CHAPTER 5

Covert attention effects on spatial resolution

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Abstract: First, we review the characteristics of endogenous (sustained) and exogenous (transient) spatial covert attention. Then we examine the effects of these two types of attention on spatial resolution in a variety of tasks, such as acuity, visual search, and texture segmentation. Both types of covert attention enhance resolution; directing attention to a given location allows us to better resolve the fine details of the visual scene at that location. With exogenous attention, but not with endogenous attention, this is the case even when enhanced spatial resolution hampers performance. The enhanced resolution at the attended location comes about at the expense of lower resolution at the unattended locations.

Keywords: covert attention; exogenous attention; transient attention; endogenous attention; sustained attention; texture segmentation; spatial resolution; visual search; acuity

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 separating the wheat from the chaff, selecting relevant information out of the irrelevant noise. Attention is what turns looking into seeing, allowing us to select a certain location or aspect of the visual scene and to prioritize its processing. Such selection is necessary because the limits on our capacity to absorb visual information are severe. They may be imposed by the fact that there is a fixed amount of overall energy consumption available to the brain, and by the high-energy cost of the neuronal activity involved in cortical computation. Attention is crucial in optimizing the use of the system's limited resources, by enhancing the representation of objects appearing at the relevant locations or composed of relevant features while diminishing the representation of objects appearing at the less relevant locations, or composed of less relevant aspects of our visual environment.

The processing of sensory input is facilitated by knowledge and assumptions about the world, by the behavioral state of the organism, and by the (sudden) appearance of possibly relevant information in the environment. For example, spotting a friend in a crowd is much easier if you know two types of information: where to look and what to look for. Indeed, numerous studies have shown that directing attention to a spatial location or to distinguishing features of a target can enhance its discriminability and the neural response it evokes.

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Spatial covert attention

Attention can be allocated by moving one's eyes toward 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. Cognitive, psychophysical, electrophysiological, and neuroimaging studies provide evidence for the existence of covert attention in both humans and nonhuman primates. Humans deploy covert attention routinely in many everyday situations, such as searching for objects, driving, crossing the street, playing sports, and dancing, as well as in social situations such as when deception about intentions is desired, in competitive activities like sports, or when moving the eyes would provide a cue to intentions that the individual wishes to conceal.

Covert attention improves perceptual performance — accuracy and speed — on many detection, discrimination, and localization tasks. Moreover, covert attention affects performance and appearance of objects in several tasks mediated by dimensions of early vision, such as contrast sensitivity (reviewed in Carrasco, 2006; Reynolds and Chelazzi, 2004), spatial resolution, and acuity.

In this chapter we review a series of psychophysical studies showing that when spatial attention is directed to a given location, performance improves in visual search, texture segmentation, and acuity tasks, which are limited by spatial resolution. For instance, when attending to a location observers can resolve information that is unresolvable without attending to that location, and can discriminate finer details than they can without directing attention to the cued location. The finding that attention improves spatial resolution has inspired neuronal models that implement the role of visual attention in object recognition (Deco and Zihl, 2001), and has been captured in computational models proposing that interactions among visual filters result in both increased gain and sharpened tuning (Lee et al., 1999).

Spatial attention: endogenous and exogenous

A growing body of behavioral evidence demonstrates that there are two covert attention systems that deal with facilitation and selection of information: "endogenous" and "exogenous". The former is a voluntary system that corresponds to our ability to willfully monitor information at a given location; the latter is an involuntary system that corresponds to an automatic orienting response to a location where sudden stimulation has occurred. Endogenous attention is also known as "sustained" attention and exogenous attention is also known as "transient" attention. These terms refer to the temporal nature of each type of attention: whereas observers seem to be able to sustain the voluntary deployment of attention to a given location for as long as needed to perform the task, the involuntary deployment of attention is transient, meaning it rises and decays quickly (Muller and Rabbitt, 1989; Nakayama and Mackeben, 1989). The different temporal characteristics and degrees of automaticity of these systems suggest that they may have evolved for different purposes and at different times — the transient, exogenous system may be phylogenetically older.

To investigate covert attention, it is necessary to keep both the task and the stimuli constant across conditions while manipulating attention. Psychophysical studies have shown that we can differentially engage endogenous and exogenous attention by using different spatial cues. In the endogenous condition, a central cue — typically an arrow at the center of the visual field — points to the most likely location of the subsequent target. In the exogenous condition, a brief peripheral cue is typically presented next to one of the target locations. A central cue directs attention in a goal- or conceptually driven fashion in about 300 ms and engages endogenous, sustained attention. Because about 200–250 ms are needed for goal-directed saccades to occur (Mayfrank et al., 1987), the stimulus onset asynchrony (SOA) for the sustained cue may allow observers to make an eye movement toward the cued location. Thus, to verify that the outcome of this manipulation is due to covert attention one has to ensure that eye movements do not take place. In our studies, we used an infrared camera to monitor the observers' eyes, ensuring

that central fixation is maintained throughout each trial. A peripheral cue presented in a location near the relevant location draws attention in a stimulus-driven, automatic manner in about 100 ms and engages exogenous attention in a transient manner, even when the cue is uninformative with regard to the target location or identity.

Covert attention affects spatial resolution

The "resolution hypothesis" states that attention can enhance spatial resolution. The following sets of studies have provided evidence for this

hypothesis. In these studies we have employed peripheral or central cues to manipulate either exogenous or endogenous attention in a variety of tasks, such as acuity, visual search, and texture segmentation, which are mediated by spatial resolution. Figure 1 includes an example of experimental trials with central or peripheral cues, to manipulate sustained or transient attention respectively, and a texture segmentation task.

Acuity tasks

Acuity tasks are designed to measure the observer's ability to resolve fine details. Performance in
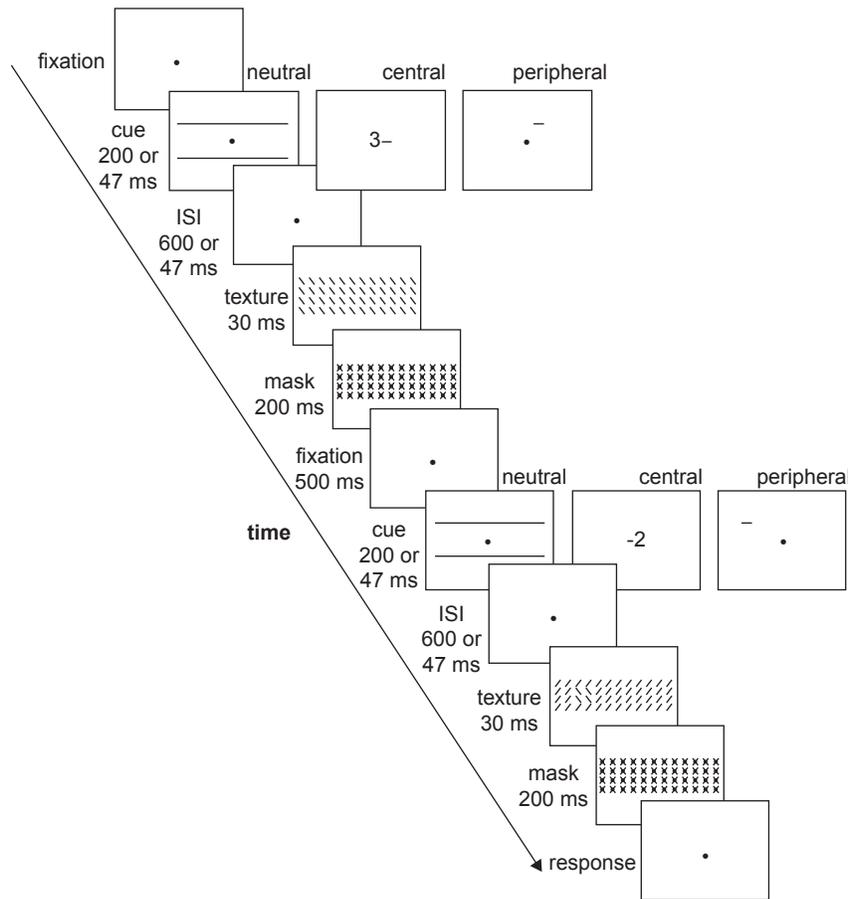

Fig. 1. Schema of the frame sequence in a typical trial with a central (sustained attention) or peripheral (transient attention) cue in a 2IFC texture segmentation task. The participants had to indicate which of the two intervals included a texture target whose orientation was orthogonal to that of the texture background. In this example the target is present in the second interval. The peripheral cue is a small horizontal bar appearing above the target location, and the central cue is composed of a digit indicating the eccentricity at which the target may appear and a line indicating the hemifield in which the target may appear. Adapted from Yeshurun et al. (2008).

