CHAPTER 3

Covert attention increases contrast sensitivity: psychophysical, neurophysiological and neuroimaging studies

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Abstract: This chapter focuses on the effect of covert spatial attention on contrast sensitivity, a basic visual dimension where the best mechanistic understanding of attention has been achieved. I discuss how models of contrast sensitivity, as well as the confluence of psychophysical, single-unit recording, and neuroimaging studies, suggest that attention increases contrast sensitivity via contrast gain, an effect akin to a change in the physical contrast stimulus. I suggest possible research directions and ways to strengthen the interaction among different levels of analysis to further our understanding of visual attention.

Keywords: visual attention; early vision; contrast sensitivity; psychophysics; neurophysiology; neuroimaging

Our understanding of visual attention has advanced significantly over the last two decades thanks to a number of factors: psychophysics research on humans has systematically characterized distinct attentional systems, and single-unit neurophysiological research has made possible the recording of neuronal responses in monkeys under attention-demanding tasks. The coupling of the results from these two approaches, as well as the findings emerging from combining fMRI (functional magnetic resonance imaging) and psychophysics, have begun to provide a mechanistic characterization of this fundamental process, which lies at the crossroads of perception and cognition.

This chapter focuses on the effect of covert spatial attention on contrast sensitivity, a basic visual dimension where the best mechanistic understanding of attention has been achieved. This is due to the existence of models of contrast sensitivity, as well as to the confluence of psychophysical, single-unit recording, and neuroimaging studies, all indicating that attention increases contrast sensitivity. Growing evidence supports the idea that this effect is mediated by contrast gain, an effect akin to a change in the physical contrast stimulus.

In the first section, I introduce the construct of selective attention, and discuss the idea that it arises from the high bioenergetic cost of cortical computation and the brain's limited capacity to process information. Then I provide an overview of the two systems of covert attention — transient (exogenous) and sustained (endogenous) — and of the mechanisms that underlie attentional effects — signal enhancement and external noise reduction.

The second section deals with the psychophysical effects of transient and sustained attention on contrast sensitivity. After introducing some ways in which attention is manipulated in psychophysical experiments, I discuss studies of transient attention indicating that contrast sensitivity is increased at the attended location across the contrast sensitivity function and the contrast psychometric function. Conversely, compared to a neutral condition, contrast sensitivity is decreased at the unattended location. I then document how the effect of transient attention on appearance is consistent with its effects on performance: apparent contrast increases at the attended location and decreases at the unattended location. At the end of the psychophysics section, I discuss a study comparing the effects of transient and sustained attention on contrast sensitivity; specifically with regard to the mechanism of signal enhancement and the contrast gain and response gain functions.

The third section presents neurophysiological studies of visual attention. Single-unit recording studies in the monkey have provided detailed, quantitative descriptions of how attention alters visual cortical neuron responses. I provide an overview of the studies showing that attentional facilitation and attentional selection may come about by increasing contrast sensitivity in extrastriate cortex in a way comparable to increasing stimulus contrast. In addition, I discuss parallels between contrast and attentional effects at the neuronal level, which advance our understanding of how effects of attention may come about.

In the fourth section, I discuss a human fMRI study that provides a retinotopic neuronal correlate for the effects of transient attention on contrast sensitivity with a concomitant behavioral effect. This study illustrates how neuroimaging studies, in particular fMRI, offer an intermediate level of analysis between psychophysics and singleunit studies.

To conclude, I discuss how models of contrast sensitivity, as well as the confluence of psychophysical, single-unit recording, and neuroimaging studies, suggest that attention increases contrast sensitivity via contrast gain, i.e., in such a way that its effect is indistinguishable from a change in stimulus contrast. Finally, I offer some thoughts regarding possible research directions and ways to strengthen the interaction among different levels of analysis to further our understanding of visual attention.

Selective attention

Limited resources

Each time we open our eyes we are confronted with an overwhelming amount of information. Despite this fact, we have the clear impression of understanding what we see. This requires selecting relevant information out of the irrelevant noise, selecting the wheat from the chaff. In *Funes el Memorioso* [Funes the Memoirist], Borges suggests that forgetting is what enables remembering and thinking; in perception, ignoring irrelevant information is what makes it possible for us to attend and interpret the important part of what we see. Attention often turns looking into seeing.

Attention allows us to select a certain location or aspect of the visual scene and to prioritize its processing. The limits on our capacity to absorb visual information are severe. They are imposed by the high-energy cost of the neuronal activity involved in cortical computation (Lennie, 2003). Neuronal activity accounts for much of the metabolic cost of brain activity, and this cost largely depends on the rate at which neurons produce spikes (Attwell and Laughlin, 2001). The high bioenergetic cost of firing pressures the visual system to use representational codes that rely on very few active neurons (Barlow, 1972). As only a small fraction of the machinery can be engaged concurrently, energy resources must be allocated flexibly according to task demand. Given that the amount of overall energy consumption available to the brain is constant, the average discharge rate in active neurons will determine the number of neurons that can be active at any time. The bioenergetic limitations provide a neurophysiological basis for the idea that selective attention arises from the brain's limited capacity to process information (Lennie, 2003).

As an encoding mechanism, attention helps the visual system to optimize the use of valuable processing resources. It does so by enhancing the representation of the relevant locations or features while diminishing the representation of the less relevant locations or aspects of our visual environment. The processing of sensory input is enhanced by knowledge and assumptions of the world, by the behavioral state of the organism, and by the (sudden) appearance of possibly relevant information in the environment.

Throughout the 19th and early 20th centuries. scientists such as Wundt, Fechner, James, and Helmholtz proposed that attention plays an important role in perception. It is necessary for effortful visual processing, and may be the 'glue' that binds simple visual features into an object. In the 1980s and 1990s, cognitive psychologists developed experimental paradigms to investigate what attention does and which perceptual processes it affects (Neisser, 1967; Posner, 1980; Treisman and Gelade, 1980). Over the last decade, cognitive neuroscientists have investigated the effects of attention on perception using three different methodological approaches. The physiological brain systems that underlie attention have been explored using two different methodological approaches. One has enabled studying how and where attention modulates neuronal responses by using single-unit recording; this method yields a precise estimate of local activity, but largely ignores behavioral consequences. The second approach has employed brain scanners (fMRI systems) to study the human brain while engaged in attentional tasks. This has enabled the identification of many of the cortical and subcortical brain areas involved in attention, and these experiments have yielded insights into the global structure of the brain architecture employed in selectively processing information. A third approach has focused on behavior; researchers have used cognitive and psychophysical techniques to explore what attention does and what perceptual processes it affects. More recently, they have started to investigate the mechanisms of visual attention, including how visual attention modulates the spatial and temporal sensitivity of early filters. and how it influences the selection of stimuli of interest, and its interaction with eye movements (Baldassi, Burr, Carrasco, Eckstein & Verghese, 2004).

Recent studies show that attention affects early visual processes such as contrast discrimination, orientation discrimination, and texture segmentation — which until recently were considered to be preattentive. Electrophysiological studies have established that neural activity increases at attended locations and decreases at unattended locations. Consequently, we can now infer that attention helps manage energy consumption. 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. Because of bioenergetic limitations, the allocation of additional resources to an attended location implies a withdrawal of resources from unattended locations. Indeed, we have recently published a study showing that when only two stimuli are present in a display, compared to a neutral attentional state, attention enhances the signal at the attended location, but impairs it at the unattended location (Pestilli and Carrasco, 2005).

Systems of covert attention: transient and sustained

Attention can be allocated by moving one's eyes towards a location, or by attending to an area in the periphery without actually directing one's gaze toward it. This peripheral deployment of attention, known as covert attention, aids us in monitoring the environment, and can inform subsequent eye movements (Posner, 1980). Many human psychophysical studies as well as monkey single-unit recording studies have likened attention to increasing visual salience.

A growing body of behavioral evidence demonstrates that there are two systems of covert attention, which deal with facilitation and selection of information: 'sustained' (endogenous) and 'transient' (exogenous). The former corresponds to our ability to monitor information at a given location at will; the latter corresponds to an automatic, involuntary orienting response to a location where sudden stimulation has occurred. Experimentally, these systems can be differentially engaged by using distinct cues. Symbolic cues direct sustained attention in a goal- or conceptually- driven fashion in about 300 ms, whereas peripheral cues grab attention in a stimulus-driven, automatic manner in about 100 ms. Whereas the shifts of attention by sustained cues appear to be under conscious control, it is extremely hard for observers to ignore transient cues (Nakayama and Mackeben, 1989; Cheal and Lyon, 1991; Yantis, 1996; Giordano et al., 2003). This involuntary transient shift occurs even when the cues are uninformative or may impair performance (Yeshurun and Carrasco, 1998, 2000; Yeshurun, 2004; Pestilli and Carrasco, 2005).

Transient and sustained attentions show some common perceptual effects (Hikosaka et al., 1993; Suzuki and Cavanagh, 1997), but some differences in the mechanisms mediating increased contrast sensitivity have been reported (Lu and Dosher, 2000; Ling and Carrasco, 2006). Of interest, these systems have different temporal characteristics and degrees of automaticity (Nakayama and Mackeben, 1989; Cheal and Lyon, 1991; Yantis, 1996), which suggest that these systems may have evolved for different purposes and at different times - the transient system may be phylogenetically older. There is no consensus as to whether common neurophysiological substrates underlie sustained and transient attention. On the one hand, all single-cell recording studies have manipulated sustained attention; on the other hand, some fMRI studies have found no difference in the brain networks mediating these systems (Peelen et al., 2004); others have reported differences. For example, sustained attention is cortical in nature, but transient attention also activates subcortical processing (Robinson and Kertzman, 1995; Zackon et al., 1999), and partially segregated networks mediate the preparatory control signals of sustained and transient attention. Sustained attention is mediated by a feedback mechanism involving delayed reentrant feedback from frontal and parietal areas (e.g., Martinez et al., 1999; Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002).

Mechanisms of covert attention: signal enhancement and external noise reduction

Although it is well established that covert attention improves performance in various visual tasks (e.g., Morgan et al., 1998; Lu and Dosher, 1998, 2000;

Carrasco et al., 2000, 2001, 2002, 2004a,b; Baldassi and Burr, 2000; Baldassi and Verghese, 2002; Blanco and Soto, 2002; Cameron et al., 2002; Solomon, 2004), 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 changes observers' decision criteria and reduces spatial uncertainty (Davis et al., 1983; Sperling and Dosher, 1986; Kinchla, 1992; Palmer, 1994; Shiu and Pashler, 1994; Nachmias, 2002), to proposals asserting that attention actually improves sensitivity by reducing external noise (Lu and Dosher, 1998; Morgan et al., 1998; Baldassi and Burr, 2000; Dosher and Lu, 2000; Cameron et al., 2004) or by enhancing the signal (Bashinski and Bacharach, 1980; Carrasco et al., 2000, 2002; Dosher and Lu. 2000: Cameron et al., 2002: Ling and Carrasco, 2006).

