas, during the preparatory period and/or while the stimuli are present, and in higher areas that may be the origin of top-down signals; (8) paradigms that directly measure the differences and interactions between space-based and FBA in humans; and (9) paradigms that directly measure the differences and interactions between space-based and FBA in awake behaving monkeys to develop systems models of them. In addition, as we continue investigating visual attention it would be critical to establish a more rigorous link between the 'attentional control' literature, and the 'how attention affects perception' literature reviewed here.

In a certain sense, the task of reviewing the evolution of the field of attention over several decades is analogous to the phenomena of vision and attention themselves. The field out there is vast, dynamic and complex, and the reviewer – this reviewer at least – has limited bandwidth and processing power, as well as a finite amount of available time and energy. As with any review, there are many interesting psychophysical and neurophysiological examples that could have also been included in this review article. I began this review by evoking the Borges short story, “*Funes el memorioso*,” an apt parable of the dilemmas of perception and memory. During the preparation of this review, as I tried to take in, and do justice to, hundreds of carefully constructed scientific papers, another Borges parable on “*Scientific Rigor*” kept coming to mind: that of the emperor who ordered his court cartographer to create a perfect map of his realm on a scale of 1:1. The result, of course, was less a legible map and more a rather useless skin that covered – and became part of – the emperor's vast domains. Borges knew well that selection, abstraction, simplification and attention simultaneously limit and enable all human endeavors, and that the myth of total coverage is, well, a myth. I hope that this incomplete, pocket-sized map of a vast and mobile territory will at least help orient those researchers who traverse the terrain, and do at least some justice to the scientists who have inhabited and cultivated its land over the last decades.

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Appendix A. Neurophysiological techniques for the study of attention

A.1. Single-unit recording studies

The development of techniques to record the electrical activity of single neurons in awake-behaving animals (e.g., monkeys) has enabled researchers to probe the biological foundations of attention while monkeys perform attention-demanding tasks. Such studies have provided detailed, quantitative descriptions of how endogenous attention alters the responses of neurons in striate and extrastriate visual cortex, yielding attentional facilitation and selection. Attentional facilitation results when spatial

attention enhances the responses evoked by a single stimulus appearing alone in a neuron's RF, so that neurons respond to an attended stimulus much as they would were its luminance increased. However, one must consider that given that stimuli rarely appear in isolation, attentional selection of behaviorally relevant targets from among distracters arguably serves a more ecologically relevant purpose. In studies considering multiple stimuli appearing within a neuron's RF, the firing rate is characteristically determined primarily by the task-relevant stimulus. Numerous studies have compared the response when attention is directed either to one of the two stimuli in the RF or outside the RF while fixation is maintained. Attending to the preferred stimulus (for which the neuron is tuned) increases the neuron's response evoked by the pair of stimuli whereas attending to the non-preferred stimulus (for which the neuron is not tuned) decreases such response.

A.2. Neuroimaging studies

Neuroimaging has yielded information on the integrated brain activity underlying visual attention in humans. Studies documenting the neural correlates of covert attention have used several techniques, among them functional magnetic resonance imaging (fMRI), event-related potentials (ERP), and steady-state visual evoked potentials (SSVEP) and magnetoencephalography (MEG).

fMRI non-invasively measures hemodynamic processes in the human brain by providing temporally integrated maps of regional cerebral blood flow across the whole brain. It is based on the increase in blood flow to the local vasculature that accompanies neural activity in the brain. There is wide agreement that attention increases fMRI responses in visual cortical areas in a retinotopically specific manner, corresponding to attended spatial locations, as well as in some regions of parietal and frontal areas, both for endogenous and exogenous attention.

ERPs are electrophysiological responses that arise during sensory, cognitive and motor processing, which provide precise information about the time course of information processing. ERP recordings can help reveal the timing and organization of stimulus selection processes in the brain's attentional network. ERP studies provide support for a mechanism of early sensory facilitation, at the level of extrastriate visual cortex, during the spatial cueing of attention.

SSVEP is a continuous oscillatory electrical response elicited in the visual pathways when a visual stimulus is presented repetitively at specific frequencies (at a rate of ≥ 5 Hz). The SSVEP can be recorded from the scalp as a nearly sinusoidal waveform. This waveform is usually found to have the same fundamental frequency as the driving stimulus, and often includes higher harmonics. The amplitude of the SSVEP can also be substantially increased when the flickering stimulus is being attended, in relation to when it is ignored.

MEG is an imaging technique used to measure the magnetic fields produced by electrical activity in the brain via extremely sensitive devices such as superconducting quantum interference devices (SQUIDS). MEG offers a direct measurement of neural electrical activity (compared to fMRI for example) with very high temporal resolution but relatively low spatial resolution. The advantage of measuring the magnetic fields produced by neural activity is that they are not distorted by surrounding tissue, unlike the electric fields measured by EEG (particularly the skull and scalp).

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