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some of these tasks, like the detection of a small gap in a Landolt-square, is limited by the retinal mosaic, while in other tasks, like identification of offset direction with Vernier targets, it is limited by cortical processes (e.g., Levi et al., 1985; Olzak and Thomas, 1986). By combining such tasks with attentional cueing we were able to demonstrate that directing transient attention to the target location improves performance in both acuity and hyperacuity tasks even when a suprathreshold target is presented without distracters. Specifically, we investigated whether covert attention can enhance spatial resolution via signal enhancement in a visual acuity task. We used a suprathreshold target (Landolt-square), which appeared at one of four possible eccentricities along the vertical or horizontal meridian and asked observers to indicate which side of the Landolt-square had a gap (Yeshurun and Carrasco, 1999). When a peripheral cue indicates the location of the upcoming target, observers' performance improves in terms of both speed and accuracy; they are able to detect a smaller gap appearing on a Landolt-square. Similarly, directing attention to the location of a Vernier target allowed observer to identify smaller horizontal offsets (Fig. 2; Yeshurun and Carrasco, 1999).

The same pattern of results is found whether or not a mask follows a target; that is, when all sources of added external noise-distracters, global masks, and local masks- have been eliminated from the display (Fig. 3; Carrasco et al., 2002). The decrement in performance with eccentricity is more pronounced along the vertical than horizontal meridian. The magnitude of the cueing effect increased with eccentricity but the magnitude of this effect was similar at different isoeccentric locations (Carrasco et al., 2002; Yeshurun and Carrasco, 1999). The finding that this effect becomes more pronounced as target eccentricity increases is consistent with the idea that attention enhances spatial resolution.

It is worth noting that the magnitude of the attentional effect is similar when comparing performance at the cued location with a central-neutral cue (a small circle at the center of the display) or with a distributed-neutral cue (four copies of the peripheral cue, simultaneously presented at the centers of each of the four quadrants). This finding rules out the possibility that the results are due to the fact that the central-neutral cue reduces the extent of the attentional spread.

It has long been postulated that attention helps manage limited resources and that the benefit exerted at the attended location is often accompanied by a cost at the unattended location(s). Indeed, this trade-off in processing is present with simple displays and in tasks mediated by early vision. For instance, both exogenous (Pestilli and Carrasco, 2005; Pestilli et al., 2007) and endogenous (Ling and Carrasco, 2006a) attention enhance contrast sensitivity at the attended location at the expense of decreasing sensitivity at the unattended location.
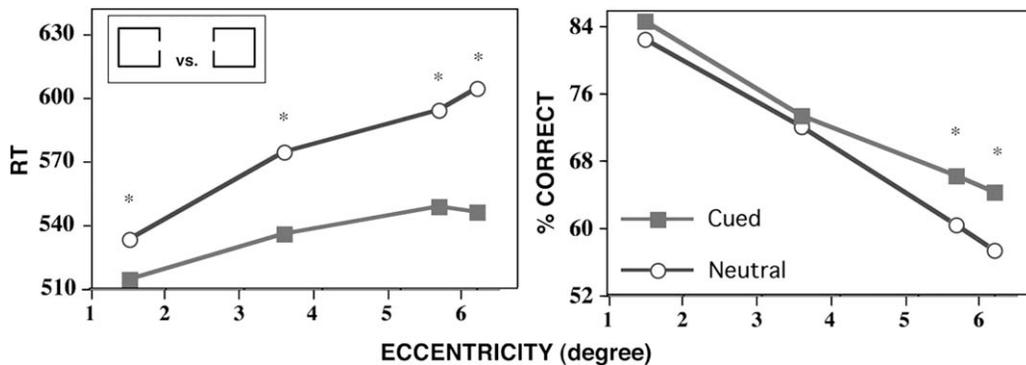

Fig. 2. RT (left panel) and accuracy (right panel) for detection of a gap in a Landolt-square (inset). Adapted from Yeshurun and Carrasco (1999).

a   with local post mask
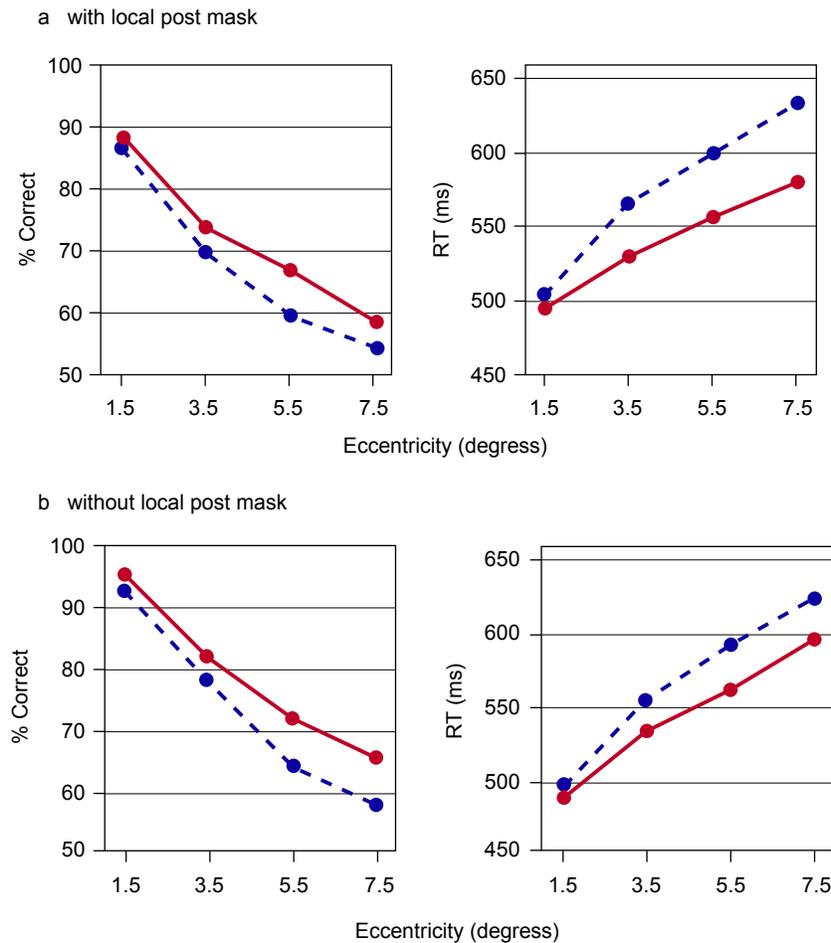

b   without local post mask

Fig. 3. Accuracy and RT for detection of a gap in a Landolt-square as a function of eccentricity: (a) with a local mask following the Landolt-square and (b) without a local mask. Continuous gray line indicates cued condition and the dashed black line indicates neutral condition. Adapted from Carrasco et al. (2002).

Once we established that covertly attending to a stimulus location increases spatial acuity (Carrasco et al., 2002; Yeshurun and Carrasco, 1999), we investigated whether increased spatial acuity is coupled with a decreased acuity at unattended locations (Montagna et al., 2009). We measured the effects of exogenous (transient, involuntary) and endogenous (sustained, voluntary) attention on observers' acuity thresholds for a Landolt gap resolution task at both attended and unattended locations, and compared the pattern of their trade-offs by maintaining task and stimuli identical while selectively engaging either type of attention. The fact that the attentional effect was evaluated

against a neutral baseline condition for each type of attention allowed us to establish whether it represented a benefit, a cost, or both.

Spatial covert attention was manipulated via cues preceding stimulus presentation (Fig. 4). On each trial, a pre-cue either indicated a specific stimulus location (cued trials) or indicated both stimulus locations (neutral trials). Different types of cues selectively engaged either exogenous (peripheral uninformative cue) or endogenous (central informative cue) attention. Observers reported the location of a gap (top or bottom side) in the target Landolt-square indicated by a response cue following stimuli offset. The two
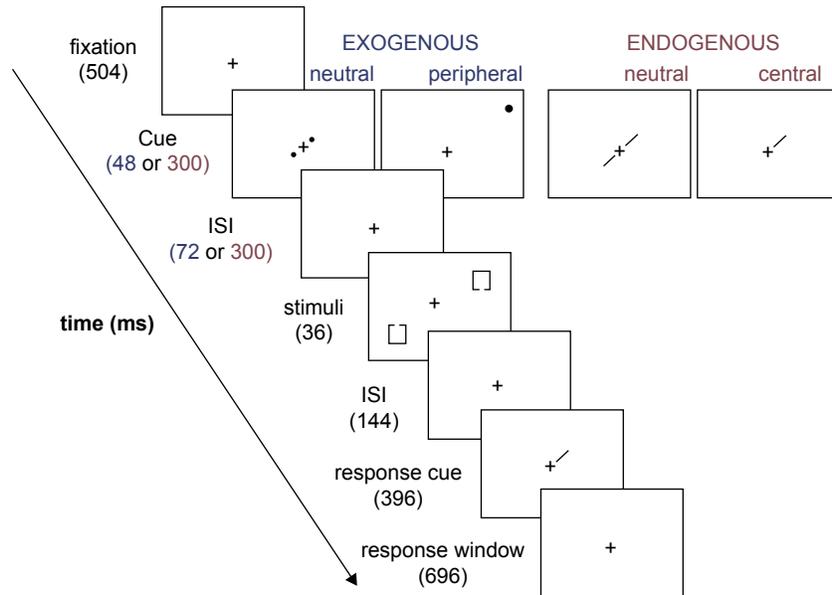
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Fig. 4. Trial sequence. The trial sequence was identical for the exogenous and endogenous attention conditions except for the spatiotemporal characteristics of the peripheral and central cues. Adapted from Montagna et al. (2009).

attentional conditions, exogenous and endogenous, were blocked per session and each had its corresponding neutral cue baseline condition to quantify the magnitude of the attentional effects.

