Research Article

TRANSIENT SPATIAL ATTENTION DEGRADES TEMPORAL RESOLUTION

Yaffa Yeshurun and Liat Levy

University of Haifa, Haifa, Israel

Abstract—*To better understand the interplay between the temporal and spatial components of visual perception, we studied the effects of transient spatial attention on temporal resolution. Given that spatial attention sharpens spatial resolution, can it also affect temporal resolution? To assess temporal resolution, we measured the two-flash fusion threshold. When two flashes of light are presented successively to the same location, the two-flash fusion threshold is the minimal interval between the flashes at which they are still perceived as two flashes, rather than a single flash. This assessment of temporal resolution was combined with peripheral precuing—a direct manipulation of transient spatial attention. This allowed us to demonstrate, for the first time, that spatial attention can indeed affect temporal resolution. However, in contrast to its effect on spatial resolution, spatial attention degrades temporal resolution. Two attentional mechanisms that could account for both attentional effects—enhanced spatial resolution and reduced temporal resolution—are discussed.*

The importance of the selection processes termed attention is rarely doubted. By giving priority to relevant information over nonrelevant information, these processes help observers comprehend the overwhelming amount of visual information confronting them at any given moment. Although much of the investigation of spatial attention—the allocation of attention to a specific location of the visual display—has focused on spatial processes, there is growing interest in attentional effects on the complementary temporal aspect of visual perception (e.g., Carrasco & McElree, 2001; Shore, Spence, & Klein, 2001; Visser & Enns, 2001). Previously, we demonstrated that spatial attention can aid performance by enhancing spatial resolution (Yeshurun & Carrasco, 1998, 1999, 2000). In the current study, we investigated whether the same attentional manipulation that affected spatial resolution can also affect visual temporal processes, specifically, temporal resolution, and if so, what the nature of this attentional effect is.

Visual temporal resolution is typically defined as the ability to follow rapid changes in light intensity over time, or the ability to resolve temporal details (e.g., Levine, 2000). For example, temporal resolution can be expressed as the ability to recognize that two brief visual events, presented in close succession, are indeed two separate events rather than a single continuous event. Many circumstances in everyday life, such as driving on a busy highway, involve the processing of such rapidly varying information. High temporal resolution is critical for successful performance in such circumstances. Although understanding the way in which spatial attention affects temporal resolution is essential for comprehending and optimizing behavior in such situations, these effects have not been studied. Exploring attentional effects on temporal resolution was, therefore, the main goal of this study.

Address correspondence to Yaffa Yeshurun, Department of Psychology, University of Haifa, Haifa 31905, Israel; e-mail: yeshurun@research.haifa.ac.il.

Successful navigation through the environment depends also on spatial resolution—the ability to resolve small details in the visual scene. We have conducted several studies demonstrating that spatial attention enhances the spatial resolution at the attended location. Directing attention to a target location improved performance in both acuity and hyperacuity tasks (Yeshurun & Carrasco, 1999). Similarly, in a visual search task, attention improved performance more for peripheral than for central targets, a result implying that attention can reduce resolution differences between the fovea and the periphery (Carrasco & Yeshurun, 1998). Furthermore, we explored the effects of attention on a texture-segmentation task in which performance is expected to decline with heightened resolution. In this task, performance peaks at midperiphery and then drops at more central or more peripheral locations (e.g., Gurnsey, Pearson, & Day, 1996). Presumably, performance drops because spatial linear filters, tuned to a specific band of spatial frequency and orientation, are too small at the fovea or too large at the far periphery for the scale of the texture (i.e., resolution is too high or too low). We found that attention enhanced performance where the resolution was too low (periphery), but impaired performance where the resolution was already too high (fovea). These findings clearly support the hypothesis that attention enhances spatial resolution, possibly by reducing the size of the corresponding filters (Yeshurun & Carrasco, 1998, 2000).

These studies indicate that spatial attention allows observers to better resolve the various details in the environment, but could it also improve the ability to tell apart events occurring at different points in time? That is, can spatial attention also enhance temporal resolution? Furthermore, if attention affects temporal resolution, would these effects be a direct consequence of the changes in spatial resolution, or could attention affect temporal processing independently?

