

Isoluminant stimuli and red background attenuate the effects of transient spatial attention on temporal resolution

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Abstract

The effects of transient spatial attention on temporal resolution were recently studied and compared with attentional effects on spatial resolution. It was found that in contrast to the attentional enhancement of spatial resolution, transient attention impairs temporal resolution. To account for these findings a novel attentional mechanism was suggested. This attentional mechanism facilitates parvocellular neurons at the attended location, which in turn inhibit the activity of magnocellular neurons at the same location [Yeshurun & Levy, *Psychol. Sci.* 14 (3) (2003a) 225]. The goal of the present study was to replicate the attentional decrement in temporal resolution (Experiment 1), and perform direct tests of this ‘parvo facilitation—magno inhibition’ hypothesis. The employment of isoluminant stimuli (Experiments 2a and 2b) or a red background (Experiment 3) ensured that the parvo system was the main system mediating performance. Consequently, any parvo–magno inhibitory processes elicited by the attentional mechanism should only have a minor effect on performance. As predicted, these manipulations either significantly attenuated or completely eliminated the attentional decrement in temporal resolution. These findings provide direct support to the hypothesis that attention favors parvocellular over magnocellular neurons.

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Processes that select a specific location in space and grant priority in processing to information gathered at that location are often grouped under the term spatial attention, and transient attention is the involuntary, stimulus-driven component of spatial attention. In previous studies we examined the effects of transient attention on spatial and temporal resolution. By utilizing different stimuli and tasks, like gap detection with ‘Landolt-squares’, discrimination of offset-direction with Vernier targets (e.g., Yeshurun & Carrasco, 1999) and texture segmentation (e.g., Yeshurun & Carrasco, 1998, 2000), we were able to show that transient attention enhances the spatial resolution at the attended location. That is, it enhances our ability to resolve small details in the visual scene. In a recent study, we examined the effects of transient attention on temporal resolution, i.e., our ability to resolve rapid changes in light intensity over time (Yeshurun & Levy, 2003a). Observers saw two

flashes of light presented successively to the same location. The minimal interval between the flashes at which observers can still perceive them as two separate flashes, rather than a single continuous flash reflects the limit of their temporal resolution. The shorter this critical interval is, the higher the temporal resolution required to resolve it (e.g., Artieda, Pastor, Lacruz, & Obeso, 1992; Reeves, 1996). This measurement of temporal resolution was combined with peripheral precueing—a common method to manipulate transient attention. On the *cued trials*, a peripheral cue indicated the target onset and location. This exogenous cue allows observers to focus their attention, in advance, on the target location, and is assumed to capture attention in a stimulus-driven, “automatic” manner (e.g., Jonides, 1981; Müller & Rabbitt, 1989; Posner, 1980). On the *neutral trials*, a neutral cue indicated the target onset but not its location (i.e., it was equally likely to appear at any location). This combined paradigm allowed us to demonstrate, that spatial attention can affect temporal resolution. However, in contrast to its effect on spatial resolution, spatial attention *degrades* temporal resolution. That is, we

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found that observers were less accurate in the cued than the neutral trials.

In a search for a single attentional mechanism that can account for both the enhancement of spatial resolution and the decrement in temporal resolution, we first examined the possibility that transient attention merely reduces the size of receptive fields at the attended location (e.g., Desimone & Duncan, 1995; Moran & Desimone, 1985). Smaller receptive fields allow for enhanced spatial resolution. Temporal resolution, however, requires large receptive fields because with large receptive fields spatial summation—the summation of signals from adjacent 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). If transient attention indeed reduces receptive fields' size, attending the target location should diminish spatial summation as it occurs over a smaller area, and therefore should result in a lower temporal resolution. Thus, an attentional mechanism that limits spatial summation via a reduction in receptive fields' size could account for both attentional effects: spatial resolution enhancement and temporal resolution decrement.