Gap-size thresholds (75% localization accuracy) were measured for each attention condition (exogenous and endogenous) and each cueing condition (cued, neutral, and uncued). For exogenous attention, observers were informed that the peripheral cue was uninformative, that is, it was not predictive of target location or gap side. For endogenous attention, observers were informed that the cue would indicate the target location on 70% of the central-cue trials, and were instructed to allocate their voluntary attention to the cued location. For both exogenous and endogenous attention, acuity thresholds were lower in the cued and higher in the uncued condition compared to the neutral baseline condition (Fig. 5). Both types of attention increased acuity at the attended and decreased it at unattended locations relative to a neutral baseline condition. The fact that acuity trade-offs emerge for very simple, non-cluttered displays, in which only two stimuli are competing for processing challenges the idea that perceptual processes are of unlimited capacity (e.g., Palmer et al., 2000), or that attentional selection is required only once the perceptual load exceeds the capacity limit of the system (e.g., Lavie, 1995). On the contrary, it suggests that trade-offs are a mandatory and basic characteristic of attentional allocation and that such a mechanism has a general effect across different stimulus and task conditions.

Visual search

In a visual search task, observers are typically required to detect the presence of a predefined target appearing among other nonrelevant items; for instance, a red vertical line appearing among red tilted lines in a feature search, or a red vertical line appearing among red tilted and blue vertical lines (e.g., Treisman, 1985). It was previously demonstrated that performance in visual search tasks, for both features and conjunctions, deteriorates as the target is presented at farther peripheral locations (Carrasco et al., 1995). This reduction in performance is attributed to the poorer spatial resolution at the periphery (e.g.,

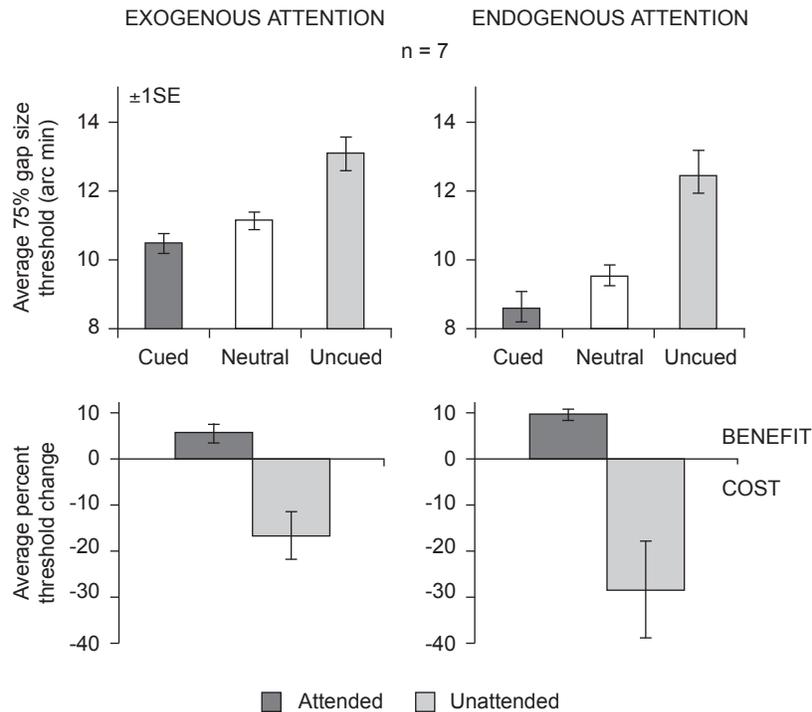EXOGENOUS ATTENTION   ENDOGENOUS ATTENTION

n = 7

Fig. 5. Average gap-size thresholds (75% localization accuracy) for both exogenous (upper-left panel) and endogenous (upper-right panel) attention for the cued, neutral, and uncued conditions. The lower panels depict the average percent change in acuity thresholds at cued and uncued locations as compared to the neutral condition for exogenous (left) and endogenous (right) attention. Values below zero indicate a cost in acuity, whereas values above zero indicate a benefit. Error bars show ± 1 SE. Adapted from Montagna et al. (2009).

Carrasco et al., 1995, 1998; Carrasco and Frieder, 1997). We have found that when observers direct their attention to the target location prior to the onset of the search display, the performance deterioration with target eccentricity is significantly reduced for both features and conjunctions (Carrasco and Yeshurun, 1998; Fig. 6). The ability of the peripheral cue to reduce this performance decrement supports the resolution hypothesis because it implies that attention can reduce resolution differences between the fovea and the periphery.

Texture segmentation

We performed a crucial test of the resolution hypothesis by exploring the effects of transient attention on a task in which performance is diminished by heightened resolution (Yeshurun and Carrasco, 1998). If attention indeed enhanced resolution, performance at the attended location should be impaired rather than improved. The task is a basic texture segmentation task that involves the detection of a texture target embedded in the background of an orthogonal orientation (Fig. 7). Observers' performance in this task does not peak when the target is presented at foveal locations, where resolution is highest. Instead, performance peaks at mid-peripheral locations, and drops as the target appears at more central or farther peripheral locations (e.g., Gurnsey et al., 1996; Joffe and Scialfa, 1995; Kehrer, 1989). Moreover, when the scale of the texture is manipulated, performance peaks at different eccentricities. Enlarging the scale of the texture shifts the peak of performance to farther locations, whereas decreasing this scale shifts the peak of performance toward the center
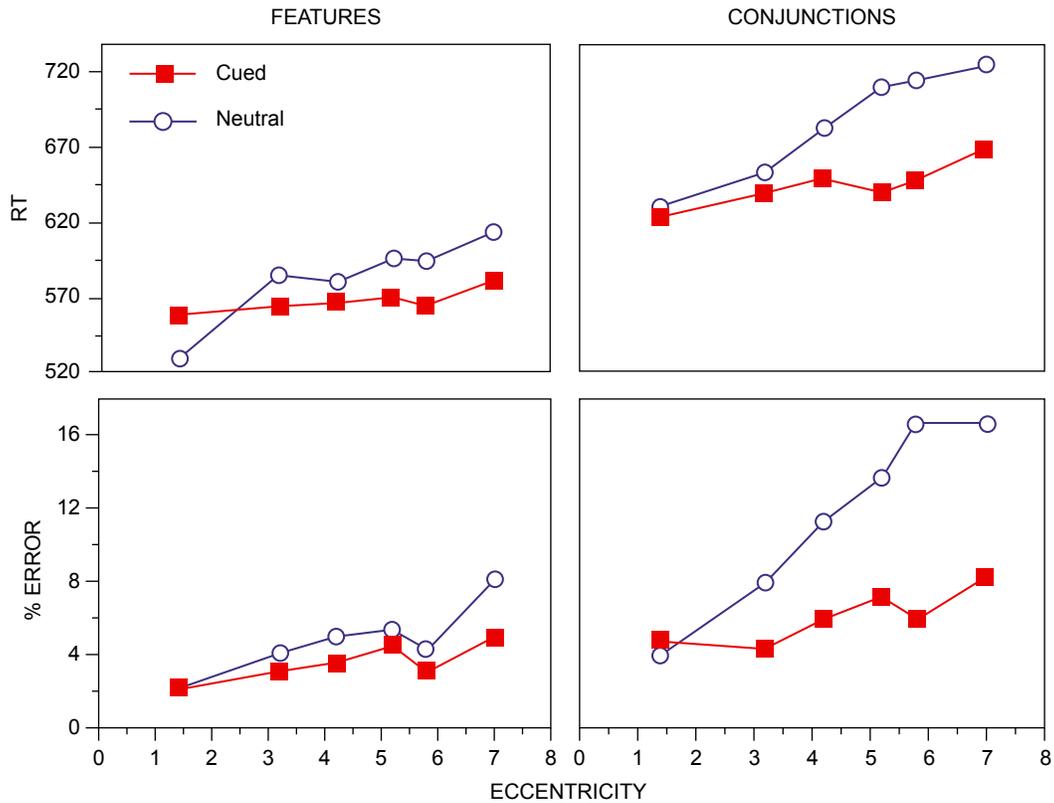
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Fig. 6. RT and error rate for feature search (left panel — a search for a red vertical line appearing among red tilted lines) and conjunction search (right panel — a search for a red vertical line appearing among red tilted and blue vertical lines). Adapted from Carrasco and Yeshurun (1998).
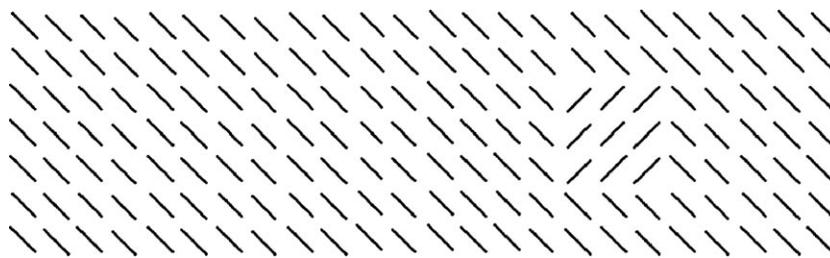