To date, the relationship between the spatial and temporal characteristics of the visual system is unclear. On the one hand, it has been suggested that these two dimensions are relatively independent. For instance, it was suggested that the visual system operates via a collection of spatiotemporal mechanisms whose spatial and temporal functions are separable (e.g., Lehky, 1985; Wilson, 1980). On the other hand, physiological and psychophysical experiments demonstrate interactions between the spatial and temporal domains (e.g., Carrasco, 1990; Drum, 1984). Furthermore, there seems to be a trade-off between spatial and temporal resolution (e.g., Wilson, 1980; Wilson & Bergen, 1979). For instance, whereas spatial resolution is highest at the fovea, temporal resolution may be higher at more peripheral regions, and whereas spatial resolution requires small receptive fields, large receptive fields may mediate temporal resolution (e.g., Allen & Hess, 1992; Schiller & Logothetis, 1990; Shapley & Perry, 1986).

Given these divergent findings, it is not obvious what the effects of attention on temporal resolution would be. Specifically, if spatial and temporal resolution are mediated by relatively independent factors, then spatial attention may be able to adapt its operation to also enhance temporal resolution. Alternatively, depending on the degree to which these factors interact, and given the contrasting characteristics of the two kinds of resolution, attention may produce a reverse effect on temporal resolution. For example, if attention enhances spatial resolution by reducing the size of receptive fields, and temporal resolution requires large receptive fields, attention may impair temporal resolution instead of enhancing it.

To test these contrasting predictions, we coupled a classic method for measuring temporal resolution—the two-flash fusion threshold—with peripheral precuing, which is a common way to manipulate transient spatial attention. The main question was whether spatial attention could affect temporal resolution, and if so, what direction the effect would take (enhancement vs. decrement).

EXPERIMENT 1

To assess temporal resolution, we measured the two-flash fusion threshold. Two flashes of light were presented successively to the same location, and we determined the minimal interval between the flashes at which they were still perceived as two separate flashes, rather than as a single continuous flash. The shorter this critical interval is, the higher the temporal resolution (e.g., Artieda, Pastor, Lacruz, & Obeso, 1992; Reeves, 1996). This measurement of temporal resolution was combined with a direct manipulation of transient spatial attention. In half the trials, the *cued trials*, a peripheral cue indicated the target's onset and location. This exogenous cue, a small horizontal bar, allowed observers to focus their attention, in advance, on the target location, and was assumed to capture attention in a stimulus-driven, automatic manner (e.g., Jonides, 1981). In the rest of the trials, the *neutral trials*, two long horizontal lines indicated the target's onset but not its location (i.e., the target was equally likely to appear at any location).

Given the finding that spatial attention enhances spatial resolution, and given that there may be a trade-off between spatial and temporal resolution, we reasoned that attending to the location of this temporal target might decrease temporal resolution. Alternatively, the effects of attention on temporal resolution might not be constrained by its effects on spatial resolution. That is, when the task at hand requires high temporal resolution, the attentional mechanism may be able to adapt itself to the task requirements and enhance temporal resolution.

Method

Eighteen observers with normal or corrected-to-normal vision viewed a 21-in. monitor of a PowerMac G4 computer, and had to indicate whether the target was composed of two flashes of light separated by a brief interval or a single continuous flash (Fig. 1). The flash was composed of a 37-cd/m^2 disk with a diameter of 3°. It appeared on a black background at one of 11 possible locations along the horizontal meridian, with eccentricity (distance from the center) ranging from 0 to 16.5°. The cue in the cued trials was a $1° \times 0.3°$ green horizontal bar (43 cd/m^2) appearing 0.5° above the target's location. In the neutral trials, two $17° \times 0.3°$ green horizontal lines appeared above and below the entire display.

Each trial began with a fixation point followed by the attentional cue (Fig. 1). The cue was present until the target's offset, to prevent confusion between the flickering of the cue and that of the target. The target was presented 94 ms after onset of the cue: On 50% of the trials, two disks appeared, each for 47 ms, separated by a variable interval (interstimulus interval, ISI, of 11–34 ms). On the rest of the trials, a single disk was presented for a duration ranging from 105 to 130 ms. These brief durations ensured that eye movements could not occur between cue onset and target offset (Mayfrank, Kimmig, & Fischer, 1987). Each observer viewed 864 trials presented in a randomized order. Both accuracy and reaction time (RT) were recorded.