To test this hypothesis observers were again asked to detect a temporal gap separating two brief flashes. However, the 3° flickering disk, used before, was replaced with a much smaller disk (0.3° diameter). If the attentional disadvantage in temporal resolution resulted from a decrement in spatial summation it should be eliminated (or at least reduced) because with a disk smaller than 1°–2°, spatial summation is negligible (e.g., Brown, 1966), and therefore should not affect performance. We found, however, that the attentional disadvantage, found with a large disk, was present even with a much smaller disk. Performance was still significantly less accurate in the cued than the neutral trials. This finding suggests that the attentional decrement in temporal resolution is not due to a mere decrement in the extent of spatial summation (Yeshurun & Levy, 2003a).

An alternative hypothesis suggests that transient attention facilitates the activity of parvocellular neurons at the attended location, and that due to inhibitory interactions between parvocellular and magnocellular channels (e.g., Breitmeyer & Williams, 1990; Tassinari, Marzi, Lee, Di Lollo, & Campara, 1999) this facilitation then leads to inhibition of magnocellular neurons at the same location (Yeshurun & Levy, 2003a). Parvocellular neurons typically have smaller receptive fields than magnocellular neurons, greater sampling density, and they demonstrate higher spatial resolution. However, their response duration is longer, and their temporal resolution is low (e.g., Derrington & Lennie, 1984; Gouras & Zrenner, 1979; Merigan & Maunsell, 1993; Schiller & Logothetis, 1990; Schiller, Logothetis, & Charles, 1990; Solomon, White, & Martin, 1999). Thus,

an attentional mechanism that favors parvocellular over magnocellular neurons could also account for both effects of transient attention—enhancement of spatial resolution and decrement in temporal resolution. Evidently, because parvocellular neurons typically have smaller receptive fields, one of the outcomes of favoring parvocellular over magnocellular neurons is a reduction in the average size of receptive fields at the attended location. Even so, with this attentional mechanism, smaller receptive fields is just one outcome out of several possible outcomes of parvocellular facilitation, and it may not be the one responsible for the decrement in temporal resolution. For example, the temporal resolution decrement might be due to the fact that parvocellular neurons have longer response duration. Longer response duration means lowered temporal resolution because when two stimuli are separated by a brief interval, their corresponding neural responses are more likely to be integrated over time if their response duration is longer. Thus, while the former outcome—smaller receptive fields—could be responsible for the spatial resolution enhancement, the latter outcome—prolonged response duration—could account for the impaired temporal resolution. Because in this case the reduction in temporal resolution is not attributed to a reduction in spatial summation, this attentional mechanism could also account for the temporal resolution decrement found with the small disk.

The goal of the present study was to directly test the hypothesis that transient attention facilitates parvocellular neurons and that this facilitation leads to inhibition of magnocellular neurons. To that end, two different methods were employed. In one, the flickering stimuli were isoluminant, and in the other, a red background was used. Presumably, both methods ensure that the parvo system is the predominant system involved in the processing of the flickering stimuli, either because the magno system is relatively colorblind (e.g., Merigan & Maunsell, 1993; Schiller & Logothetis, 1990) or because it is inhibited by diffused red light (e.g., Kruger, 1977; Livingstone & Hubel, 1984; Schiller & Malpeli, 1978; Van Essen, 1985). Given that in both cases, the magno system has only a negligible effect on performance, any parvo–magno inhibitory effects elicited by such attentional mechanism should only have a minor effect on performance, and the attentional decrement in temporal resolution should be greatly attenuated.

To test this hypothesis four experiments were performed. Resembling our previous study (Yeshurun & Levy, 2003a), all four employed a combination of two-flash-fusion threshold measurements and attentional precueing. Experiment 1 was designed to replicate the previously found attentional disadvantage in temporal resolution, but with a control for local temporal interference. It also served as the baseline to which performance in Experiments 2a and 2b was compared.