The external noise reduction hypothesis maintains that attention selects information by diminishing the impact of stimuli that are outside its focus. Noise-limited models incorporate internal noise arising from such sources as spatial and temporal uncertainty of targets and distracters, as well as external noise resulting from distracters 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 distracters. According to these models, performance decreases as spatial uncertainty and the number of distracters increase, because the noise they introduce can be confused with the target signal (Shiu and Pashler, 1994; Solomon et al., 1997; Morgan et al., 1998; Baldassi and Burr, 2000; Dosher and Lu, 2000). 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. According to 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 distracters appear with the target (distracter exclusion), but not when the target is presented alone, and are more pronounced as the number of distracters increases (Palmer, 1994; Shiu and Pashler, 1994, 1995; Eckstein and Whiting, 1996; Foley and Schwarz, 1998; Verghese, 2001; Cameron et al., 2004). These studies assert that attention allows us to exclude distracters that differ along some relevant dimension from the signal by narrowing a filter that processes the stimulus.

The signal enhancement hypothesis proposes that attention directly improves the quality of the stimulus representation of the signal within the locus of attention enhancement (Bashinski and Bacharach, 1980; Luck et al., 1996; Muller et al., 1998; Lu and Dosher, 1998; Carrasco et al., 2000, 2002; Cameron et al., 2002; Ling and Carrasco, 2006). In my lab, we have conducted a series of studies to evaluate whether signal enhancement (or internal noise) occurs in addition to external noise reduction. An attentional benefit can be attributed with certainty to signal enhancement only when all the factors that according to the external noise reduction model, are responsible for the attentional effects are eliminated. Presenting a suprathreshold target alone, without added external noise such as distracters or local or multiple masks, and eliminating spatial uncertainty, have allowed us to conclude that transient attention can increase contrast sensitivity (Carrasco et al., 2000; Cameron et al., 2002; Ling and Carrasco, 2006) and spatial resolution (Yeshurun and Carrasco, 1999; Carrasco et al., 2002) via signal enhancement (for a review, see Carrasco, 2005). However, 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. Indeed, under some experimental conditions it has been shown that signal enhancement and noise reduction mechanisms coexist (e.g., Lu and Dosher, 2000; Carrasco et al., 2004a,b; Pestilli and Carrasco, 2005).

Neurophysiological (e.g., Luck et al., 1997; Reynolds et al., 1999, 2000; Martinez-Trujillo and Treue, 2002; Reynolds and Chelazzi, 2004), psychophysical (Carrasco et al., 2000; Carrasco and McElree, 2001; Cameron et al., 2002, 2004; Talgar et al., 2004) and neuroimaging (Pinsk et al., 2004; Liu et al., 2005) studies indicate that both mechanisms affect the processing of visual stimuli. Singlecell studies show that attention can alter the responses of V1 neurons and can result in stronger and more selective responses in both V4 and MT neurons (Motter, 1994; Desimone and Duncan, 1995; McAdams and Maunsell, 1999; Reynolds and Desimone, 1999; Treue and Martinez-Trujillo, 1999). Likewise, signal enhancement is reflected in brain-imaging studies showing that attentional modulation is accompanied by stronger stimulus-evoked brain activity, as measured by scalp potential (see review by Hillyard and Anllo-Vento, 1998) and fMRI in both striate and extrastriate visual areas (e.g., Gandhi et al., 1999; Martinez et al., 1999; Pessoa et al., 2003; Yantis and Serences, 2003; Liu et al., 2005). All these studies support the psychophysical finding that attention affects the quality of sensory representation.

Psychophysical studies

Effects of transient attention on early vision

Much research has focused on the time course and degree of automaticity of the allocation of sustained and transient attention. However, less is known about the ways in which these systems, in particular sustained attention, affect fundamental visual dimensions. In past research, my laboratory has been particularly interested in characterizing the effects of transient attention on early visual processes. Given that transient attention highlights salient changes in the environment, its default, heuristic-like operation may be to enhance the quality of the signal and to reduce the external noise, enabling one to react accurately and quickly in most instances.

Indeed, we have found that transient attention affects spatial and temporal aspects of vision in remarkable ways. Compared to a neutral condition, it enhances contrast sensitivity (Carrasco et al., 2000; Cameron et al., 2002; Ling and Carrasco, 2006; Pestilli and Carrasco, 2005) and apparent contrast (Carrasco et al., 2004a,b) at the attended location, and decreases sensitivity (Pestilli and Carrasco, 2005) and apparent contrast (Carrasco et al., 2004a,b) at the unattended location. Transient attention also enhances spatial resolution (Yeshurun and Carrasco, 1998, 1999, 2000; Carrasco et al., 2002), and apparent spatial frequency (Gobell and Carrasco, 2005). In addition to improving discriminability, transient attention also speeds up information accrual (Carrasco and McElree, 2001; Carrasco et al., 2004a,b, 2006).

By improving discriminability, transient attention enables us to selectively extract relevant information in a noisy environment; by accelerating processing, it enables us to extract this information efficiently in a dynamic environment, before potentially interfering stimuli occur. However, purportedly because of its automatic fashion, transient attention does not always result in improved performance. It causes enhanced contrast sensitivity and spatial resolution; even when doing so leads to deviations from veridical perception (Carrasco et al., 2004; Gobell and Carrasco, 2005), makes us more prone to perceive an illusion (Santella and Carrasco, 2003), or impairs performance (Yeshurun and Carrasco, 1998, 2000; Talgar and Carrasco, 2002; Yeshurun, 2004).

Using fMRI, we have demonstrated a retinotopically specific neural correlate in striate and extrastriate areas for the enhanced contrast sensitivity engendered by transient attention (Liu et al., 2005). The attentional effect increases along the hierarchy of visual areas, from V1 to V4. Because attention can boost the signal by increasing the effective stimulus contrast via contrast gain (Reynolds et al., 2000; Carrasco et al., 2000, 2004a,b; Martinez-Trujillo and Treue, 2002; Cameron et al., 2002; Ling and Carrasco, 2006), 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 et al., 1990). Thus, a feedforward mechanism in which attentional modulation accumulates across sequential levels of processing can underlie the transient attention gradient.

Manipulations of spatial covert attention

To interpret the psychophysical results reported here, some methodological issues need to be clarified upfront. First, to investigate attention, it is best to keep the task and stimuli constant across conditions and to explicitly manipulate attention, rather than to infer its role (unfortunately, this has often not been the case in attention studies). We compare performance in conditions where attention is deliberately directed to a given location (attended condition) with performance when attention is distributed across the display (neutral or control condition), and in some cases, with performance in conditions where attention is directed to another location (unattended condition).

In cued trials, attention is directed to the target location via either a transient or a sustained cue. To effectively manipulate transient attention and to prevent forward spatial masking, the transient cue is presented $\sim 100 \,\mathrm{ms}$ before the display onset, adjacent to the location of the upcoming stimulus. In contrast, sustained cues typically appear at the display center \sim 300 ms before stimulus onset (e.g., Jonides, 1981; Muller and Rabbitt, 1989; Nakayama and Mackeben, 1989; Cheal and Lyon, 1991; Yantis, 1996). Because \sim 200–250 ms are needed for goaldirected saccades to occur (Mayfrank et al., 1987), the stimulus-onset-asynchrony (SOA) for the sustained cue may allow observers to make an eve movement toward the cued location. Thus, observers' eyes are monitored to ensure that central fixation is maintained throughout each trial.

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 lines encompass the whole display (distributed neutral cue), indicating that the target is equally likely to occur at any possible location. We have found that performance is comparable with these 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 letter identification task contingent on contrast sensitivity (Talgar et al., 2004), an acuity task (Cameron et al., 2002), and a temporal resolution task (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.

The following are some critical methodological issues to be considered when using spatial cues to test for sensory effects of attention: 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., Carrasco and Yeshurun, 1998). Many experiments manipulate sustained attention in detection tasks with cues indicating that a certain location has a given probability of containing the target (e.g., Posner, 1980). 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; Fig. 1), 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. A second 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 highcontrast pedestals (Foley and Schwarz, 1998). Uncertainty about the target location produces a more noticeable degradation at low than at high performance levels (Pelli, 1985; Eckstein and Whiting, 1996), and uncertainty is larger for less discriminable stimuli (Nachmias and Kocher, 1970; Cohn, 1981; 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., Pelli, 1985; Eckstein and Whiting, 1996; Solomon et al., 1997; Palmer et al., 2000; Carrasco et al., 2000, 2002).

In some studies, we have explored the conditions for which the effect of attention can be attributed to



Fig. 1. Sequence of events in a given trial. Observers perform a 2AFC orientation discrimination task on a tilted target Gabor patch, which appears at one of eight isoeccentric locations. The target is preceded by a sustained cue (instructing observers to deploy their attention to the upcoming target location), a transient cue (reflexively capturing attention to the upcoming target location), or a neutral cue (baseline). The timing (precue and interstimulus interval (ISI)) for sustained and transient conditions differs (along with their respective neutral conditions), in order to maximize the effectiveness of the cues (Ling and Carrasco, 2005, Fig. 2).

signal enhancement. To do so, 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. That is, the target should be suprathreshold (to reduce spatial uncertainty) and presented alone, without distracters and local or multiple masks (Lu and Dosher, 1998, 2000; Carrasco et al., 2000, 2002; Cameron et al., 2002; Golla et al., 2004; Ling and Carrasco, 2006).

Many of the studies I describe in this chapter involve an orientation discrimination task because this dimension has been well characterized both psychophysically and neurophysiologically, and a link between these two levels of analysis has been well established (Regan and Beverley, 1985; De Valois and De Valois, 1988; Graham, 1989; Ringach et al., 1997). In addition, we use orientation discrimination to assess the effect of attention on stimulus contrast because performance on this task improves with increasing contrast (Nachmias, 1967; Skottun et al., 1987; Lu and Dosher, 1998; Cameron et al., 2002), and because fMRI response increases monotonically with stimulus contrast (Boynton et al., 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 and Treue, 2005; Reynolds, 2005).