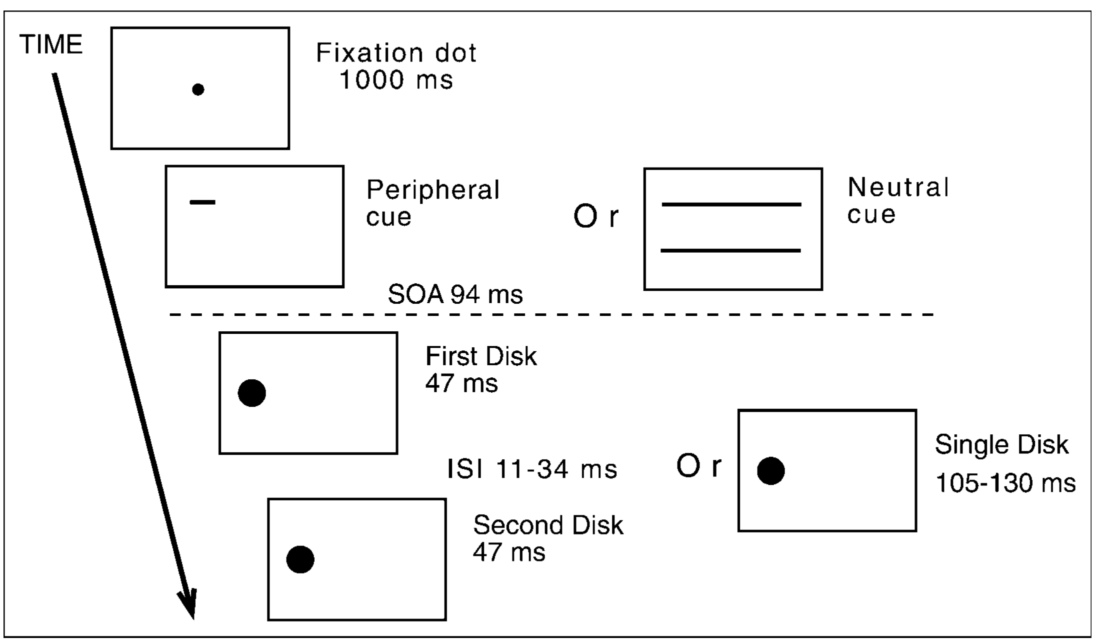

Fig. 1. Sequence of presentation of each experimental trial. ISI = interstimulus interval. SOA = stimulus onset asynchrony.