Experiments 2a,b were similar to Experiment 1, but their flickering stimuli were isoluminant. Finally, Experiment 3 compared performance with a gray background to that with a red background. We expect to find the attentional decrement in temporal resolution in Experiment 1 and with the gray background of Experiment 3. In contrast, if attention indeed favors parvocellular over magnocellular neurons, this decrement should be greatly attenuated in Experiments 2a, 2b and with the red background of Experiment 3.

1. Experiment 1

This experiment examined whether the previously found performance decrement in the cued trials reflects a real attentional effect on temporal resolution or merely a local temporal interference between the attentional cue and the target. A simple local interference (e.g., forward masking) was already ruled out in a previous control experiment (Yeshurun & Levy, 2003a). There, the attentional manipulation was identical to the one used in the original experiment (Fig. 1a): the peripheral attentional cue was a small horizontal bar that appeared above the target location, and the neutral cue was composed of two long horizontal lines appearing above and below the entire display. The task employed in the control experiment, however, required high spatial resolution rather than measuring temporal resolution. 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 in the cued trials was a mere artifact of this specific cueing manipulation, it should have also been found in that control experiment, because the same cueing manipulation was employed. We found, however, that when the task required high spatial resolution the precue improved performance. The fact that the same attentional cue led to performance decrement

when the task required high temporal resolution rules out the possibility that this decrement was caused by some simple local interference between the cue and the target.

Still, the attentional decrement in temporal resolution might be due to a more complex temporal interference. For example, to successfully attract transient attention, the attentional cue appeared in an adjacent location to the target. Because of this proximity, the neural activity generated by the cue might be somehow integrated with the activity generated by the target, resulting in a more complex temporal pattern of activity that hampers observers' ability to detect the temporal gap. The end result would be lowered performance with the attentional cue than with the neutral cue. Such temporal interference might not be evident unless a temporal task is employed.

This possibility does not seem highly likely to us given that the cue and target were very different in appearance (a $1^\circ \times 0.3^\circ$ green horizontal bar vs. a 3° gray disk); they did not occupy the same spatial location, but were separated by 0.5° ; and the cue was present till target offset, so it was clear that these are two separate objects. Nevertheless, to ensure that the temporal resolution decrement is not due to such interference Experiment 1 employed a similar temporal resolution task—indicating whether the target was flickering or continuous, but with a 'multi-bar' neutral cue that simultaneously cues all possible locations, resembling the cue employed successfully by Talgar, Pelli, and Carrasco (2004). Instead of the two long horizontal lines, the 'multi-bar' neutral cue was composed of nine $1^\circ \times 0.3^\circ$ green horizontal bars that appeared 0.5° above each one of the nine possible target locations (Fig. 1b). Each of these bars was identical to the bar used as the peripheral cue. Thus, with such a neutral cue the local information present in the vicinity of the target is identical in both cueing conditions. The sole difference is that only with the attentional cue observers know in advance where the target is about to appear. If the attentional impairment of temporal resolution at the attended location is due to local temporal interference it should be greatly reduced with this neutral cue because such temporal interference should be present in both cueing conditions. Alternatively, if this decrement truly reflects the effects of transient attention on temporal resolution, it should be replicated even with this 'multi-bar' neutral cue.

1.1. Method

Observers: 16 students with normal or corrected to normal vision, who were naive as to the purpose of the study.