Fig. 7. Example of the texture stimuli used in Yeshurun and Carrasco (1998).

(Gurnsey et al., 1996; Joffe and Scialfa, 1995; Kehrer, 1989).

The finding that in this texture segmentation task performance drops at central locations — central performance drop (CPD) — is attributed to a mismatch between the average size of spatial filters at the fovea and the scale of the texture (Gurnsey et al., 1996; Kehrer, 1997). There is ample evidence that we process visual stimuli by means of parallel spatial filters. These are

low-level analyzers that are tuned to a specific band of spatial frequency and orientation (e.g., De Valois and De Valois, 1988; Graham, 1989; Phillips and Wilson, 1984). It has been suggested that the size of these filters at the fovea may be too small for the scale of the texture, as if spatial resolution at the fovea is too high for the task. At more peripheral regions, the filters' average size increases gradually, and is presumably optimal around the peak of performance. At farther locations, the filters are too big and their low resolution limits performance. Consequently, the finding that performance with a larger texture scale peaks at farther eccentricities may reflect the fact that the processing of this enlarged texture requires larger filters that are more abundant at farther eccentricities, and vice versa (Gurnsey et al., 1996; Kehrer, 1997).

We hypothesized that if attention indeed enhances spatial resolution, attending to the target location should enhance performance at the periphery, where the resolution is too low, but should impair performance at the fovea, where the resolution is already too high for the task. Moreover, if attention enhances resolution by effectively decreasing the average size of filters at the attended location (e.g., Moran and Desimone, 1985; Reynolds and Desimone, 1999), then for a larger texture scale, attention should impair performance for a wider range of eccentricities; for a smaller texture scale, attention should impair performance in a narrower range of eccentricities. This is due to the fact that with a larger texture scale the mismatch between the texture scale and the size of the filters would extend farther toward the periphery and vice versa (Yeshurun and Carrasco, 1998). To test these predictions we combined peripheral cues with this texture segmentation task. On the cued trials a peripheral cue indicated the target location prior to its appearance, allowing observers to focus their attention, in advance, on the target location without having time to move their eyes to the location. On the neutral trials a pair of lines, appearing above and below the display, indicated that the target was equally likely to appear at any location. The texture target appeared at any of 17 possible eccentricities, and the scale of the texture was manipulated by viewing the display from three different distances — 228, 57, or 28 cm (see neutral and peripheral conditions in Fig. 1).

For all three viewing distances the pattern of the results conformed to the resolution hypothesis (Fig. 8). Accuracy was higher for the cued than the neutral trials at the more peripheral locations but was lower at central locations. Hence, attending to the target location improved performance at peripheral locations, where the resolution was too low for the scale of the texture, but impaired performance in central locations, where the resolution was already too high. Moreover, as predicted, with a larger texture scale (middle panel), performance was impaired in a larger range of eccentricities (0–5°), compared to the medium texture scale (0–1°, left panel). Similarly, with a smaller texture scale (right panel), performance was impaired at a smaller range of eccentricities (0–0.66°). This study demonstrated that (a) attention helps performance that is limited by resolution that is too low, but hinders performance that is limited by resolution that is too high; (b) the range of eccentricities in which attention hinders performance depends on the scale of the texture and the average size of the filters at a given eccentricity. Although no other existing model of attention could predict an attentional impairment, this impairment is predicted by the resolution hypothesis (Yeshurun and Carrasco, 1998).

We obtain the same pattern of results when we present the texture along the vertical rather than the horizontal meridians. Interestingly, when the texture was presented along the vertical meridian performance peaked at farther eccentricities in the lower than in the upper vertical meridian, indicating that resolution was higher in the lower half. Furthermore, the peripheral cue affected performance along the vertical meridian uniformly, indicating that the degree of enhanced resolution brought about by transient attention was constant along the vertical meridian (Talgar and Carrasco, 2002). Consistent with findings in contrast sensitivity (Cameron et al., 2002; Carrasco et al., 2001), performance on texture segmentation indicates that the vertical meridian asymmetry for spatial resolution is
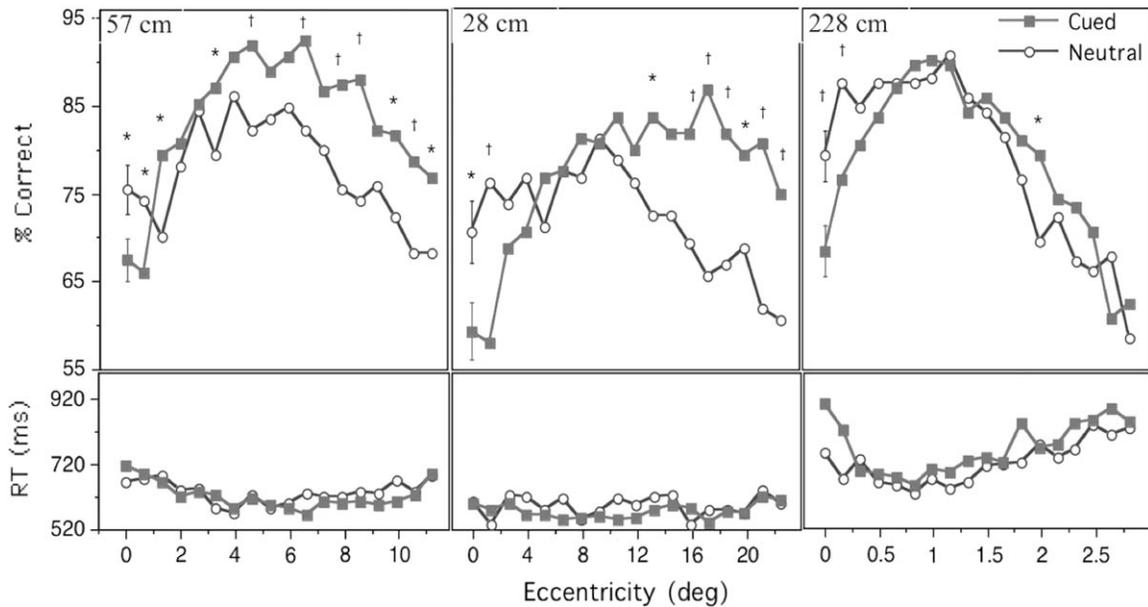
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Fig. 8. Observers' performance as a function of target eccentricity and cueing condition for the three viewing distances. Because viewing distance varied, the eccentricity values (abscissa) differ in the three panels. Adapted from Yeshurun and Carrasco (1998).

determined by visual, not attentional, constraints. These findings shed light on the nature of the attentional mechanism by lending strong support to the hypothesis that attention enhances the spatial resolution at the attended location, possibly by reducing the average size of the corresponding filters.

We conducted another study to investigate the level of visual processing at which these attentional effects take place (Yeshurun and Carrasco, 2000). At the level of the visual cortex, texture segmentation theoretically involves passage of visual input through two layers of spatial linear filters, separated by a point-wise nonlinearity. The first-order linear filters are assumed to perform a more local analysis of spatial frequency and orientation, and are thought to correspond to simple cortical cells in area V1. The second-order linear filters are considered to be of a larger scale and assumed to perform a more global analysis on the output of the first-order filters plus the intermediate nonlinearity (e.g., Bergen and Landy, 1991; Fogel and Sagi, 1989; Graham et al., 1992; Malik and Perona, 1990; Sutter et al., 1989, 1995). To assess the level of

processing at which attention affects spatial resolution we used textures of a different nature (Yeshurun and Carrasco, 2000). These textures were composed of narrow-band stimuli, ensuring that only filters of a specific scale were activated (Fig. 9; Graham et al., 1992).