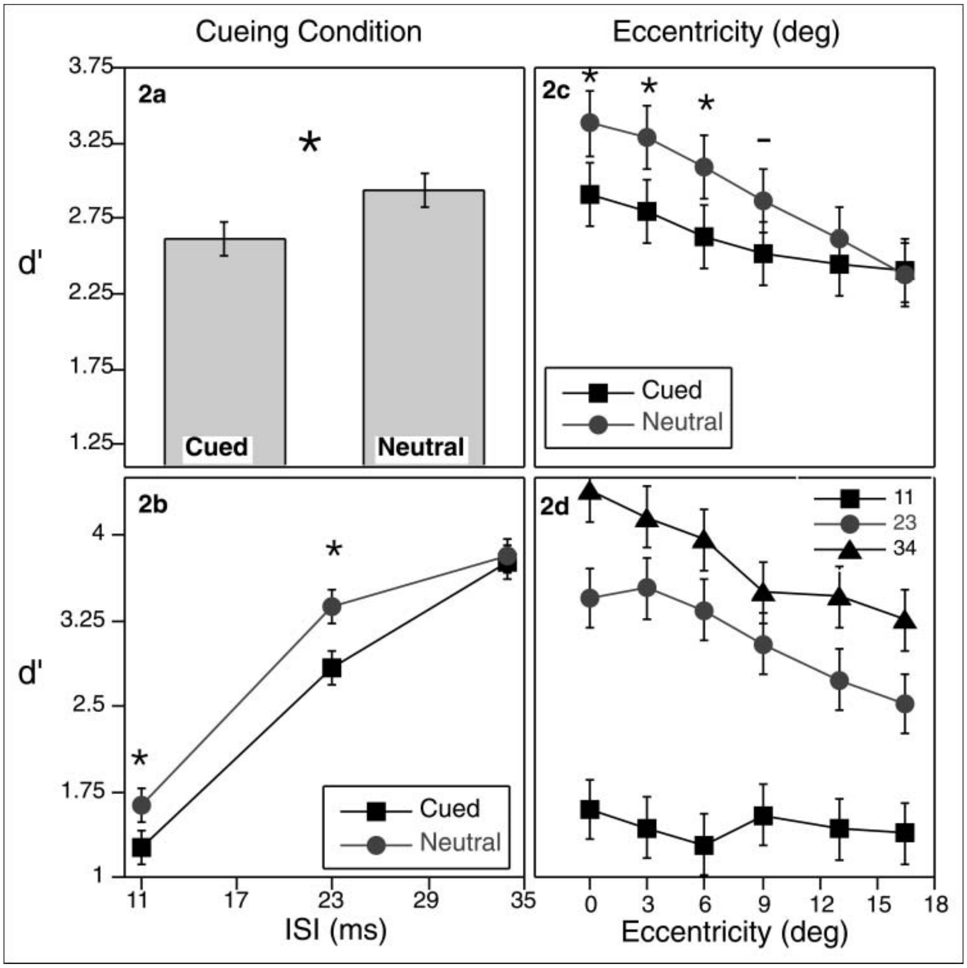

Fig. 2. Observers' accuracy in Experiment 1 as a function of (a) cuing condition, (b) cuing condition and interstimulus interval (ISI), (c) cuing condition and target eccentricity, and (d) ISI and target eccentricity. Results of LSD post hoc comparisons are shown; marginally significant differences ($p < .1$) are indicated by a minus sign, and significant differences ($p < .05$) by an asterisk.

Results and Discussion

A within-observers three-way analysis of variance (ANOVA; Cuing $\times$ Eccentricity $\times$ ISI) was performed on the accuracy (d')[1] and RT data collected on trials with correct responses. As can be seen in Figure 2a, performance was significantly less accurate in the cued than the neutral trials, $F(1, 17) = 8.01$, $p \leq .01$. Although the Cuing $\times$ ISI, Cuing $\times$ Eccentricity, and ISI $\times$ Eccentricity interactions were not significant, the performance decrement in the cued trials was more pronounced for shorter ISIs (i.e., when a higher temporal resolution is required) than for longer ISIs and for more central, compared with more peripheral, eccentricities (Figs. 2b–2d, respectively). Effects on RTs were not statistically significant but resembled the effects on accuracy, indicating that there was no speed-accuracy trade-off.

The difference in d' between the cuing conditions was accompanied by a small but significant difference in response bias,[2] $F(1, 17) = 27.14$, $p \leq .0001$. Observers adopted a mildly conservative criterion in the cued trials (i.e., a tendency to report a continuous target; $c = 0.155$) and a mildly liberal criterion in the neutral trials ($c = -0.163$).

In sum, attending the target location degraded observers' ability to detect the temporal gap. This decrement may have been a side effect of the fact that attention enhances spatial resolution. That is, because attention enhances spatial resolution, and there seems to be a trade-off between spatial and temporal resolution, attention may actually harm temporal resolution. Alternatively, the performance decrement in the cued trials may simply have been an artifact of the specific cuing manipulation used (e.g., there may have been forward-masking effects

1. The following equation was used to calculate d': $d' = z(\text{hit}) - z(\text{false alarm})$ (Macmillan & Creelman, 1991).

2. The following equation was used to calculate response bias: $c(\text{criterion}) = -0.5(z(\text{hit}) + z(\text{false alarm}))$ (Macmillan & Creelman, 1991).

between the cue and the target). To test this latter alternative, we performed Experiment 2.

EXPERIMENT 2

This experiment was designed to rule out the possibility that the performance decrement in the cued trials of Experiment 1 was due to some local interference between the cue and the target. To that end, we used the same attentional manipulation used in Experiment 1, but instead of measuring temporal resolution, we employed a task that requires high spatial resolution: detection of a spatial gap rather than a temporal gap. Instead of the flickering disk, a circle with a small gap in one of its sides was presented, and observers had to indicate the side of the circle with the gap. If the performance decrement of Experiment 1 was an artifact of the cuing manipulation, the decrement would also be expected in this experiment, because the same cuing manipulation was employed. In contrast, if the decrement in temporal resolution was a consequence of the same attentional operation that enhances spatial resolution, the decrement would be expected to disappear when the task requires high spatial resolution.

Method

Experiment 2 was the same as Experiment 1, except for the following: Instead of the disk, a circle 3° in diameter, with a 0.06° gap in one of its sides, was presented for 80 ms at one of seven possible locations, with eccentricity ranging from 0 to 6°. Thirteen observers viewed 416 trials each, and indicated whether the gap appeared on the right or the left side of the circle.