Stimuli and apparatus: The stimuli were presented using PsyScope™ (Cohen, MacWhinney, Flatt, & Provost, 1993) on a 21" monitor of a PowerMac G4

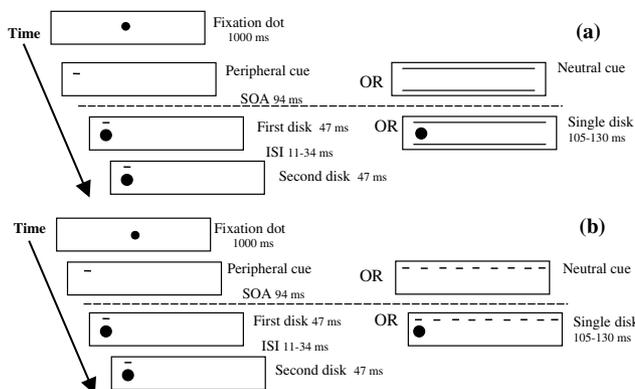


Fig. 1. This diagram depicts the sequence of presentation of each experimental trial of (a) the previous study of Yeshurun and Levy (2003a); (b) Experiment 1 and 2a of this study.

computer (resolution: 1280×1024 85 Hz). The target was composed of two flashes of light separated by a brief interval (flickering target) or a single continuous flash (continuous target). The flash was composed of a gray disk (50% of maximum brightness) with a diameter of 3°, appearing on a black background at one of nine possible locations along the horizontal meridian: one at the center and four to each side of fixation point (eccentricity: 3°, 6°, 9°, 13°). The cue in the cued trials was a 1°×0.3° green horizontal bar (CIE coordinates: $x=0.34$, $y=0.56$; 76% of maximum monitor brightness) appearing 0.5° above the target location. In the neutral trials, nine 1°×0.3° green horizontal bars appeared 0.5° above each one of the nine possible locations.

Procedure: Each trial began with a fixation point (1000 ms) followed by the cue. To prevent confusion between the flickering of the cue and that of the target, the cue was present till target offset. The target was presented 94 ms after cue onset: On 50% of the trials, two disks appeared, each for 47 ms, separated by a variable interval (ISI: 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). The observers had to report whether the target was flickering or continuous, and each one of them viewed 840 trials presented in a randomized order. Although observers were only encouraged to be accurate not fast, reaction times (RT) were also measured to test for speed-accuracy tradeoffs.

Because the disk of the flickering target was ‘on’ for a shorter duration than its corresponding continuous disk, it could have been perceived as dimmer. To rule out this possibility a pilot test was conducted prior to the actual data collection and it indicated that observers could not perform the task based on brightness differences between the flickering and continuous target.

1.2. Results and discussion

A within-observers three-way ANOVA (cueing*eccentricity*ISI) on accuracy (in d')¹ revealed that all main effects were significant. Observers performance deteriorated as target eccentricity increased [$F(4, 60) = 2.65$, $p \leq 0.05$; Fig. 2a] and as the ISI was shorter [$F(2, 30) = 180.56$, $p \leq 0.0001$; Fig. 2b]. Most importantly, observers were significantly more accurate in the neutral than the cued trials [$F(1, 15) = 29.13$, $p \leq 0.001$; Fig. 2a and b]. This attentional disadvantage was found for all eccentricities, apart for the 3° eccentricity in which the difference between the cued and

neutral condition was only marginally significant ($p = 0.066$), and for all ISIs. Only the ISI*eccentricity interaction attained statistical significance [$F(8, 120) = 4.02$, $p \leq 0.0005$] and it indicated that performance decreased with increasing eccentricities only for the two longer ISIs, (Fig. 2c). The analysis of the correct RTs (excluding values >3SD) indicated that there were no speed-accuracy tradeoffs.

A similar analysis of variance was performed on a measurement of response bias.² A significant effect of target eccentricity and ISI emerged. There was a growing tendency to adopt a more liberal criterion as target eccentricity increased and as the ISI was longer [Eccentricity: $F(4, 60) = 30.47$, $p \leq 0.0001$; ISI: $F(2, 30) = 65.1$, $p \leq 0.0001$]. However, as opposed to the significant precueing effect on d' , the response bias did not differ significantly between the cueing conditions, and in both cases it was not significantly different from 0—a neutral criterion.