Transient attention increases contrast sensitivity

Transient attention increases sensitivity across the contrast sensitivity function

A number of psychophysical studies have shown that in the presence of competing stimuli contrast sensitivity for the attended stimulus is enhanced (Solomon et al., 1997; Lee et al., 1997, 1999; Foley and Schwartz, 1998). We assessed whether attention increases sensitivity in a wide range of spatial frequencies, spanning the contrast sensitivity function. To evaluate whether increased contrast could be mediated by signal enhancement, we explored if this effect also emerges when a suprathreshold target is presented alone (Carrasco et al., 2000).

We compared the stimulus contrast necessary for observers to perform an orientation discrimination task at a given performance level when the target location was preceded by a peripheral cue appearing adjacent to the target location, and

when it is preceded by a neutral cue appearing at fixation, which indicates that the target is equally likely to occur at any of the eight isoeccentric locations. We assessed the effect of transient attention across a wide range of spatial frequencies and found that it increases sensitivity across the contrast sensitivity function (Fig. 2a). Less contrast was necessary to attain the same performance level when a transient cue preceded the Gabor than when a neutral cue did (Fig. 2b). The results are consistent with a signal enhancement mechanism. The display did not contain any added external noise; there were no distracters, or local or global masks, which according to the external noise reduction model are responsible for attentional effects (e.g., Davis et al., 1983; Solomon et al., 1997; Morgan et al., 1998; Dosher and Lu, 2000; Lu and Dosher, 2000; Baldassi and Burr, 2000; Nachmias, 2002).

We found that a signal detection model (SDT) of external noise reduction could account for the cueing benefit in an easy discrimination task (e.g., vertical vs. horizontal Gabor patches). However, such a model could not account for this benefit when location uncertainty was reduced, either by increasing overall performance level, increasing stimulus contrast to enable fine discriminations of slightly tilted suprathreshold stimuli, or presenting a local postmask. An SDT model that incorporates



Fig. 2. (a) Data for two individual observers (CPT and YY) illustrating that for a target of constant contrast, precueing the target location enhances sensitivity across the contrast sensitivity function (CSF; Carrasco et al., 2000, Fig. 3). (b) The stimulus contrast necessary to attain the same performance level for a range of spatial frequencies is lower when the target location is precued by a peripheral cue (bottom squares) than by a neutral cue (top squares). The contrast differences depicted in the Gabor patches are based on data reported by Carrasco et al. (2000).

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 that predicted by uncertainty reduction. Thus, the cueing effect could not be explained by the mere reduction of location uncertainty. 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. The finding that transient attention operates via signal enhancement under low-noise conditions has been corroborated using the external noise plus attention paradigm (Lu and Dosher, 1998, 2000).

Transient covert attention enhances letter identification without affecting channel tuning

To explore how the enhancement of contrast sensitivity at the attended location comes about we investigated whether covert attention affects the tuning of a spatial frequency channel (Talgar et al., 2004) (see Fig. 3). We chose a task that isolates a spatial frequency channel that mediates the identification of broadband stimuli. A broadband stimulus could be seen through channels with various tunings, allowing us to test for shifts of peak frequency of the channel as a result of directing covert attention. Given that observers have multiple independent channels with various peak frequencies, one would expect a broadband stimulus such as a letter to activate many channels. However, using a critical-band-masking paradigm with unfiltered letters, the same filter tuning is found for detection of narrowband gratings and identification of broadband letters (Solomon and Pelli, 1994). Critical-band masking of letters allows us to test the effects of covert attention on a single spatial frequency channel using a broadband stimulus.

In auditory detection tasks observers are able to switch channels to avoid noise and attain a lower threshold than they would without switching channels, a process termed off-frequency listening (Patterson and Nimmo-Smith, 1980). Correspondingly, in a visual task observers might be able to 'switch channels' to use the noise-free part of the spectrum to reduce their thresholds. When narrow-band noise is superimposed on a broadband stimulus (e.g., a letter), an ideal observer could use the noise-free region of the signal spectrum to perform perfectly.



Fig. 3. A schematic representation of a trial sequence. In one third of the blocks, the target was preceded by a central–neutral cue (a dot in the center of the display), in another third by a distributed–neutral cue (a dot adjacent to each of the eight possible target locations), and in the remaining block by a peripheral cue (a single dot adjacent to the actual target location). Note that the eight noise patches were outlined in black to demarcate the locations (Talgar et al., 2004; Fig. 1).

To assess whether transient covert attention affects the spatial frequency tuning of a single channel, we used a task that isolates a single spatial frequency channel which mediates the identification of broadband stimuli (e.g., letters), in conjunction with the critical-band masking paradigm (Solomon and Pelli, 1994). In particular, we investigated the following two hypotheses:

First, covert attention shifts the peak frequency of the channel. Studies dealing with acuity and hyperacuity tasks (Yeshurun and Carrasco, 1999; Carrasco et al., 2002) as well as with texture segmentation tasks (Yeshurun and Carrasco, 1998, 2000; Talgar and Carrasco, 2002) have supported the hypothesis that attention increases spatial resolution at the attended location. Hence, we hypothesized that the peak frequency of the channel may shift to higher spatial frequencies when the low portion of the letter spectrum is masked (high-pass noise), and to lower spatial frequencies when the higher portion of the letter spectrum is masked (low-pass noise).

Second, covert attention alters the channel bandwidth, making it better matched to the signal. There is no consensus as to whether attention increases the selectivity of the neuronal response. Some have reported that attention narrows the tuning for orientation and color of neurons in V4 (Spitzer et al., 1988; Reynolds and Desimone, 1999; Reynolds et al., 2000), whereas others have found an increased gain but unchanged tuning for orientation in area V4 (McAdams and Maunsell, 1999), and for direction of motion in areas MT/MST (Treue and Martinez-Trujillo, 1999). Increased contrast sensitivity for a grating of a given frequency could be mediated by a narrowing of the channel tuning, but increased sensitivity for a broadband stimulus such as a letter would arise from a widening of the bandwidth. In general, better matching the channel to the noise-normalized signal would increase sensitivity.

To investigate these two hypotheses, we used critical-band masking of letters (Solomon and Pelli, 1994) and tested the effects of covert attention on a single spatial frequency channel using a broadband stimulus. The target letter (N, Z, or X; presented in low- or high-pass noise with different cut-off frequencies) followed the transient cue at 1 of 8 locations. Distracter letters (V's) occupied the remaining locations. All stimuli appeared at isoeccentric non-cardinal locations for which contrast sensitivity is similar (Carrasco et al., 2001; Cameron et al., 2002). We measured the energy threshold elevation for each observer at each of the low- and high-pass cut-off noise frequencies with both a peripheral and a neutral cue.

To quantify the attentional benefit, we used two control conditions. The central-neutral cue appeared at the center of the display. To test for the possibility that this cue reduces the extent of the attentional spread by attracting attention to its location, away from the peripheral target locations (Pashler, 1998), we also employed a distributedneutral cue presented at all possible target locations. By simultaneously stimulating the detectors at all candidate locations, the distributed-neutral cue should also reduce uncertainty as well as any differences in the onset time of activation in response to the central-neutral and the peripheral cues.

We derived the power gain of the inferred filter from the threshold energy elevation at each noise cut-off frequency, by assuming a parabola-shaped filter

$$[\log G(f) = b_0 + b_1 \log f + b_2 (\log f)^2].$$

The low- and high-pass noises are additive if their sum leads to a threshold energy elevation that is equivalent to the sum of threshold energy elevations yielded by each noise alone. If observers exhibit channel switching and utilize the noise-free part of the signal spectrum to perform the task, noise additivity would be violated (Majaj et al., 2002). We assume E to be linearly related to the total power passed through the channel filter mediating letter identification (Solomon and Pelli, 1994; Majaj et al., 2002):

$$E = E_0 + a \int_0^\infty 2\pi f G(f) N(f) df,$$

where E_0 is the threshold at 0 noise, N the noise spectrum, f the spatial frequency, and G the power gain of the channel. We estimate its parameters by maximum likelihood methods. The ratio of the E obtained in the peripheral- and neutral-cue conditions is computed to quantify the attention effect.



Fig. 4. Transient attention decreases threshold (a), but does not alter a channel's peak spatial frequency (b) or its bandwidth (c) (Talgar et al., 2004; Adapted with permission from Talgar et al., 2004, Figs. 3, 4, and 5.)

We found that directing attention to the target location reduces energy threshold by a factor of 2 (Fig. 4a). The magnitude of the effect is consistent with neurophysiological findings, indicating that attention increases the effective contrast of the attended stimulus by a factor of 1.5 (e.g., Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002; Reynolds and Desimone, 2003). Contrary to our hypotheses, there is no change in the tuning of the channel mediating this task, as assessed by the peak channel frequency (Fig. 4b) and the channel bandwidth (Fig. 4c) in each condition for each observer. The channel characteristics are remarkably stable; neither center frequency nor bandwidth was affected. The absence of channel switching makes it clear that transient covert attention does not induce observers to perform this task in a flexible way. Recently, we have reported that sustained attention yields the same pattern of results. It also increases contrast sensitivity in this task, without affecting the channel's center frequency or bandwidth (Pestilli et al., 2004). Lu and Dosher (2004) have corroborated these results.

Transient attention increases sensitivity across the contrast psychometric function

Two types of gain control mechanisms have been considered in neural responses to luminance-modulated stimuli — contrast gain and response gain (Sclar et al., 1989; Fig. 5). The signature of contrast gain is a shift in the 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 signature of a response gain is an increase in firing rate proportional with stimulus intensity. Some have supported a contrast gain model (Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002), but others have reported findings consistent with a response gain model (McAdams and Maunsell, 1999; Treue and Martinez-Trujillo, 1999). How do attentional changes at the neural level affect the psychophysical contrast response functions?

We have examined the effect of transient attention across a range of performance levels, from subthreshold to suprathreshold, when the target was presented alone at 1 of 8 isoeccentric locations (Cameron et al., 2002). We found that transient attention decreased the threshold of the psychometric function for contrast sensitivity in this orientation discrimination task (Fig. 6a). The results were consistent with a contrast gain mechanism; the effect of attention was more pronounced within the dynamic range. However, the high asymptotic level for the neutral condition may have precluded the emergence of response gain.