Results and Discussion

A within-observers two-way ANOVA (Cuing $\times$ Eccentricity) indicated that, unlike in Experiment 1, performance was significantly more accurate in the cued than the neutral trials, $F(1, 12) = 34.29$, $p \leq .0001$ (Fig. 3a). This attentional benefit was present at all target eccentricities (Fig. 3b). As in Experiment 1, there was no speed-accuracy trade-off. Finally, there was no significant response bias.

The finding that transient attention improves performance in a task that measures spatial resolution is consistent with our previous studies demonstrating an attentional benefit with acuity and hyperacuity tasks (Carrasco, Williams, & Yeshurun, 2002; Yeshurun & Carrasco, 1999), and with the results of studies using many other psychophysical tasks that require heightened spatial resolution, such as visual search (Carrasco & Yeshurun 1998), luminance detection, and letter identification (Posner, Snyder, & Davidson, 1980).

Taken together, Experiments 1 and 2 demonstrate that when the task required high temporal resolution (Experiment 1), precuing attention to the target location diminished performance. In contrast, when the task required high spatial resolution (Experiment 2), the same precue improved performance. The fact that the same attentional cue led to a performance decrement only in Experiment 1 rules out the possibility that this decrement was caused by some local interference between the cue and the target. Instead, the findings imply that attention indeed degrades temporal resolution, possibly as a consequence of the enhancement of spatial resolution.

EXPERIMENT 3

It seems, then, that whether spatial attention decreases or enhances performance depends on the type of resolution required for optimal performance. Could the same mechanism of spatial attention account for both outcomes? That is, is there a single attentional mechanism that enhances spatial resolution on the one hand but degrades temporal resolution on the other?

Some researchers have suggested that attention enhances spatial resolution by reducing the size of receptive fields at the attended location (e.g., Desimone & Duncan, 1995; Moran & Desimone, 1985). These authors proposed that, initially, top-down signals bias activity in

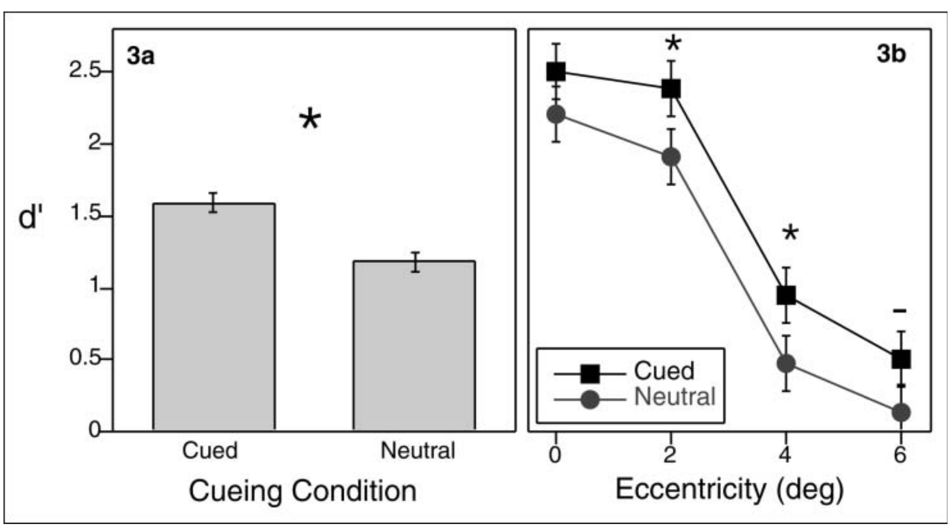

Fig. 3. Observers' accuracy in Experiment 2 as a function of (a) cuing condition and (b) cuing condition and target eccentricity. Results of LSD post hoc comparisons are shown; marginally significant differences ($p < .1$) are indicated by a minus sign, and significant differences ($p < .05$) by an asterisk.

favor of the neurons representing the attended location. These favored neurons compete with other neurons and ultimately inhibit their response. The outcome of this competition could effectively reduce the size of the relevant receptive fields. Smaller receptive fields indeed allow for enhanced spatial resolution. Temporal resolution, however, requires large receptive fields because with large receptive fields spatial summation—the summation of signals from neighboring areas—is performed over larger areas, resulting in a larger sum of signals and therefore an increased signal-to-noise ratio (e.g., Mäkelä, Rovamo, & Whitaker, 1994; Raninen & Rovamo, 1987). Given that spatial summation is diminished with smaller receptive fields, because it occurs over smaller areas, and given that attention may reduce the size of receptive fields, attending the target location may reduce temporal resolution. Thus, an attentional mechanism that limits spatial summation via a reduction in the size of receptive fields could account for both the enhancement of spatial resolution and the decrement in temporal resolution.