By manipulating the spatial-frequency content of the texture we were able to replicate our previous findings (Yeshurun and Carrasco, 1998), demonstrating that these effects are robust and can generalize to textures of a very different nature. More importantly, we could differentially stimulate first or second-order filters of various scales. We found that the pattern of the attentional effects on texture segmentation depended only on the second-order frequency of the texture. As can be seen in Fig. 10, the attentional effect was the same regardless of the first-order content: for both the low-frequency (top-left panel) and the high-frequency (top-right) conditions, a significant interaction emerged; accuracy was higher for cued trials than neutral trials at more peripheral eccentricities, but accuracy was lower at central locations (0–2°). In contrast, the attentional effect differed when the second-order content was
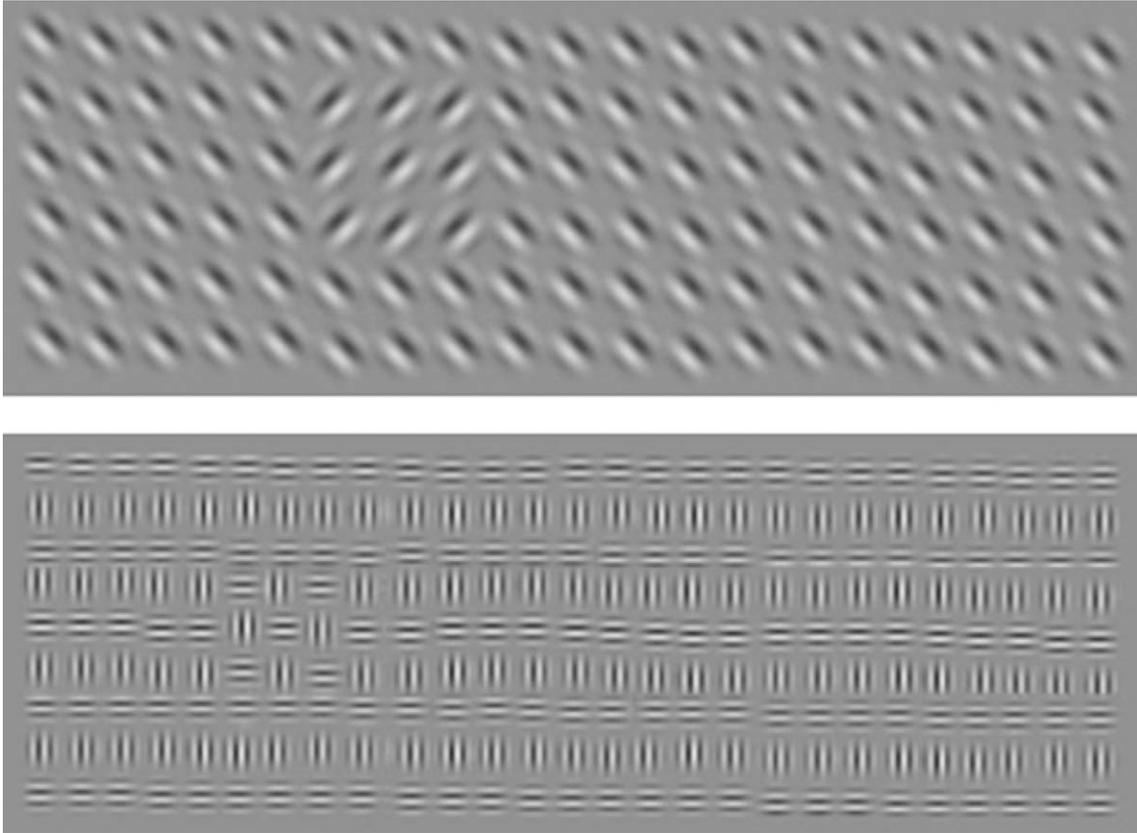
Fig. 9. An example of the first-order (top) and second-order (bottom) textures used in Yeshurun and Carrasco (2000).

varied: attention impaired performance in a greater range of eccentricities for the low-frequency (bottom-left) than the high-frequency (bottom-right) conditions (0–7.76° vs. 0–3.33°), and an attentional benefit emerged only for the high-frequency condition. This suggests that attention operates at the second stage of filtering, possibly by reducing the size of the second-order filters, resulting in enhanced spatial resolution. This finding indicates that attention can modulate processing as early as at the primary visual cortex. Thus, these attentional effects suggest a link between task performance (behavior) and physiological studies demonstrating attentional modulation of activity in area V1, either by means of single cell recording (Ito and Gilbert, 1999; Motter, 1993) or by fMRI (Brefczynski and DeYoe, 1999; Gandhi et al., 1999; Kastner and Ungerleider, 2000; Martinez et al., 1999).

To test directly whether covert attention enhances spatial resolution by increasing sensitivity to high spatial frequencies, we employed a cueing procedure in conjunction with selective adaptation (Carrasco et al., 2006). The selective adaptation procedure is used to assess the spatiotemporal properties of the visual system. It has long been demonstrated that prolonged exposure to one type of stimulus reduces sensitivity to those stimulus parameters and other similar stimuli, thus allowing for the selective adaptation for a particular variable or set of variables, such as spatial frequency and orientation (Blakemore and Campbell, 1969; Graham, 1989; Movshon and Lennie, 1979; Saul and Cynader, 1989). While keeping the stimulus content identical, we manipulated the availability of spatial-frequency information by reducing observers' sensitivity to a range of frequencies.
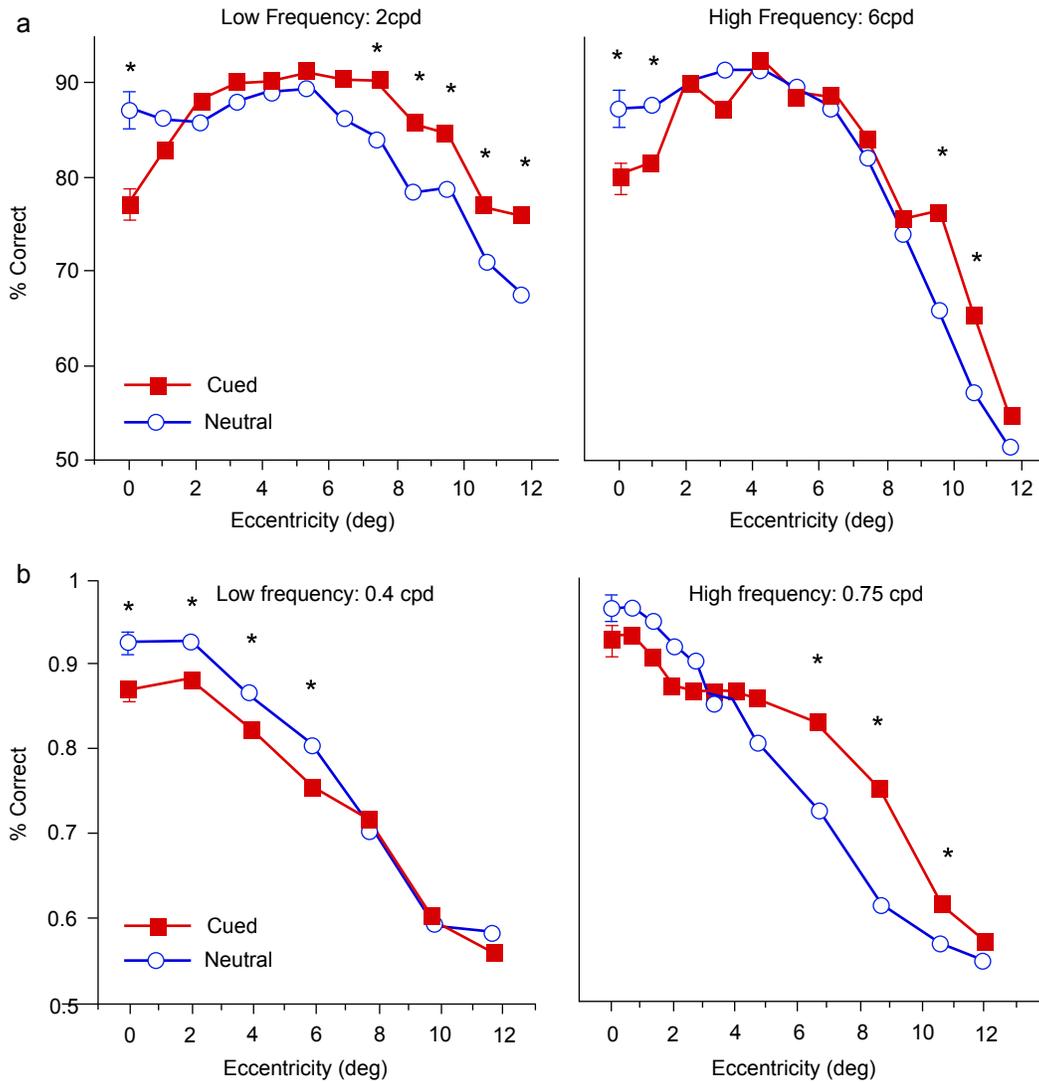
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Fig. 10. Performance with first-order (a) and second-order (b) textures of low (left) or high (right) frequency as a function of cueing condition and target eccentricity. Adapted from Yeshurun and Carrasco (2000).