To assess the role of spatial uncertainty in the precue effect, we conducted two control experiments. First, we made the discrimination task harder by decreasing the tilt of the targets from 15 to 4° . Observers required higher stimulus contrasts to perform this discrimination task, and this in turn diminished spatial uncertainty. Even though the target contrast was higher, an



Fig. 5. Possible effects of attention on the contrast response function. 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 (C50) 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 shifts leftward — boosting the effective contrast of the stimulus. 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}). C50, threshold; R_{max} , asymptote, n, slope, C, contrast level, N, attentional modulation, M, response at lowest stimulus intensity.



Fig. 6. (A) Psychometric functions (percent correct as a function of target contrast) for two of the spatial frequencies used (4 and 8 cpd), for two observers. Neutral precued condition is represented with open symbols and dotted lines; peripheral precue condition is represented with filled symbols and solid lines. Attention shifts the psychometric function to the left, and in some instances, makes the slope shallower (adapted from Cameron et al.,2002, Fig. 3). (B) The peripheral cue increases contrast sensitivity throughout the psychometric function of contrast sensitivity to the same extent in an orientation discrimination task (top panels) for stimuli that differ in spatial uncertainty, 4° vs. 15° tilted (bottom panels), as assessed by localization performance (Cameron et al., 2002, Fig. 10).

attentional effect of similar magnitude was observed (Fig. 6b). In addition, to directly assess the ease with which observers can localize the stimulus, we also performed a localization task. When the target was tilted 15°, discrimination and localization performance were tightly coupled. However, when the targets were tilted 4° , performance on the localization task was much better than performance on the discrimination task. Notwithstanding the superior localization performance on the 4° discrimination task, the attentional effect was comparable for both orientation conditions. Importantly, at contrasts that yielded perfect localization, there was still an attentional effect in the discrimination tasks. Thus, given that we used suprathreshold stimuli, excluded all sources of added external noise (distracters, local and global masks) and showed experimentally that spatial uncertainty cannot explain this decrease in threshold, the observed attentional benefit is consistent with a signal enhancement mechanism.

Transient attention increases contrast at the cued location and decreases it at the uncued location

It had been proposed that very few neurons can be concurrently engaged, but this proposition only recently became tractable and has now been systematically evaluated. The calculations are astonishing — the cost of a single spike is high and severely limits (possibly to about 1%) the number of neurons that can be (substantially) active concurrently (Lennie, 2003). The limited energy expenditure that the brain can afford necessitates machinery for the system to allocate energy according to task demand. This limited capacity entails selective attention, which enables us to process effectively vast amounts of visual information by selecting relevant information from noise. In this study we investigated the possibility that covert attention helps to control the expenditure of cortical computation by trading contrast sensitivity across attended and unattended areas of the visual field, even with impoverished displays and simple tasks. Specifically, we assessed contrast sensitivity at both cued and uncued locations (Pestilli and Carrasco, 2005).

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 and Hoffman, 1974; Rock and Gutman, 1981; Kinchla, 1992). Although most hypotheses regarding the distribution of attention in the visual field assume that information outside the attended area is not processed, many studies have shown that information beyond the focus of attention affects performance, indicating that it is processed to a certain degree (Carrasco and McElree, 2001; Carrasco et al., 2004a,b; Cameron et al., 2004).

When manipulating attention, a cue is considered valid when it indicates the target location, and it is considered invalid when it indicates a nontarget location. Although assessing the effects of attention by comparing performance in the valid and invalid conditions is useful for distinguishing between sensitivity-based and decisionalbased explanations of the cueing effect, this comparison cannot determine whether such an effect is due to an enhanced signal at the cued location, a diminished signal at the uncued location, or both. To pinpoint the source of the attentional effect, it is necessary to compare performance in both the valid and invalid conditions with a neutral condition, in which the cue does not indicate a stimulus location but only the timing of the display onset (Hawkins et al., 1990; Luck et al., 1994; Carrasco and Yeshurun, 1998).

We evaluated the effect of transient attention on contrast sensitivity at both the attended and unattended locations. As discussed above, at the attended area transient attention increases sensitivity in an orientation discrimination task with an informative cue, i.e., when the cue indicates target location but not its orientation (Lu and Dosher, 1998; Carrasco et al., 2000; Cameron et al., 2002). When a peripheral cue is always valid in terms of location, however, some of its effect could be due to a conceptually driven, voluntary component of attention. To eliminate this possible contamination, we ensured cue unpredictability by cueing the target only 50% of the time, and by asking observers to report the orientation of the stimulus indicated by a response cue (a line displayed after stimuli offset). Indeed, observers could have entirely disregarded the cue and based

their responses only on the information accumulated during stimulus presentation and still attained the same overall performance level. The use of the nonpredictive cue and the response cue enabled us to isolate the purely automatic orienting of attention. Given that the transient peripheral cue is thought to be automatic (Yantis and Jonides, 1984; Jonides and Yantis, 1988), even an uninformative cue (which indicates neither target location nor orientation) should exert an effect on performance.

Previous studies have examined the effect of attention on contrast sensitivity at parafoveal locations (e.g., Lee et al., 1997; Lu and Dosher, 1998, 2000; Cameron et al., 2002; Solomon, 2004). We investigated the effects of transient attention at both parafoveal and peripheral locations to assess whether the benefit and cost varied as a function of the distance between the attended and unattended stimuli. Observers were asked to discriminate the orientation of 1 of 2 Gabor patches simultaneously presented left and right of fixation (at either 4 or 9° of eccentricity). 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). Based on models of signal enhancement, which propose that attention directly improves the quality of the stimulus representation (Bashinski and Bacharach, 1980; Lu and Dosher, 1998; Muller et al., 1998; Carrasco et al., 2000; Cameron et al., 2002), we hypothesized that sensitivity would be increased at the cued location. Based on models of distracter exclusion, which propose that attention allows us to exclude distracters from the signal by narrowing the filter processing the stimulus (Davis et al., 1983; Palmer, 1994; Solomon et al., 1997; Foley and Schwarz, 1998; Morgan et al., 1998; Baldassi and Burr, 2000), we hypothesized that sensitivity will be reduced at the uncued location.

Following a peripheral or a central-neutral transient cue, two slightly tilted Gabor patches were simultaneously presented to the left and right of fixation (Fig. 7). A response cue was presented after the Gabors, indicating to the observer for which Gabor the orientation was to be reported, thus defining valid and invalid trials (cue location and response-cue match and do not match, respectively). We estimated contrast thresholds under each attention condition at each eccentricity. Usually, with invalid cue trials attention is diverted away from the target location at stimulus onset, but observers have information regarding the target location because its identity differs from the distracter. However, in this study, observers did not know where the target was, and they had to process the identity of the stimuli presented at both locations to perform the task (Fig. 7).

To quantify the magnitude of the attentional effect, we calculated the ratio of the contrast sensitivity (1/median threshold) for valid vs. neutral cue, and invalid vs. neutral cue at both eccentricities. No difference between the two conditions would yield a ratio equal to 1. A benefit in contrast sensitivity is indicated by values >1; a cost by values <1. All observers followed the same pattern of responses: values >1 for the valid:neutral ratio (cost). Figure 8 (left panel) shows the values for one observer.

The data for individual observers were consistent with the overall frequency distributions. The histograms represent the threshold values obtained in each cue condition at each eccentricity. Although the absolute contrast threshold and the spread of the distribution varied across observers, the valid cue (blue histograms) improved performance and the invalid cue (red histograms) impaired performance with respect to the neutral cue for each individual observer at both eccentricities. Fig. 8 (right panel) illustrates the frequency distribution for the same observer. The same pattern of results, and of comparable magnitude, was obtained at both parafoveal and peripheral locations.

Results from all observers indicate that despite the fact that they were told that the cue was uninformative as to the target location and orientation, and 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. This indicates that information at the attended location is processed to a greater degree than in the neutral condition, and that



Fig. 7. (a) *A trial sequence*. Following a fixation point, a cue appeared either above one of the two Gabor locations (peripheral cue) or at fixation (neutral cue). After an ISI, two Gabors were 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 pointed to a precued Gabor. On another third of the trials it pointed 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 matched. In an invalid trial the locations indicated the left Gabor in half of the trials and the right Gabor in the other half (Pestilli and Carrasco, 2005, Fig. 1).



Fig. 8. The *left panel* depicts the ratios of the medians of the sensitivity (1/median threshold) for one observer for 4°(left two bars) and 9° (right two bars) eccentricity. A ratio >1 indicates a benefit of allocating attention to the target location (valid:neutral ratio: sensitivity in the valid condition is higher than sensitivity in the neutral condition). A ratio <1 indicates a cost of allocating attention to the nontarget location (invalid:neutral ratio: sensitivity in the invalid condition is lower than sensitivity in the neutral condition). The black vertical lines reflect the overall attentional effect, i.e., the valid:invalid ratio. The right panel contains six histograms representing the thresholds obtained for the same observer in each cue condition at 4° and 9° eccentricity. Blue histograms represent the threshold obtained for the valid condition; black histograms represent the neutral cue condition; red histograms represent the invalid cue condition. Black vertical lines indicate the median values. (Adapted from Pestilli and Carrasco, 2005, Fig. 2.)

information processed outside of the focus of attention is processed to a lesser degree. 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 — the sensory representation of the relevant stimuli is boosted — and distracter exclusion at the uncued location — the influence of the stimuli outside the attentional focus is reduced.

By illustrating that transient attention can help in managing the overall bioenergetic expenditure across the attended and unattended locations of the visual field, this study provides evidence for the notion that transient attention directs observers' attention to the cued location in an automatic fashion (Muller and Rabbitt, 1989; Nakayama and Mackeben, 1989; Cheal and Lyon, 1991; Yantis, 1996).

Transient attention increases apparent contrast

From recent 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; James, 1890). Surprisingly, very little direct empirical evidence has been brought to bear on the issue (Tsal et al., 1994; Prinzmetal et al., 1997, 1998), and a number of methodological concerns limit the conclusions we can draw from these studies (Carrasco et al., 2004a,b; Luck, 2004; Treue, 2004; Gobell and Carrasco, 2005).

To directly investigate this issue, Carrasco et al., (2004a,b) implemented a novel paradigm that enables us to assess the effects of spatial cueing on appearance and to test subjective contrast. This paradigm allows one to objectively assess observers' subjective experience while circumventing methodological limitations of previous studies, and to address other questions about phenomenological experience, making it possible to study subjective experience more objectively and rigorously (Luck, 2004; Treue, 2004).