Experiment 3 was designed to test the possibility that the attentional decrement in temporal resolution is indeed due to a decrement in spatial summation. Observers were again asked to detect a temporal gap. However, the flickering disk, which had a diameter of 3° in Experiment 1, had a much smaller diameter of 0.3° in this experiment. If the attentional disadvantage in temporal resolution resulted from a decrement in spatial summation, that disadvantage would be eliminated (or at least reduced) in this experiment. This is because with a disk smaller than 1 to 2°, spatial summation is negligible (e.g., Brown, 1966), and therefore should not affect performance. Alternatively, if the cued trials' disadvantage in temporal resolution remained, this result would indicate that the attentional mechanism underlying the resolution decrement does not merely reduce the effective area over which information is summed.

Method

Experiment 3 was the same as Experiment 1, except for the following: Instead of the 3° disk, a 0.3° disk appeared in one of five possible locations. Floor effects were avoided by presenting the disk with a variable ISI of 23 or 34 ms, and at eccentricities ranging from 0 to 5° only. Each of the 9 observers viewed 816 trials.

Results and Discussion

A within-observers three-way ANOVA (Cuing × Eccentricity × ISI) revealed that the attentional disadvantage found with a large disk is present even with a much smaller disk. Performance was still significantly less accurate in the cued than the neutral trials, $F(1, 8) = 17.13$, $p \leq .005$ (Fig. 4a). This performance decrement was more pronounced for the 34-ms than for the 23-ms ISI, $F(1, 8) = 6.02$, $p \leq .05$ (Fig. 4b), but did not vary as a function of target eccentricity (Fig. 4c). Performance differences between the two ISIs were more pronounced at far than at near eccentricities, $F(2, 16) = 4.73$, $p \leq .05$ (Fig. 4d). As before, there was no speed-accuracy trade-off. A response bias was found only for the neutral trials (a conservative criterion; $c = 0.251$).

Because spatial summation can take place only across the area covered by the stimulus, the benefits of spatial summation are negligible when the stimulus covers a very small area (e.g., Brown, 1966). Hence, neurons with large receptive fields lose their advantage over neurons with smaller receptive fields. If the attentional decrement in temporal resolution was due to a decrement in spatial summation, brought about by an attentional decrease in receptive-field size, it should have been eliminated once spatial summation was no longer a relevant factor. The fact that the attentional impairment was not eliminated or even reduced with a small disk suggests that this decrement in temporal resolution is not due to a decrement in the extent of spatial summation.

GENERAL DISCUSSION

This study examined whether transient spatial attention can affect visual temporal resolution, and if so, how these effects on temporal resolution are related to attentional effects on spatial resolution. Experiments 1 and 3 revealed that spatial attention can indeed affect temporal resolution. In both experiments, attending the target location reduced observers' ability to detect a temporal gap. Experiment 2 further demonstrated that this performance decrement was not a mere artifact of the cuing manipulation, because the same attentional cue improved performance when the task required high spatial resolution. Taken together, these experiments demonstrate that in contrast to its effects on spatial resolution, attention lowered observers' temporal resolution.

What mechanisms could possibly lead to this attentional decrement in temporal resolution? An attentional mechanism that reduces the size of receptive fields could account for both an enhancement in spatial resolution and a decrement in temporal resolution. Whereas smaller receptive fields allow for enhanced spatial resolution, they limit spatial summation, which may, in turn, harm temporal resolution. Experiment 3 indicates, however, that the attentional mechanism underlying the decrement in temporal resolution does not merely reduce the size of receptive fields, because a lower temporal resolution was found even when spatial summation was not a relevant factor.