At central locations when high-frequency non-optimal filters participate in the normalization process the weakened response of the optimal filters would result in the CPD. Thus by adapting to high spatial frequencies, the nonoptimal filters would be removed from the normalization process and the CPD would be diminished. Furthermore, were the central attentional impairment (Talgar and Carrasco, 2002; Yeshurun and Carrasco, 1998, 2000) due to an increased sensitivity to high frequencies and a reduced sensitivity to lower frequencies, adapting to high spatial frequencies should eliminate the attentional impairment at central locations and diminish the benefit in the peripheral locations. If the contribution of the nonoptimal high frequencies is diminished in the normalization process, cueing the target location could no longer inhibit the optimal filters for the scale of the texture and performance would not be impaired, that is, no central attentional impairment would emerge.

Observers performed a 2-AFC discrimination task after selectively adapting to 0-cpd (baseline), 1-cpd (low spatial frequency), or 8-cpd (high spatial frequency). The results indicate that the CPD was present in the baseline and the low-spatial-frequency neutral conditions but was eliminated in the high-spatial-frequency neutral condition (Fig. 11). Furthermore, the central attentional impairment present in the baseline and low-frequency exogenous cueing conditions was eliminated in the high-frequency exogenous cueing condition. In other words, we found that by adapting to low spatial frequencies, performance in this texture segmentation task does not change. However, by adapting to high spatial frequencies, the CPD is diminished and the central attentional impairment is eliminated. These results indicate that the CPD is primarily due to the dominance of high-spatial-frequency responses, and that transient covert attention enhances spatial resolution by increasing sensitivity to higher spatial frequencies.

In another study we examined the adaptability of transient attention regarding spatial resolution. In particular, we investigated whether the scale of the information that attracts attention (the size of the attentional cue) can modulate the effects of transient attention on the spatial resolution at the attended location (Yeshurun and Carrasco, 2008). Various studies have manipulated the size of the attended region by employing cues of different sizes or dual tasks (e.g., Goto et al., 2001; Greenwood and Parasuraman, 2004; Hock et al.,

1998; Müller et al., 2003). These studies have found that the larger the attended region, the lower the resolution. Although these studies manipulated sustained attention, they suggest that transient attention may also be able to modulate its effect on spatial resolution as a function of the cue size, so that the larger the cue the lower the resolution.

To test this hypothesis, we used a texture segmentation task that was similar to the one employed in our previous studies (e.g., Yeshurun and Carrasco, 1998; Fig. 7), and systematically manipulated the size of the attentional cue (Fig. 12). If the gradual increase in the size of the attentional cue leads to a gradual resolution decrement, then performance at central locations should gradually improve and at peripheral locations should gradually deteriorate as the cue size increases. Moreover, as cue size increases the eccentricity at which performance peaks should gradually shift to nearer eccentricities reflecting the gradual decrease in resolution, with the performance peak of the largest cue being at the nearest eccentricity (as it designates the largest area — the whole display). Alternatively, if transient attention does not alter its operation based on the size of the attentional cue, its effect on spatial resolution should not change in a gradual fashion with changes in cue size.

The findings consistently replicated the attentional enhancement of spatial resolution reported previously with a small cue (Carrasco et al., 2006;
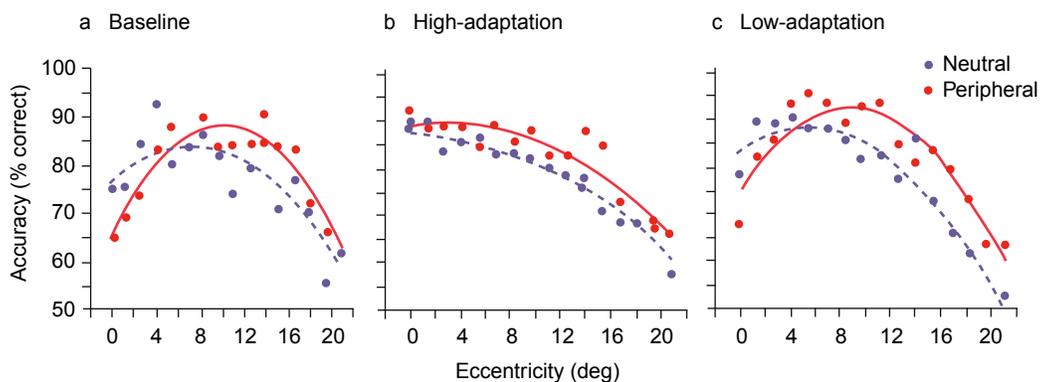

Fig. 11. Observers' performance as a function of cue type and target eccentricity. (a) Baseline, (b) high-spatial-frequency adaptation grating, and (c) low-spatial-frequency adaptation grating. Adapted from Carrasco et al. (2006).
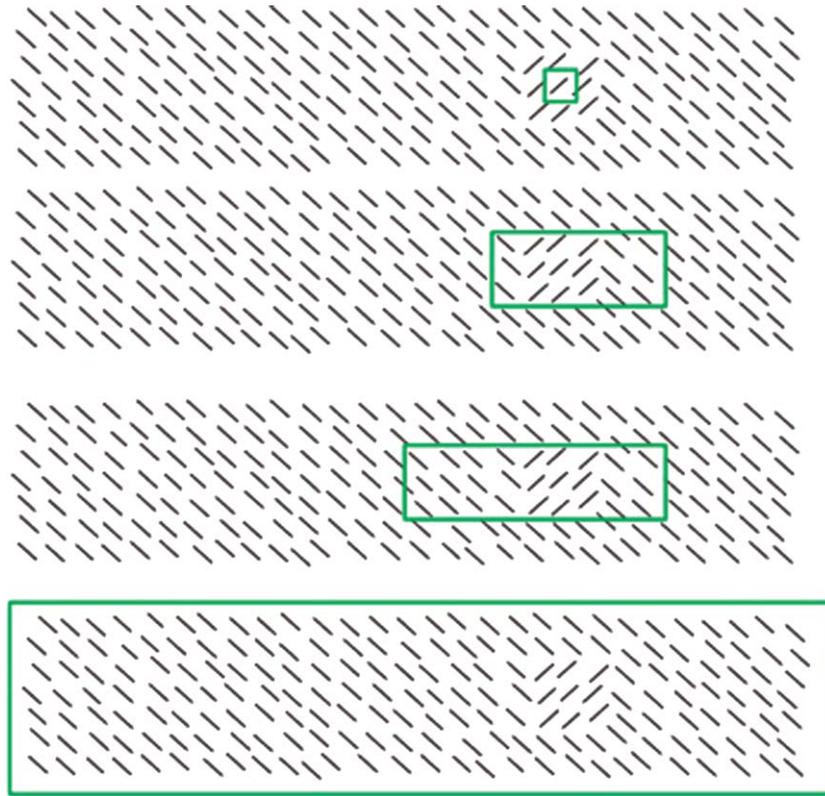
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Fig. 12. An example of cues of different sizes and the textures used in Yeshurun and Carrasco (2008). The largest cue (bottom) was similar to the neutral cue employed previously (e.g., Yeshurun and Carrasco, 1998), and since it carried no information regarding the target location this cue served as the baseline to which performance with smaller cues was compared.

Talgar and Carrasco, 2002; Yeshurun and Carrasco, 1998), but there was no evidence of gradual resolution decrement with large cues. Specifically, a differential effect was found for the different cue sizes, but it mainly reflects an attentional effect for the small cue sizes and no effect for larger cues (Fig. 13). There was no gradual change in performance with increasing cue size. These findings indicate that in this texture segmentation task, transient attention exerts its effects on spatial resolution only when it is directed to a small region by a small cue. There is no evidence that transient attention can flexibly lower resolution when it is attracted to a broader spatial region by large cues.