Observers were briefly presented with either a peripheral or neutral cue, followed by two Gabor patches (tilted to the left or right) to the left and right of fixation (Fig. 9). The contrast of one of the Gabors was presented at a fixed contrast (standard), whereas the other varied in contrast randomly from a range of values around the standard (test patch). The orientation of each Gabor was chosen randomly. We manipulated transient attention with an uninformative peripheral cue. We asked the observers: what is the orientation of the stimulus that is higher in contrast? These instructions emphasized the orientation judgment, when in fact we were interested in their contrast judgments; i.e., the orientation discrimination task served as a 'cover story' task, which de-emphasized the fact that we were interested in the observers' subjective experience.

The results showed that transient attention significantly increased perceived contrast (Fig. 10). When a Gabor 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.

We conducted multiple control experiments to rule out alternative accounts of these findings: (1) We increased the temporal separation between the cue onset and the display onset from 120 ms, the optimal time for transient attention, to 500 ms, when transient attention is no longer active. Consistent with the quick decay of transient attention to the cued location, this manipulation yielded no contrast enhancement of the cued stimulus, i.e., there is no appearance effect (data not shown). This result shows that observers were not biased to report the orientation of a cued stimulus per se. (2) When observers are asked to report the orientation of the Gabor of lower contrast, they select the cued stimulus less often if it is of the same contrast as the uncued stimulus (data not shown). This result is consistent with the enhanced apparent contrast of the cued stimulus observed in the main experiment. This control rules out the possibility



Fig. 9. (a) Sequence of events in a single trial. Each trial began with a fixation point followed by a brief neutral or peripheral cue. The peripheral cue had equal probability of appearing on the left- or right-hand side, and was not predictive of the stimulus contrast or orientation. The timing of this sequence maximized the effect of transient attention and precluded eye movements. (b) Task. Observers performed a 2×2 forced choice (2×2 AFC) task: they were asked to indicate the orientation (left vs. right) for the stimulus that appeared higher in contrast. In this trial, they would report the orientation for the stimulus on the right. (Carrasco et al., 2004a,b, Fig. 1.)

that observers report the orientation of a cued stimulus more often simply because they find its orientation easier to judge or are subject to some type of cue bias.

This study provides evidence for a contrast gain model (Reynolds et al., 1999, 2000) in which attention allows for greater neuronal sensitivity, suggesting that attention changes the strength of a stimulus by enhancing its effective contrast or salience. It is as if attention boosts the actual stimulus contrast. The finding that the cue not only enhanced the cued stimulus' appearance but also improved the observers' performance supports the hypothesis that the increased saliency at the target location seems to be the basis of perceptual judgments. Many have considered the saliency map to be the basis of perceptual judgments and a tool for directing gaze to potential relevant locations of the visual environment (Itti and Koch, 2001; Treue, 2004; Gobell et al., 2004; Itti, 2005; Zhaoping, 2005).

Sustained attention and contrast sensitivity

Single-unit studies have evaluated the effects of attention on the contrast response function by manipulating sustained attention (Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002). To evaluate the similarity of the transient and sustained systems of attention, it is important to characterize their effects on early vision, and to investigate whether the same mechanism(s) can underlie such effects. Recently, Ling and Carrasco (2006) obtained contrast psychometric functions for both sustained and transient attention to further bridge the gap between neurophysiological and psychophysical results. We systematically compared sustained and transient covert attention using the same task, stimuli, and observers. We tested whether a signal enhancement mechanism underlies both types of attention. Moreover, we investigated the neural model underlying signal enhancement by measuring the psychometric functions for both sustained and



Fig. 10. Attention alters appearance. Top panel: Appearance psychometric function. Percentage of responses in which observers reported the contrast of the test patch as higher than the standard, plotted as a function of the physical contrast of the test patch. Data are shown for the neutral and peripheral conditions (test cued and standard cued). The standard was 22% contrast and that is the contrast at which the test and standard stimuli attained subjective equality (50%). Bottom panel: Effect of covert attention on apparent contrast. If you were looking at one of the two fixation points (black dots), and the grating to the left of that fixation point was cued, the stimuli at both sides of fixation would appear to have the same contrast. A cued 16% contrast grating appears as if it were 22% contrast. (Adapted from Carrasco et al., 2004a,b, Figs. 4 and 5.)

transient attention to assess whether they have similar or different effects on the contrast response function.

As mentioned above, two types of gain control mechanisms have been considered in neural responses to luminance-modulated stimuli — contrast gain and response gain (Sclar et al., 1989; see Fig. 5). We had provided evidence in support of a contrast gain mechanism for transient attention (Cameron et al., 2002). However, in that study, performance asymptoted close to 100%, leaving little room at the higher contrasts for a possible test of response gain. Neurophysiological studies of sustained attention

that have evaluated these two mechanisms have avoided levels at which neural saturation occurs. Similarly, to properly compare contrast gain and response gain psychophysically, the psychometric functions should arise from a demanding task that ensures that performance on the neutral baseline condition does not asymptote at 100%, leaving room to test for response gain.

Observers performed a 2AFC orientation discrimination task on a slightly tilted Gabor patch. We first established the contrast range required to measure the full extent of the psychometric function with an asymptote that occurs at a performance level that allows room for benefit. We used the method of constant stimuli to measure performance as a function of target contrast in the neutral, transient, and sustained cue conditions. In each trial, a Gabor is presented in 1 of 8 possible isoeccentric locations. The cues (sustained and its neutral control vs. transient and its neutral control) are constant throughout a block, but the spatial frequency and contrast levels are randomized within each block.

Using a nested hierarchical model, for each observer we estimated the probability that the same Weibull distribution can describe the data sets for both cue conditions (sustained vs. its neutral control; transient vs. its neutral control), as opposed to two separate distributions. Additionally, to test the models of response gain vs. contrast gain, we fit the data to their respective models, along with a hybrid model of both response and contrast gain, and compare likelihoods to assess which model describes the data better. Whereas response gain predicts an increasing effect of attention with contrast (a multiplicative effect across the psychometric function), contrast gain predicts only a shift in sensitivity with attention (an overall additive effect independent of stimulus intensity). The hybrid model predicts both a shift in sensitivity as well a multiplicatively increasing effect of attention.

Results indicate that whereas sustained attention operates via contrast gain (Fig. 11; top panel; characterized by a shift in threshold), transient attention operates via a mixture of contrast and response gain (bottom panel; characterized by an effect even at high-contrasts asymptotic levels; Ling and Carrasco, 2006). An uncertainty reduction model of attention



Fig. 11. Psychometric functions for sustained and transient attention. The solid line represents the fits for the neutral condition, and the dashed line represents the fits for the precued. (a) Sustained attention consistently shifted the function to the left, having little impact on its shape, but increasing contrast sensitivity. (b) Transient attention consistently led to an elevation in asymptote, and the fits suggest a decrease in contrast threshold as well. Error bars correspond to mean ± 1 standard error. (Adapted from Ling and Carrasco, 2005, Fig. 3.)

would predict that the attention effect should be most prominent with low-contrast stimuli (where uncertainty is greatest and performance would benefit most from uncertainty reduction) and decrease with increasing stimulus contrast (where uncertainty is diminished and performance would not benefit from uncertainty reduction). However, this was not the case in this study. Moreover, different signature responses across the psychometric function emerged notwithstanding the fact that the reduction of location uncertainty is the same in both cases.

Using the external noise paradigm, Lu and Dosher (1998, 2000) reported that transient covert attention seems to operate via both signal enhancement and external noise reduction. They showed that 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. However, they have attributed sustained attention effects only to an external noise reduction mechanism (Dosher and Lu, 2000a,b; Lu and Dosher, 2000, 2002).

With regard to transient attention, these and previous findings are in agreement; under low external noise conditions, it operates via signal enhancement. However, the results for sustained attention are inconsistent with those reported previously by Dosher and Lu. The most relevant difference that could help reconcile the discrepancy lies in the amount of time observers were given to deploy their sustained attention. The SOA in their studies was 150 ms because it has been reported that this time was enough for experienced observers to deploy sustained attention (Cheal and Lyon, 1991). Perhaps this short timing precluded emergence of the signal enhancement mechanism. It is possible that the observers who failed to show an effect were not trained optimally to deploy sustained attention within the allotted time; had they had longer time to deploy sustained attention an effect could have emerged.

In a sustained attention task, using a dual-task paradigm in which observers performed tasks under conditions of full or poor attention, evidence for pure response gain has been reported (Morrone et al., 2004). However, a subsequent psychophysical study suggested that dual task, sustained attention may operate via a hybrid model, involving both contrast gain and response gain (Huang and Dobkins, 2005). Whereas the dual-task paradigm has some advantages, such as eliminating location uncertainty reduction as an alternative explanation, it has disadvantages that may have hampered their conclusions. 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., Sperling and Dosher, 1986; Pashler, 1998). The difference with the present results 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 we directed attention toward the target.

This study systematically compared sustained and transient covert attention using the same task, stimuli, and observers. On the one hand, both types of attention had a similar effect on performance; they increased contrast sensitivity under zero-noise conditions (the display contained nothing to be suppressed, since there was no added external noise). Hence, we conclude that both attentional systems can be mediated by a signal enhancement mechanism. Furthermore, because this effect occurred even with very high-contrast stimuli, it cannot be explained by uncertainty reduction. On the other hand, sustained and transient attention had different effects on the contrast response function. Sustained attention enhances contrast sensitivity strictly via contrast gain, whereas, in addition to contrast gain, transient attention revealed response gain.

Neurophysiological studies of attentional modulation of apparent stimulus contrast: attentional facilitation and selection

The development of techniques to record the activity of neurons in awake-behaving animals has enabled researchers to probe the biological foundations of sustained attention. Single-unit recording studies in the monkey have provided detailed, quantitative descriptions of how attention alters visual cortical neuron responses.

A number of neurophysiological studies have shown that directing 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 Reynolds and Chelazzi, 2004; Martinez-Trujillo and Treue, 2005; Reynolds, 2005).

With regard to attentional facilitation, consistent with psychophysical findings, 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., Motter, 1993; Ito and Gilbert, 1999; McAdams and Maunsell, 1999; 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. The contrast response function (CRF) summarizes the way in which changes in stimulus contrast are translated into changes in neuronal firing rate via a nonlinear sigmoid function (Fig. 5). Consistent with a contrast gain, in V4, an extrastriate visual area at an intermediate stage of the ventral processing stream, attention shifts the CRF 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), it fails to elicit a response, when unattended. However, when the monkey attended to its location in the RF the same 10% contrast elicits the neuron to respond. Attention does not alter the neuronal response when the stimulus is above saturated contrast. Across a population of V4 neurons, the greatest increments in firing rate were observed at contrasts in the dynamic range of each neuron's CRF (Fig. 12). The finding that similar results were found for preferred and poor stimuli indicates that the lack of attentional effect at high contrast did not reflect an absolute firing rate limit; instead, it reflected a leftward shift in the contrast response function.