An alternative explanation is that spatial attention facilitated the activity of parvocellular neurons at the attended location, possibly by enhancing their sensitivity, and that this in turn inhibited the activity of magnocellular neurons at the same location. Because parvocellular neurons typically have smaller receptive fields than magnocellular neurons, one of the outcomes of favoring parvocellular over magnocellular neurons is a reduction in the size of receptive fields. Nevertheless, this is just one of several outcomes brought about by parvocellular facilitation. For instance, in addition to their smaller receptive fields, parvocellular neurons have longer response duration (e.g., Merigan & Maunsell, 1993; Schiller & Logothetis, 1990). Accordingly, attentional facilitation of parvocellular neurons will have at least two outcomes: reduction in the average size of receptive fields and prolonged response periods. When two stimuli are separated by a brief interval, longer response duration means that their corresponding neural responses are more likely to be integrated over time, yielding lowered temporal resolution. Thus, an attentional mechanism that favors parvocellular over magnocellular neurons could account for both the enhancement in spatial resolution (because of smaller receptive fields) and the decrement in temporal resolution (because of longer response duration). Because in this case the reduction in temporal resolution is not attributed to a reduction in spatial summation, this attentional mechanism can accommodate the findings of all three experiments reported here.

The notion of inhibitory interactions between parvocellular and magnocellular channels has been raised in several studies exploring various phenomena (e.g., Breitmeyer & Williams, 1990; Tassinari, Marzi, Lee, Di Lollo, & Campara, 1999). The possibility that such "parvo-magno" inhibition underlay the attentional decrement in tem-

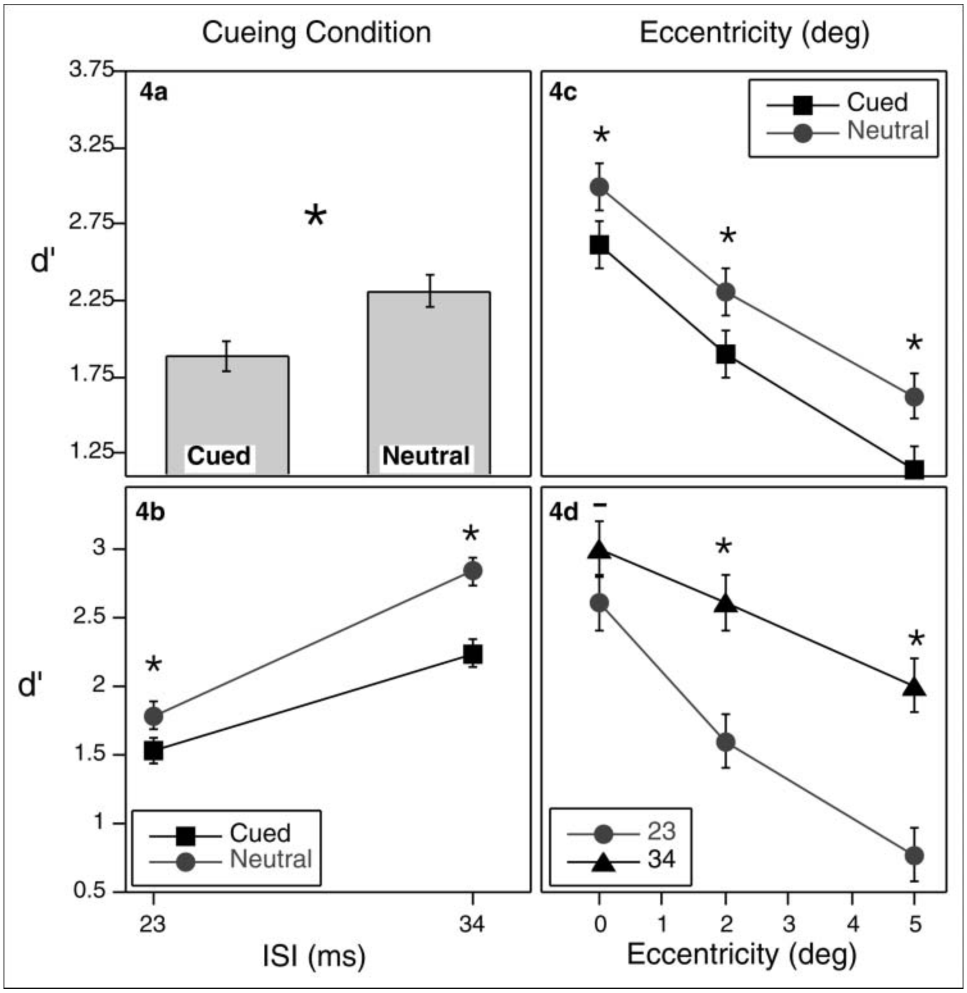

Fig. 4. Observers' accuracy in Experiment 3 as a function of (a) cuing condition, (b) cuing condition and interstimulus interval (ISI), (c) cuing condition and target eccentricity, and (d) ISI and target eccentricity. Results of LSD post hoc comparisons are shown; marginally significant differences ($p <$ .1) are indicated by a minus sign, and significant differences ($p < .05$) by an asterisk.