The texture segmentation studies described thus far employed a peripheral cue to measure the effects of transient attention. Transient

attention increases spatial resolution even when it is detrimental to the task at hand. Improved resolution due to transient attention is advantageous because most everyday tasks — such as reading, searching for small objects, or identifying fine details — benefit from heightened resolution. Thus, an attentional mechanism that increases spatial resolution by default can be very effective. However, in certain situations resolution enhancement is not beneficial. For example, when a more global assessment of a scene is required (e.g., viewing an impressionist painting) enhancing resolution is not optimal. Likewise, a high-resolution analysis of the scene will not provide optimal results when navigating through the world under poor atmospheric conditions (e.g., fog or haze). We wondered how sustained attention, given its top-down nature, would affect performance in a
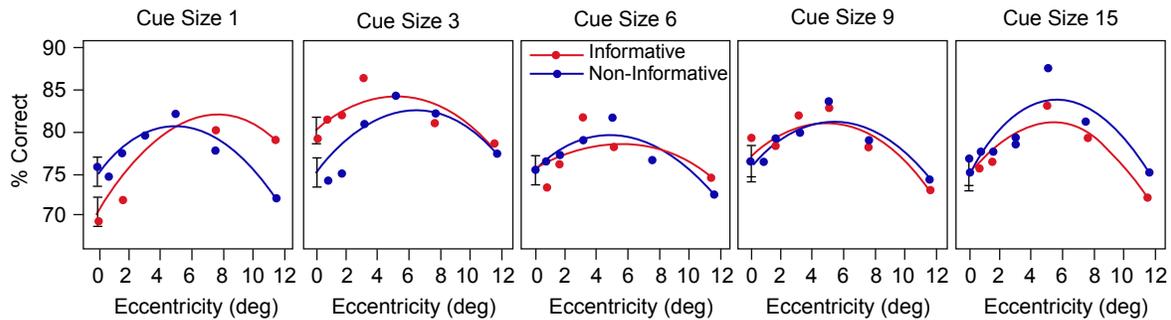
Fig. 13. Observers' performance as a function of cue size and target eccentricity. "Informative" refers to the trials in which the cue carried some information regarding the target location (the larger the cue the less precise this information is). "Noninformative" refers to the trials in which the cue carried no information regarding the target location (the largest cue). The number of cue size indicates the number of texture columns encompassed by the cue frame. Adapted from Yeshurun and Carrasco (2008).

texture segmentation task in which enhanced spatial resolution is detrimental to performance.

In a recent study (Yeshurun et al., 2008) we employed a central cue to test whether sustained attention can also affect performance in a texture segmentation task, and whether this effect will be similar to that found with peripheral cues. In some of the experiments of this study the texture segmentation task was the same as the one employed with transient attention in previous studies (Talgar and Carrasco, 2002; Yeshurun and Carrasco, 1998, 2008; Fig. 1). In other experiments the texture was modified from a homogeneous to a heterogeneous background to preclude the need for a post-mask and thus ensure that performance is limited only by spatial factors (Fig. 14). The average orientation of line elements in the texture display was $\pm 45°$ from vertical, the actual orientation of each line element was chosen at random from a uniform distribution of orientations. As the range of sampled orientations around the mean increases, the target patch becomes harder to detect. The resulting texture stimuli were very similar to the ones used by Potechin and Gurnsey (2003). With these texture stimuli we used a Yes–No detection task rather than the 2IFC task employed before. The central cue was composed of a digit indicating the eccentricity at which the target may appear and a line indicating the quadrant in which the target may appear.

The pattern of results was very similar for both types of texture stimuli and tasks: sustained attention, like transient attention, can affect texture segmentation. However, in contrast to transient attention, the effects of sustained attention did not vary as a function of eccentricity (Fig. 15). Directing sustained attention to the target location improved performance at all eccentricities (unless performance was at chance level). There was no attentional impairment at central locations. These findings indicate that the attentional benefit that emerged in both experiments is robust and can be generalized to different textures and tasks.

In this study we also evaluated the contribution of location uncertainty at the decisional level to the effect of sustained attention. We compared the effect of the central pre-cues with the effect of post-cues, which indicate the target location *after* the offset of the texture display. Spatial post-cues, like post-masks, are considered to effectively reduce location uncertainty (e.g., Carrasco et al., 2000; Carrasco and Yeshurun, 1998; Kinchla et al., 1995; Luck et al., 1994, 1996; Lu and Dosher, 2004; Smith, 2000). Both pre- and post-cues reduce location uncertainty, as both allow the observer to assign lower weights to information extracted from the non-cued locations; however, only the pre-cues allow for a change in the quality of the texture representation due to the advanced allocation of attention to the location of the upcoming target. Thus, any additional benefit yielded by pre-cues compared to post-cues could be ascribed to an attentional modulation of the
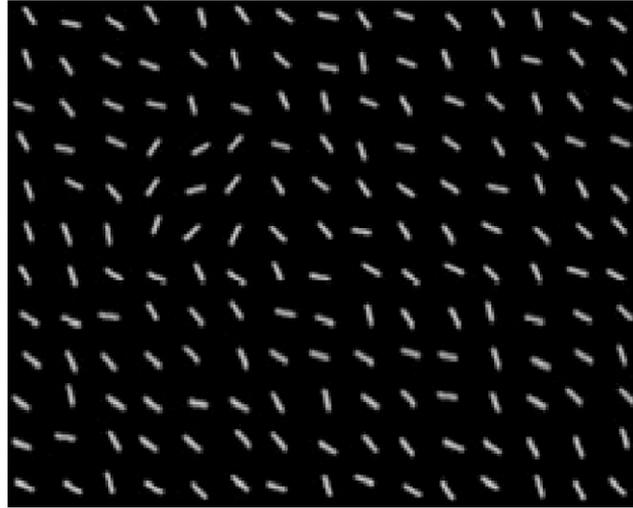
80

Fig. 14. An example of the heterogeneous textures used in Yeshurun et al. (2008).
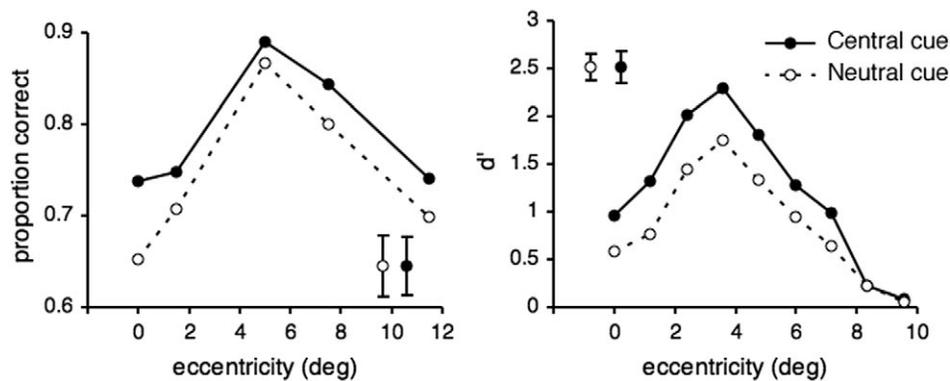

Fig. 15. Observers' performance as a function of cue condition and target eccentricity, for texture stimuli with homogeneous (left panel; see Fig. 7) or heterogeneous (right panel; see Fig. 14) background. Adapted from Yeshurun et al. (2008).

quality of the texture representation rather than to the mere reduction of location uncertainty at the decisional stage. The results showed that performance with the central pre-cue, which triggers sustained attention, was significantly higher than performance with its neutral condition, whereas performance for the central post-cue was only marginally higher than its neutral condition. Moreover, the central pre-cue elicited a significantly better performance than the central post-cue. These results indicate that the benefit of the central pre-cue went well beyond the mere effect of location uncertainty at the decisional stage — it improved the quality of the texture representation.

Discussion

The various studies we described thus far were designed to test the effects of transient and sustained attention on performance by employing

peripheral and central pre-cues, respectively. The studies of transient attention clearly demonstrate that transient attention can affect performance in various basic tasks like acuity and texture segmentation. Directing transient attention to the target location reduced performance differences between the center and the periphery in visual search tasks (Carrasco and Yeshurun, 1998), improved performance in tasks that were limited by acuity or hyperacuity (Carrasco et al., 2001; Montagna et al., 2009; Yeshurun and Carrasco, 1999), and improved or impaired texture segmentation depending on the combination of the eccentricity of the texture target and the scale of the texture (Carrasco et al., 2006; Talgar and Carrasco, 2002; Yeshurun and Carrasco, 1998, 2000, 2008).