Under the conditions of this experiment, 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). This value has been corroborated by other studies that have also quantified spatial attention in units of luminance contrast, including studies in MT (Martinez-Trujillo and Treue, 2002) and in V4 (Reynolds and Desimone, 2003), whose estimates were 50% and 56%, respectively. As mentioned above, this effect of attention is indistinguishable from a change in stimulus contrast (see also Maunsell and McAdams, 2000).

Given our limited ability to process information, it is also crucial to understand how attentional selection of behavioral relevant stimuli from among competing distracters (Wolfe, 1994; Palmer et al., 2000; Carrasco and McElree, 2001; Verghese, 2001; Cameron et al., 2004) 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 taskrelevant 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



Fig. 12. Response of an example neuron from area V4 as a function of attention and stimulus contrast. (A) The contrast of the stimulus in the receptive filed 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 with permission from Reynolds et al., 2000.)

Attend away

Rate change

% Change

Attend RF

nonpreferred stimulus. Several labs have replicated this observation that the attentional modulation depends on the similarity between the attended stimulus properties and the sensory preferences of the neuron, both in the ventral (Chelazzi et al., 1993, 1998, 2001; Reynolds et al., 1999; Sheinberg and Logothetis, 2001; Reynolds and Desimone, 2003) and in the dorsal (Treue and Maunsell, 1996; Treue and Martinez-Trujillo, 1999) streams.

For instance, 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 nonpreferred. 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 nonpreferred stimulus the response is reduced so that it approaches the low response elicited when it is presented by itself (Fig. 13). In short, attending to the preferred stimulus increases the response to the pair but attending to the poor stimulus reduces the response evoked by the pair. This results 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. Martinez-Trujillo and Treue (2002) presented two pairs of random dot patterns, one inside the RF and one outside the RF. In each pair, the potential target moved in the null direction and the distracter moved in the preferred direction. They recorded the cell's responses to various contrast levels of the distracter patterns, moving in the preferred direction, in two attentional conditions, when the target was the stimulus outside or inside the receptive field (Fig. 14, top panel). Both sets of functions, attending inside and outside the RF were fit with a sigmoid function (Fig. 5). Attending to the null pattern inside the RF strongly increased threshold



Fig. 13. Effect of attention to one of two stimuli in the RF of a V4 neuron. Each function shows the response of a single V4 neuron averaged over repeated stimulus presentations, under different stimulus and attentional conditions (indicated by the icon). When the preferred stimulus is attended the response for the stimulus pair increases approaching the level of response elicited when the preferred stimulus is presented alone; conversely, when the poor stimulus is attended the level of activity is reduced, approaching the level of activity elicited when the poor stimulus is presented alone. (Adapted with permission from Reynolds et al., 1999.)



Fig. 14. (A) Two pairs of random dot patterns appeared simultaneously on the screen, one inside and the other outside the cell's receptive field. Each pair consisted of one preferred and one null pattern. The monkeys always attended to the null pattern, inside the receptive field (top row) or outside the receptive field (bottom row). From left to right the panels illustrate decreasing luminance value of the preferred patterns leading to a decrease in response. (B) Average responses of one MT neuron to different contrast levels in the attending outside and attending inside conditions. The vertical lines indicate the C50 value for each curve and the tables shows the values of four parameters (see Fig. 5 for R_{max} , C50, *n*, and *M*) (C) Average normalized responses after aligning the contrast response functions in all units to their respective C50 values in the attending outside condition. (Adapted with permission from Martinez-Trujillo and Treue, 2002.)

with only a slight change in asymptote (Fig. 14, bottom panels). This indicates that the response suppression to a distracter was stronger when the stimulus had intermediate contrast. The slight change in asymptote occurred despite the fact that the sampled cells were capable of much higher firing rates. This study demonstrates that the magnitude of attentional modulation depends on the stimulus contrast of the unattended stimuli inside the receptive field. Attention had a stronger effect on responses of direction-selective MT neurons when a distracter presented in their receptive field had intermediate, rather than low or high contrast. This result is consistent with contrast gain. Martinez-Trujillo and Treue (2002) have suggested that the attentional effects observed in MT may result from the modulation of input gain, which would be similar to a change in stimulus contrast; that the attentional effects vary nonlinearly as a function of stimulus contrast indicates that these effects are not simple multiplications of a cell's response.

Likewise, Chelazzi et al. (2001) obtained a similar pattern of results while recording in area V4 of monkeys performing a visual search task involving objects (faces and houses). The finding 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, provides support for attentional models positing that response suppression mediates the selection of one stimulus and the inhibition of the other (e.g., Desimone and Duncan, 1995; Ferrera and Lisberger, 1995; Lee et al., 1999).

The common nonlinearity between the CRF and the magnitude of attentional modulation across different areas of the dorsal and ventral pathways indicate a tight link between attentional mechanisms and the mechanisms responsible for contrast encoding. Indeed, it has been proposed that because this tight link does not seem to exist for the encoding mechanisms of other stimulus properties (e.g., motion coherence), attention can be considered a mechanism aimed at modulating stimulus saliency while leaving other stimulus properties relatively unchanged (Martinez-Trujillo and Treue, 2002).

A similar relative enhancement or suppression of stimulus representations can be obtained when varying stimulus contrast. Given that the role of contrast in modulating the visual response properties of neurons has been well documented, and that response suppression plays an important role in the models developed to account for these modulations, to better understand the role that attention may play in selecting stimuli, it is important to consider the role of suppression in the visual cortex (Reynolds and Chelazzi, 2004; Reynolds, 2005).

Contrast changes in the visual stimulus yield multiplicative changes in neuronal responses, similar to those evoked by attention (e.g., Tolhurst, 1973; Sclar and Freeman, 1982; Treue and Martinez-Trujillo, 1999). The similarity between the effects of attention and the effects of varying stimulus contrast could indicate that these two processes are closely related and probably use similar mechanisms to modulate neuronal responses. Were this the case, one would expect attentional and contrast modulation of neuronal responses to share the same properties (Martinez-Trujillo and Treue, 2005; Reynolds, 2005).

It is known that contrast modulates neuronal responses in the following ways:

- (1) Cortical neuronal responses typically saturate as contrast increases, and this saturationfiring rate is stimulus-dependent. The dynamic range is larger and the saturation point is higher for a stimulus of the neuron's preferred orientation than for a stimulus of poor but excitatory orientation, and no response is elicited by a nonpreferred stimulus. Thus, increasing contrast leads to a multiplicative increase in the response (Sclar and Freeman, 1982; Fig. 15A). Correspondingly, consistent with the idea of attentional facilitation, attention causes a leftward shift in the contrast response function by increasing the effective contrast of a stimulus (Reynolds et al., 2000; Fig. 12).
- (2)Increasing the stimulus contrast characteristically results in a multiplicative increase in the neurons' tuning curves for properties such as motion and orientation (Sclar and Freeman, 1982; Fig. 15B). The multiplicative effect of contrast on the orientation-tuning curve is due to the fact that contrastresponse functions derived for any orientations can be related to each other by a gain factor, as is the case in Fig. 12. Similarly, spatial attention causes a multiplicative increase in the orientation-tuning curve of neurons in area V4, without otherwise altering its shape. This increase in the gain of the orientation-tuning curve enables neuronal signals to better distinguish the orientation of the stimulus (McAdams and Maunsell, 1999). Likewise, attention multiplicatively increases the direction of motion-tuning curves of neurons in area MT (Treue and Martinez-Trujillo, 1999).
- (3) When two spatially superimposed gratings of different orientation appear simultaneously



Fig 15. Contrast-dependent response modulations. (A) Contrast-response functions for a stimulus of the neuron's preferred orientation (upper line), a poor but excitatory orientation (middle line), and the null orientation (bottom line). (Adapted with permission from Sclar and Freeman, 1982.) (B) Orientation tuning curves of a second neuron, stimulus contrast varied from 10% (empty circles) to 80% (filled circles). (Adapted with permission from Sclar and Freeman (1982.) (C) Responses of a neuron recorded in area V1 of an anesthetized macaque. Two superimposed gratings appeared within the receptive field: one grating was of optimal orientation, the other was of a suboptimal orientation; both gratings varied from 0% to 50% contrast. (Adapted with permission from Carandini et al., 1997.) (D–F) The contrast gain model can account for these contrast-dependent response modulations. (See text; adapted with permission from Reynolds, 2005.)

within a receptive field in V1, increasing the contrast of one of them results in an increased or decreased response depending on the neuron's selectivity for the two stimuli. In general, increasing the contrast of the preferred grating increases the response to the pair; conversely, increasing the contrast of the nonpreferred grating decreases the response to the pair. However, the highest contrast preferred stimulus seems to be virtually immune to the suppressive effect of the nonpreferred stimulus (Carandini et al., 1997; Fig. 15C). Correspondingly, this pattern of results is observed when attention is directed to one of two stimuli in the receptive field; attending to one of them will either increase or decrease the response, depending on the cell's relative preference for the two stimuli — the attended stimulus dominates the neuronal response (e.g., Luck et al., 1997; Reynolds et al., 1999; Treue and Martinez-Trujillo, 1999; Chelazzi et al., 2001; Martinez-Trujillo and Treue, 2002; Reynolds and Desimone, 2003).

(4) Similar modulations of the contrast-dependent response occur in V4 when two stimuli appear at separate locations in the visual field. On the one hand, a 5% contrast-poor stimulus has no measurable effect on the neuronal responses of the preferred stimulus but becomes increasingly suppressive as contrast increases. On the other, suppression is diminished if the preferred stimulus is elevated in contrast (Reynolds and Desimone, 2003; Fig. 16). Correspondingly, psychophysical studies show that attention increases contrast sensitivity (Pestilli and Carrasco, 2005; Fig. 8) and apparent contrast (Carrasco et al., 2004a,b; Fig. 9) at the attended location while reducing both contrast sensitivity and apparent contrast at the unattended location.

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. This model is mathematically related to models that account for the contrast-dependent effects described above. 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; Fig. 12).