poral resolution found here is supported by the fact that when temporal resolution was measured over a large range of eccentricities (Experiment 1), a larger decrement was found at near than at far eccentricities (Fig. 2c). Given that parvocellular neurons are more prevalent at near eccentricities (e.g., Merigan & Maunsell, 1993; Schiller & Logothetis, 1990), their inhibitory impact should be larger at these eccentricities and indeed lead to a greater decrement.

It is certainly possible that the enhancement in spatial resolution and the decrement in temporal resolution are brought about by two different attentional mechanisms, though this explanation is less parsimonious. Enhanced spatial resolution could be due to a mere reduction in receptive-field size, whereas lengthening the period over which visual information is integrated may bring about the decrement in temporal resolution. Although these two operations may take place independently, it is important to note that the favoring of parvocellular neurons leads to both outcomes: reduction in the size of receptive fields and longer temporal integration.

Moreover, the finding that attention lowers temporal resolution is consistent with previous studies demonstrating that attention prolongs the duration of visible persistence (Visser & Enns, 2001) and the perceived duration of the attended stimulus (e.g., Enns, Brehaut, & Shore, 1999; Mattes & Ulrich, 1998; Tse, Cavanagh, Intriligator, & Rivest, 1997). Although these previous studies did not directly manipulate transient spatial attention, as was done in the present study, all three outcomes (lower temporal resolution, longer visible persistence, and longer perceived duration) could be accounted for by attentional favoring of parvocellular over magnocellular neurons. Parvocellular neurons are typically active longer than magnocellular neurons and characterized by slower decay (e.g., Merigan & Maunsell, 1993; Schiller & Logothetis, 1990). Therefore, their facilitation could result in both longer perceived duration of stimuli and longer temporal integration that leads to longer visible persistence and lower temporal resolution. Thus, our counterintuitive finding that attention can degrade performance seems less surprising when one considers the trade-off between segregation and integration of information. The opposing nature of these two processes suggests that an attentional mechanism that enhances one should degrade the other. Indeed, attention helps performance when the task requires segregation of the scene into its fine spatial components or integration across time. In contrast, when there is a need for spatial integration or fine temporal segregation, attention degrades performance.

The hypothesis that spatial attention facilitates parvocellular neurons, which in turn inhibit magnocellular neurons, could also account for the finding that attention reduces metacontrast masking (e.g., Enns & Di Lollo, 1997). It has been suggested that metacontrast masking—backward masking between spatially separated stimuli—is produced when magnocellular channels, activated by the mask, inhibit the activity of parvocellular channels, activated by the target (e.g., Breitmeyer, 1984; Breitmeyer & Williams, 1990). If so, the attentional facilitation of parvocellular neurons should reduce the impact of such magnocellular inhibition, and therefore reduce metacontrast effects.

Finally, it is essential to emphasize that an attentional mechanism that facilitates parvocellular neurons is probably not the only mechanism operating when an observer is attending a specific location. It is very likely that different mechanisms operate when different components of attention are triggered by different experimental paradigms (e.g., central precuing, attentional blink, line-motion illusion). Even within the paradigm of peripheral precuing employed here, it is quite probable that several attentional processes take place at the same time, resulting in different outcomes depending on the task at hand. In this study, only a single target was present at any given moment, and the task required either high temporal resolution or high spatial resolution. With these conditions, attention enhanced spatial resolution but decreased temporal resolution. Different experimental conditions may reveal the operation of different attentional mechanisms. For instance, the addition of nonrelevant information to the display might reveal that spatial attention reduces interference from distractors or masking effects (e.g., Morgan, Ward, & Castet, 1998; Smith, 2000), and a task that requires temporal-order judgment may reveal an attentional advantage in access to awareness (e.g., Shore et al., 2001).

To conclude, this study is the first to demonstrate that transient spatial attention can indeed affect visual temporal resolution. However, contrary to the attentional effect on spatial resolution, attending the target location degrades performance that is limited by temporal resolution. A possible attentional mechanism that favors parvocellular over magnocellular neurons can account for both attentional effects: enhanced spatial resolution and decreased temporal resolution.

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