It is important to note that the effects of transient attention on acuity measures could not be accounted for by many of the prominent hypotheses regarding the attentional mechanism like shifts in the decisional criterion, location uncertainty reduction, or reduction of external noise (e.g., Dosher and Lu, 2000; Eckstein et al., 2002; Kinchla et al., 1995; Lu and Dosher, 2004; Shiu and Pashler, 1994) for the following reasons: because the peripheral cue did not convey information regarding the correct response and only indicated the target location (Carrasco et al., 2002; Yeshurun and Carrasco, 1999), or conveyed no information regarding either the correct response or the target location (Montagna et al., 2009), it did not associate a higher probability with one of the responses and observers could not rely on its presence to reach a decision. Moreover, the target was presented alone, without other items to introduce external noise, and it was a suprathreshold target that could not be confused with the blank at the other locations (Yeshurun and Carrasco, 1999). Additionally, we found similar results with and without a local post-mask (Carrasco et al., 2002). In contrast to these attentional mechanisms, the improved performance in acuity tasks could be accounted for by the resolution hypothesis suggesting that transient attention enhances the spatial resolution at the attended location.

The alternative mechanisms of attention mentioned above also fail to account for the effects of transient attention on texture segmentation, namely the attentional impairment of performance at central locations (Carrasco et al., 2006; Talgar and Carrasco, 2002; Yeshurun and Carrasco, 1998, 2000, 2008), because all alternative hypotheses would predict a benefit on performance throughout all eccentricities. Only the resolution hypothesis predicts the attentional impairment of performance at central locations, and therefore, the findings of the texture segmentation studies lend strong support to the resolution hypothesis.

The resolution hypothesis is in line with other psychophysical studies suggesting that attention allows a fine-scale analysis. For instance, Morgan et al. (1998) measured orientation thresholds in a visual search task. They presented a Gabor patch in one of two possible orientations, with or without distracters, and found that when distracters were present, spatially cueing target location reduced orientation thresholds to the level found when the target was presented alone. The authors suggested that focusing attention on the target location reduced thresholds through the operation of a smaller scaled "stimulus analyzer" (Morgan et al, 1998, p. 368). Likewise, when Tsal and Shalev (1996) studied the effects of cueing attention on the perceived length of short lines, they found that a briefly presented line is judged to be shorter when its location was known in advance. They suggested that the attended line was perceived as shorter because the processing of an attended stimulus is mediated by smaller "attentional receptive fields" (Tsal and Shalev, 1996, p. 242).

The resolution hypothesis is also consistent with a comparative study that evaluated the effects of spatial covert attention on Landolt acuity as a function of different SOAs for human and nonhuman primates (Golla et al., 2004). The findings for both species demonstrate a consistent enhanced acuity when the target location was pre-cued as compared to a no-cue condition (i.e., when there was no temporal or spatial indication for both trial onset and target location). As was the case in the psychophysical studies with humans described

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above (Carrasco et al., 2002; Montagna et al., 2009; Yeshurun and Carrasco, 1999), the attentional effect increased with eccentricity in human and nonhuman primates.

There may be several ways in which this attentional enhancement of spatial resolution is accomplished. First, attention may, in effect, reduce the size of receptive fields at the attended area. This hypothesis is consistent with neurophysiological studies on endogenous attention, demonstrating that a neuron's response to its preferred stimulus is greatly reduced when the preferred stimulus is not attended, and an attended, non-preferred stimulus is also presented within the neuron's receptive field. These findings suggest that attention contracts the cell's receptive field around the attended stimulus (e.g., Anton-Erxleben et al., 2009; Moran and Desimone, 1985; Reynolds and Desimone, 1999; Womelsdorf et al., 2006).

Alternatively, attention may enhance resolution by increasing the sensitivity of the smallest receptive fields at the attended area (Balz and Hock, 1997), which in turn may inhibit the sensitivity of the larger receptive fields at the same area. At central locations, when high-frequency nonoptimal filters participate in the normalization process, the weakened response of the optimal filters results in the CPD. Indeed, adapting to high spatial frequencies resulted in a diminished CPD probably due to the fact that the nonoptimal filters were removed from the normalization process. Furthermore, adapting to high spatial frequencies also eliminated the attentional impairment at central locations. Because the contribution of the nonoptimal high frequencies was diminished in the normalization process, cueing the target location could no longer inhibit the optimal filters and performance could not be impaired, that is, there was no central attentional impairment. These results support the hypothesis that the CPD is primarily due to the dominance of high-spatial-frequency responses, and that covert attention enhances spatial resolution by increasing sensitivity to higher spatial frequencies (Carrasco et al., 2006).

Like transient attention, sustained attention affects performance in basic visual tasks mediated by spatial resolution tasks (Montagna et al., 2009; Yeshurun et al., 2008). Unlike transient attention, directing sustained attention to the target location via central pre-cues improved texture segmentation at both central and peripheral locations. This finding could not be accounted for by uncertainty reduction because when we compared performance with central pre- and post-cues we found that performance with the pre-cue was significantly better than performance with the post-cue. The effects of sustained attention on texture segmentation could be accounted for by an attentional mechanism that is capable of either enhancement or decrement of spatial resolution to optimize performance. According to this view, sustained attention optimized performance at all eccentricities via resolution enhancement at the periphery where performance is limited by a resolution that is too low, and via resolution decrement at central locations where performance is limited by a resolution that is too high. This view of sustained attention portrays a highly adaptive mechanism that can adjust its operation on a trial-by-trial basis. Note, however, that the eccentricity-independent effects of sustained attention could also be attributed to an attentional mechanism that affects texture segmentation by improving the signal to noise ratio at all eccentricities through means other than resolution modification, like reduction of external noise at early levels of processing (e.g., Dosher and Lu, 2000; Lu and Dosher, 2004), possibly via distracter suppression (e.g., Shiu and Pashler, 1994).

The finding that sustained attention affects texture segmentation in a different manner than transient attention is consistent with studies demonstrating differential effects for sustained and transient attention. For instance, Briand and Klein (1987) and Briand (1998) found that with peripheral cues, but not with central cues, the effects of attention were larger for a conjunction search than for a feature search. Another study that tested the effects of sustained and transient attention under low-noise versus high-noise conditions reported that sustained attention could affect performance only under high-noise conditions, but not under low-noise conditions (e.g., Dosher and Lu, 2000). Transient attention, however, could operate under both low-noise and high-noise conditions (Lu and Dosher, 1998,

2000). A more recent study has shown that both sustained and transient attention increase contrast sensitivity, even in low-noise conditions, but whereas the former is mediated by a contrast-gain mechanism, the latter seems to be mediated by both contrast-gain and response-gain mechanisms (Ling and Carrasco, 2006b). Moreover, a population-coding model that estimates attentional effects on population contrast response given psychophysical data indicates that whereas sustained attention changes population contrast response via contrast gain, transient attention changes population contrast response via response gain (Pestilli et al., 2009).

Some studies dealing with the effects of attention on temporal aspects of processing also show differential effects for sustained and transient attention. For instance, involuntary allocation of attention (via peripheral noninformative cues) impairs temporal order judgment, whereas voluntary allocation of attention (via central informative cues) improves it (Hein et al., 2006). Furthermore, a recent study employing a speed-accuracy trade-off procedure, which enables conjoint measures of discriminability and temporal dynamics, showed that with central cues, the attentional benefits increased with cue validity while costs remained relatively constant. However, with peripheral cues, the benefits and the costs were comparable across the range of cue validities (Giordano et al., 2009).

Finally, in line with the idea of limited resources, we have demonstrated an attentional trade-off for spatial resolution: our ability to resolve small details in a stimulus increases at the attended location, while decreasing elsewhere for both exogenous and endogenous attention (Montagna et al., 2009). This trade-off was measured for spatial acuity thresholds and was found even in impoverished, non-cluttered displays in which only two stimuli (one target and one distracter) appear at known locations to compete for processing resources. This finding suggests that the cost in acuity at unattended locations may be a mandatory consequence of the attentional allocation of resources to the attended location. Together with the effects of covert attention on contrast sensitivity (Ling and Carrasco, 2006a; Pestilli and

Carrasco, 2005; Pestilli et al., 2007), this study suggests that visual processing trade-offs are a general mechanism of attentional allocation, whose perceptual consequences affect several basic visual dimensions, and it supports the idea that spatial covert attention helps regulate the expenditure of cortical computation.

Conclusions

Attentional facilitation in visual tasks reflects a combination of mechanisms such as signal enhancement, noise exclusion, and decisional factors. In this chapter we described a set of studies on sustained and transient covert attention that support one of these mechanisms — signal enhancement via enhanced resolution. These studies employ different tasks, like gap detection, visual search, and texture segmentation, and different stimuli, like squares, Vernier stimuli, textures composed of many line segments or Gabor patches. Yet all of them suggest the same conclusion — directing attention to the target location allows us to better resolve the fine details of the visual scene.

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