This effect results in a shift of the contrast response function to the left, just as in neurophysiological (Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002) and psychophysical (Dosher and Lu, 2000; Cameron et al., 2002; Carrasco et al., 2004a,b; Ling and Carrasco, 2006; Figs. 6, 10, and 11) studies. See predictions of contrast gain model Fig. 15D. 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 and Maunsell, 1999; Treue and Martinez-Trujillo, 1999). See predictions of contrast gain model Fig. 15E. Moreover, as attention shifts contrast, its effect on the neuronal response depends on whether attention is directed toward the preferred or the nonpreferred stimulus (Reynolds et al., 2000; Chelazzi et al., 2001, Martinez-Trujillo and Treue, 2002). See predictions of contrast gain model in Fig. 15F.

Although it is not the focus of this chapter, it is important to mention that with respect to sustained attention, modulations of responses in the visual cortex occur as a result of feedback from areas like the lateral intraparietal area (LIP) and the frontal eye fields (FEF). At LIP, elevated responses are associated with increased contrast sensitivity at the behavioral level. At FEF, microstimulation causes spatially localized increases in sensitivity both at the behavioral level and in visual cortical neurons, which mimic the effect of spatial attention at the behavioral and the neuronal level (reviewed in Chelazzi and Reynolds, 2004).

Transient attention enhances perceptual performance and fMRI response in human visual cortex

Studies on brain mechanisms of attention have mostly examined sustained attention, and some of them have characterized its effects on stimulus processing in the visual cortex. For instance, in single-unit recording studies, researchers have learned that sustained attention can reduce external noise by reducing the influence of unattended stimuli (Moran and Desimone, 1985; Luck et al., 1997) and that it can also boost the signal by



Fig. 16. Increasing the contrast of a poor stimulus at one location suppresses the response elicited by a fixed contrast preferred stimulus at a second location in the receptive field of a V4 neuron. The poor stimulus' contrast (left column) increased from 5 to 80%, and did not elicit a clear response at any contrast. The preferred stimulus was fixed in contrast (right column). For the response to the pair (middle column), at low contrast, the poor stimulus had no measurable effect on the response to the preferred stimulus, but as its contrast increased (moving up the column) it became increasingly suppressive. (Adapted with permission from Reynolds and Desimone, 2003.)

increasing the effective stimulus contrast (Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002). Correspondingly, human electrophysiological studies have provided evidence that attention can increase sensory gain (Johannes et al., 1995; Hillyard and Anllo-Vento, 1998), and neuroimaging studies have shown attentional modulation of neural activity in many visual areas (Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000), including the primary visual cortex (Brefczynski and DeYoe, 1999; Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999).

Less is known about the neural mechanism for transient attention and its effects on stimulus

processing. Psychophysical findings demonstrating that transient attention increases contrast sensitivity (e.g., Lu and Dosher, 1998; Carrasco et al., 2000; Cameron et al., 2002; Ling and Carrasco, 2006) suggest that transient attention should enhance neural activity in early stages of visual processing. We tested this hypothesis by measuring brain activity in early visual areas using rapid event-related fMRI in conjunction with a peripheral cueing paradigm to manipulate transient attention (Liu et al., 2005). Participants discriminated the orientation of one of two gratings preceded or followed by a nonpredictive peripheral cue.

A number of previous neuroimaging studies in humans have examined the control mechanism of attentional capture in the frontoparietal network (reviewed in Corbetta and Shulman, 2002), but those studies have not addressed the effects of transient attention on the stimulus representation in the visual cortex. This is perhaps due to a potential measurement difficulty with the peripheral cueing paradigm used to manipulate transient attention. In this paradigm, a cue is briefly presented in the periphery and quickly followed by a stimulus nearby; the cue draws attention to the location of the upcoming stimulus. Because the spatiotemporal separation between the cue and stimulus is relatively small compared to the spatiotemporal resolution of imaging techniques, it is difficult to differentiate the sensory response to the cue and attentional modulation of the stimulusevoked response and thus to rule out an explanation based on sensory summation.

We circumvented this methodological limitation with two innovations in our experimental design, involving a spatial and a temporal manipulation that complement each other. First, to anatomically separate the cue and stimulus responses we presented them above and below the horizontal meridian, respectively (Fig. 17a). Early retinotopic areas (V1, V2, and V3) form quadrant representations of the visual field (Horton and Hoyt, 1991) such that the cue and stimulus would activate the ventral and dorsal partition of the visual cortex, respectively. Because V1 has a contiguous hemifield representation, we determined the distance necessary to separate the cue and stimulus activity within V1. However, given that the hemifield representation and larger receptive fields of higher visual areas (e.g., V3a and hV4) are likely to give rise to overlapping activations of the cue and stimulus, and given subthreshold activation, imperfect image coregistration and surface reconstruction, it may not be possible to completely isolate the cortical locations activated by the cue and stimulus. Thus, in addition to the spatial control, we took advantage of the sluggishness of the hemodynamic response and evaluated the effect of postcue trials to control for the sensory effect of the cue. A postcue trial was identical to a precue trial, except that the temporal order of the cue and stimulus were reversed. The two trial types had identical amounts of visual stimulation, but the postcue does not elicit transient attention. Because of the sluggishness of the hemodynamic response compared to the cue-stimulus interstimulus-interval (50 ms), a sensory response from a region that responded to both the cue and stimulus could not differentiate the order of the two. Thus, any differential effects between the precue and postcue conditions cannot be attributed to purely sensory summation of the hemodynamic response to the cue and stimulus, and must represent attentional modulation.

We presented two Gabor patches simultaneously in the periphery, one vertical and one tilted. Participants were asked to discriminate the orientation of the tilted Gabor (target); the vertical Gabor was a distracter. We used orientation discrimination to assess the effect of attention on stimulus contrast because performance on this task improves with increasing contrast (Nachmias, 1967; Skottun et al., 1987; Lu and Dosher, 1998;



Fig. 17. The diagram on the left illustrates the locations of the cue and the Gabor stimulus, which were presented in alternating blocks. Shown on the right are data from the right hemisphere of one participant, viewed on an inflated surface representation of the posterior occipital cortex. Light and dark gray depict gyral and sulcal surfaces, respectively. Brain activity associated with the cue and the Gabor stimulus are shown in blue and green maps, respectively. Black lines indicate the borders of early visual areas defined by the retinotopic mapping procedure (solid line: vertical meridian, dashed line: horizontal meridian). The asterisk indicates the foveal confluence where borders between areas cannot be resolved. The activation of the cue and the Gabor did not overlap in V1, V2, and V3. Activity started to overlap in V3a and hV4, as they contain a hemifield representation (Liu et al., 2005, Fig. 2.)

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Cameron et al., 2002) and because fMRI response increases monotonically with stimulus contrast (Boynton et al., 1999). Each Gabor was either preceded or followed by a cue that was either valid or invalid. As mentioned above, the terms 'valid' and 'invalid' refer to whether the cue and target appeared on the same or on opposite sides, respectively. In fact, the cue was not predictive of either the location of the target (50% validity) or of its orientation. Participants were explicitly told that the cue was completely uninformative regarding both target location and orientation and that there was no benefit whatsoever in using the cue to perform the task (Carrasco et al., 2004a,b; Gobell and Carrasco, 2005).

In each experimental session, we localized cortical regions responding to the target stimuli and performed region-of-interest analyses on the fMRI signal in early visual areas V1, V2, V3, V3a, and hV4. Representative results from the localizer scan are shown in Fig. 17b on an inflated right hemisphere. The blue and green maps depict activations for the cue and the Gabor stimulus. respectively. Consistent with the known retinotopic organization of early visual areas, the cue and the Gabor stimulus largely activated ventral and dorsal regions of visual cortex, respectively. The separation between cue and Gabor activity was evident in V1 even though the dorsal and ventral representations are contiguous in that area. Activations for the cue and the Gabor remained separate in dorsal V2 and V3, whereas they started to overlap in higher areas such as V3a and hV4, which was expected as these areas contain a hemifield representation (Tootell et al., 1997; Wade et al., 2002).

Discrimination accuracy and reaction time (RT) were computed for each participant in each condition, and the group average is shown in Fig. 18a. The valid precue condition produced the highest accuracy — the accuracy of valid precue condition was higher than that of the invalid precue, valid postcue and invalid postcue conditions; accuracy did not differ for these three conditions. Correspondingly, the valid precue also yielded the shortest responses — RT in the valid precue, which in turn was faster than for the valid postcue, with the invalid postcue being the slowest. This pattern of results indicates that there was no speed-accuracy tradeoff across different conditions.

The group-averaged estimates of the fMRI response for contralateral targets and distracters are shown in Fig. 18b. A given trial always contained one target (tilted Gabor) and one distracter (vertical Gabor) in opposite hemifields. The activity level of different conditions did not differ significantly in V1, whereas activity for the valid precue condition was higher than for the other conditions in extrastriate visual areas. We tested for the possible effect of sensory summation of the cue and target, we compared valid postcue vs. invalid precue or vs. invalid postcue conditions. These comparisons yielded no significant effects in any visual area. All observers followed the same pattern of results. If a mere summation of the sensory response of the cue and target were responsible for the differences among the experimental conditions, we should have observed similar levels of fMRI response for the precue and postcue trials. The finding that activity was higher for the valid precue than for the valid postcue conditions allows us to rule out the possibility that the enhanced fMRI signal was due to lowlevel sensory effects of the cue.

Compared to control conditions, 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. Control conditions indicated that enhanced fMRI response was not due to sensory summation of cue and target signals. Thus, an uninformative precue 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 transient attention on early vision.

To further quantify the effect of transient attention, we calculated an attention modulation index, similar to that used in single-unit physiology (Treue and Maunsell, 1996). A large attentional effect leads to an AMI value close to 1, and a small effect leads to an AMI value close to 0. The attention modulation index increased gradually from V1 to extrastriate visual areas (from about 0.05 to about



Fig. 18. Group-averaged data. (a) Behavioral results. Proportion correct (left) and reaction time (right) are shown for the four cue conditions (V-Pre: valid precue, I-Pre: invalid precue, V-Post: valid postcue, I-Post: invalid postcue). Error bars are 1 s.e.m. (b) Imaging results. Mean fMRI responses across participants for each cue condition and distracter are shown for each visual area. Response was obtained from the dorsal (V1, V2, V3 and V3a) and ventral (hV4) representations of the target (the green areas in Fig. 15). The average standard error of all time-points along a curve is shown as the error bar on the first time-point. (Adapted with permission from Liu et al., 2005, Fig. 3.)

0.3). Larger attentional effects in higher visual areas have also been found in studies of sustained attention (e.g., Kastner et al., 1999; Maunsell and 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 sustained attention, a conceptually driven mechanism, is mediated by a feedback mechanism (Desimone and Duncan, 1995; Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000; Schroeder et al., 2001; Corbetta and Shulman, 2002), a feed-forward model seems more likely in the case of transient attention, a stimulusdriven mechanism. Such a feed-forward model could be implemented by steeper CRFs in extrastriate than striate areas. This higher sensitivity in extrastriate areas is due to areal summation across progressively larger receptive fields in higher areas (Sclar et al., 1990). Given that attention can boost the signal by increasing the effective stimulus contrast (Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002) via contrast gain (Reynolds et al., 2000; Cameron et al., 2002; Martinez-Trujillo and Treue, 2002; Carrasco et al., 2004a,b; Ling and Carrasco, 2006), its effect would be more pronounced in areas with steeper CRFs.

To conclude, these results show that transient attention increases neural activity at the retinotopic locations of the subsequent target stimulus. The spatial and temporal parameters used enabled us to rule out a pure sensory explanation of this effect. We demonstrated that a nonpredictive peripheral cue increased both behavioral performance and retinotopic-specific neural response to a subsequent stimulus. Our results are the first to provide a retinotopically specific neural correlate for the effects of transient attention on early vision with a concomitant behavioral effect. The increased fMRI response in visual cortex brought about by transient attention provides the neural correlate of enhanced behavioral performance in an early visual task - enhanced contrast sensitivity in orientation discrimination. Previous research in single-unit physiology (Reynolds et al., 2000;

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Martinez-Trujillo and Treue, 2002) and human psychophysics (e.g., Lu and Dosher, 1998; Lee et al., 1999; Carrasco et al., 2000, 2004a,b; Cameron et al., 2002; Ling and Carrasco, 2006; Pestilli and Carrasco, 2005) indicate that covert attention increases contrast sensitivity. By supplying evidence from an intermediate scale of analysis — neuroimaging — this study narrows the gap between single-unit physiology and human psychophysics of attention.

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 consumption available to the brain, and the cost of cortical computation is high. Attention is crucial in optimizing the systems' limited resources.

This chapter has focused on the effects of spatial attention on contrast sensitivity, for which the best mechanistic understanding of visual attention has been achieved due to the confluence of psychophysical, electrophysiological, and neuroimaging studies.

I illustrated how psychophysical studies allow us to probe the human visual system. Specifically, I discussed studies showing that attention enhances contrast sensitivity, and how these studies allow us to characterize the underlying mechanisms, namely external noise reduction and signal enhancement. It is reasonable to assume that attentional modulation may reflect a combination of mechanisms, such as reduction of external noise, reduction of spatial uncertainty, and signal enhancement (e.g., Carrasco et al., 2000, 2002; Dosher and Lu, 2000; Pestilli and Carrasco, 2005). Many of the studies conducted in my lab have been designed to isolate and evaluate the existence of signal enhancement; they indicate that increased contrast sensitivity and increased spatial resolution can be mediated by signal enhancement (Carrasco, 2005). Psychophysical studies characterizing the effects of transient and sustained attention have shown that covert attention increases the signal across the contrast sensitivity function (Carrasco et al., 2000) and across the

contrast psychometric function (Cameron et al., 2002). Both sustained and transient attention can be mediated by signal enhancement, as revealed by the finding that the increased contrast sensitivity emerges under conditions of zero-external noise (Ling and Carrasco, 2006).

We have shown that the attentional effect exceeds the effect predicted by reduction of location uncertainty. For instance, although location uncertainty is greater at low- than at high-performance levels, the magnitude of the attentional benefit is similar regardless of the likelihood of observers confusing the target with blank locations. Attention increases sensitivity throughout the psychometric function of contrast sensitivity to the same extent for stimuli that differ in spatial uncertainty (Cameron et al., 2002; Ling and Carrasco, 2006) and even when localization performance indicates that there is no uncertainty with regard to the target location (Carrasco et al., 2000). In addition, the presence of a local postmask, which reduces location uncertainty, does not affect the magnitude of the attentional benefit (Carrasco et al., 2000).

To explore how the enhancement of contrast sensitivity at the attended location comes about we investigated whether covert attention affects the tuning of a spatial frequency channel. Attention halved the contrast threshold necessary for letter identification. However, we found no change in the tuning of the channel mediating letter identification: covert attention did not affect the peak frequency of the channel or the channel bandwidth (Talgar et al., 2004; Pestilli et al., 2004).

Investigating whether the enhancement of contrast sensitivity at the attended location has a concomitant cost at other locations, we found that compared to a neutral condition, an uninformative peripheral precue improves discrimination performance at the cued location and impairs it at the uncued location. This was the case despite the simplicity of the display and despite the fact that observers knew the cue was uninformative, they were explicitly told that the cues contained no information regarding either the location or the orientation of the target (Pestilli and Carrasco, 2005). The presence of a benefit and a cost reflects the bioenergetic limitations of the system. These changes are consistent with the idea that attention elicits two types of mechanisms: signal enhancement — the sensory representation of the relevant stimuli is boosted — and external noise reduction — the influence of the stimuli outside the attentional focus is reduced. In addition, this pattern of results confirms the stimulus-driven, automatic nature of transient attention. Similar results have been reported for contrast appearance (Carrasco et al., 2004a,b), spatial frequency appearance (Gobell and Carrasco, 2005), accuracy and temporal dynamics of visual search (Giordano et al., 2004), and for accuracy of letter identification (Luck and Thomas, 1999).

Pestilli and Carrasco (2005) documented the effect of transient attention on *performance* in an orientation discrimination task. The effect of transient attention on apparent contrast is remarkably consistent: compared to a neutral cue, apparent contrast is increased at the cued location and decreased at the other location (Carrasco et al., 2004a,b). This appearance study has been considered a crucial step in completing a chain of findings that provide insights with regard to the immediate perceptual consequences of attention (Treue, 2004). This chain is composed of neurophysiological results indicating that: varying contrast levels create multiplicatively scaled tuning curves (e.g., Sclar and Freeman, 1982); attention similarly scales neural responses (McAdams and Maunsell, 1999; Treue and Martinez-Trujillo, 1999); attention influences contrast gain mechanisms (Di Russo et al., 2001; Cameron et al., 2002; Ling and Carrasco, 2006); and that attentional modulation and changes in stimulus contrast create identical and therefore indistinguishable modulation of firing rates (Reynolds et al., 2000; Treue, 2001; Martinez-Trujillo and Treue, 2002).

As mentioned above, the high bioenergetic cost of firing entails the visual system to use neural coding that relies on very few active neurons (Barlow, 1972). For many perceptual aspects, e.g., to distinguish figure and ground, it is advantageous for the system to enhance contrast in an economic fashion. Treue (2004) has pointed out that much like the center-surround organization of visual receptive fields that serves to enhance the perceived contrast of luminance edges, attention is another tool providing an organism with an optimized representation of the sensory input that emphasizes relevant details, even at the expense of a faithful representation of the sensory input. Indeed, many human psychophysical studies (e.g., Itti and Koch, 2001; Itti, 2005; Zhaoping, 2005) as well as monkey single-unit recording studies (e.g., Reynolds and Desimone, 2003; Treue, 2004) have likened attention to increasing visual salience.

Both sustained and transient attention can increase contrast sensitivity by increasing the signal; however, these attentional systems have different effects on the CRF: sustained attention enhances contrast sensitivity strictly by contrast gain, whereas transient attention does so by a mixture of contrast gain and response gain (Ling and Carrasco, 2006). Our psychophysical findings for sustained attention are consistent with single-cell studies showing that the increased sensitivity brought about by sustained attention is mediated by contrast gain (e.g., Reynolds et al., 2000, Martinez-Trujillo and Treue, 2002). Obviously, comparisons between psychophysical and neurophysiological results need to be made with caution. Whereas the results of psychophysical studies presumably represent the response of the entire visual system, neurometric response functions are based on the response of single neurons or groups of neurons confined to particular regions of the visual system. Moreover, to date, there are no studies of single-unit recordings dealing with transient attention. Nevertheless, the link between psychometric and neurometric findings is tenable; for simple visual tasks such as motion discrimination, responses from single-unit recordings in MT are capable of accounting for behavioral psychometric functions (Britten et al., 1992).

There are several ways in which the link of psychometric and neurometric functions can be strengthened. First, it would be ideal that while characterizing single-unit activity, neurophysiological studies would index behavioral effects. Second, it would be ideal to implement a paradigm that enables the investigation of the effects of transient attention in awake-behaving monkey to develop a system's model of this stimulus-driven attentional system. The lack of single-cell studies of transient attention is probably due to the fact that it is hard to disentangle the effect of transient attention from a sensory cue effect. As mentioned above, we have been able to overcome such limitations and isolate the effect of transient attention in an fMRI study (Liu et al., 2005). Although the methodological challenges and the possible way to overcome them differ, meeting this challenge would significantly advance the field.

A third way to fortify the link of psychometric and neurometric functions is to conduct neuroimaging studies, in particular fMRI, as they provide an intermediate level of analysis capable of indexing retinotopic activity. In my opinion, the usefulness of fMRI studies of attention in narrowing the gap between psychophysical and electrophysiological studies depends on our understanding of the behavioral task performed during imaging, and the degree to which these studies can provide a neural correlate for the effects of attention on vision with a concomitant behavioral effect.

A fourth way is to take more seriously the idea of including biological constraints in the modeling of attention and in the generation of psychophysical experiments. For instance, in this chapter, I discussed how the wealth of knowledge regarding contrast-dependent changes in neuronal response could account for contrast dependent modulation of the competitive interaction observed when multiple stimuli appear within a neuron's receptive field. We could implement psychophysical paradigms to exploit all aspects of this parallel.

Although not the topic of this chapter, it is worth mentioning that attention speeds information processing (Carrasco and McElree, 2001; Carrasco et al., 2004a,b), but the neural basis of this effect is unknown. We know that speed of processing increases with stimulus contrast (Albrecht, 1995; Carandini et al., 1997). We also know that the effect of attention on contrast sensitivity is akin to increasing stimulus contrast (e.g., Reynolds et al., 2000; Carrasco et al., 2004a,b). However, increasing stimulus contrast seems to accelerate information processing to a lesser degree than the speeding of processing time brought about by attention. It remains to be explored, psychophysically and neurophysiologically, to what degree the effect of attention on contrast may mediate its effect on the speed of information processing.

To close, our understanding of visual attention has been advanced by the integration of different levels of analysis and methodologies. In this chapter, it has been illustrated how combining knowledge gathered from single-unit neurophysiology, psychophysics, and neuroimaging techniques, proves useful to understanding the way in which attention increases contrast sensitivity, in particular, and how attention alters perception.

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