Thus, the finding that precueing the target location degrades temporal resolution with stimuli whose luminance is changing over time was replicated even when the neutral cue ensured that local information adjacent to the target location is identical in both cueing conditions. This finding supports the conclusion that the performance decrement in the cued trials reflects an attentional degradation of temporal resolution rather than local temporal interference.

2. Experiments 2a,b

These experiments examined directly the hypothesis that transient attention favors parvocellular over magnocellular neurons, by using isoluminant stimuli. Isoluminant stimuli are stimuli whose luminance does not change over time; only their wavelength (color) changes. The logic was that because the magno system is relatively colorblind (e.g., Merigan & Maunsell, 1993; Schiller & Logothetis, 1990), a task that involves isoluminant stimuli is primarily performed by the parvo system. In this case, any inhibition between the parvo and magno systems should only have a minor effect on performance, and if the attentional degradation in temporal resolution is indeed a result of such inhibition it should be greatly reduced.

To test this prediction two experiments were performed. Both experiments employed a very similar experimental paradigm to the one used in Experiment 1, but with isoluminant stimuli. In Experiment 2a the target changed color from yellow to blue and in

¹ d' was calculated based on the following equation: $d' = z(\text{hit}) - z(\text{false alarm})$ (Macmillan & Creelman, 1991).

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

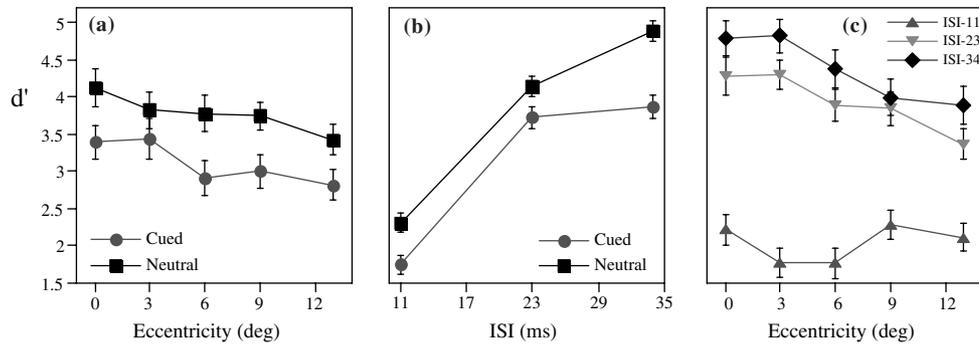


Fig. 2. Observers' performance in Experiment 1 as a function of (a) cueing condition and target eccentricity; (b) cueing condition and ISI; (c) ISI and target eccentricity. Error bars indicate ± 1 s.e.

Experiment 2b from red to green. In both cases the prediction is that the attentional disadvantage in temporal resolution will be greatly attenuated.

2.1. Experiment 2a

2.1.1. Method

Observers: 16 students with normal or corrected to normal vision, who did not participate in the previous experiment and were naive as to the purpose of the study.

Stimuli, apparatus and procedure: The stimuli, apparatus and procedure were identical to the previous experiment except for the fact that the target did not differ from its background in luminance but only in color, and its luminance stayed constant throughout target presentation. Isoluminance was established individually for each observer using the minimally distinct border method (e.g., Wagner & Boynton, 1972; Wyszewski & Stiles, 1982). In this experiment the target was yellow and it appeared on a blue background. The CIE coordinates that were most frequently chosen as isoluminant were: yellow—0.42 x , 0.50 y , and blue—0.25 x , 0.19 y . Because the green cues used in Experiment 1 were not very salient when presented on the blue background of this experiment their color was changed to light gray (90% of maximum monitor brightness).

As in Experiment 1, on 'continuous target' trials the yellow disk was present throughout target presentation, and on 'flickering target' trials, a varying ISI of the blue background separated the two disk presentations.

2.1.2. Results

A within-observers three-way ANOVA (cueing * eccentricity * ISI) on accuracy revealed that two main effects were significant. Similar to Experiment 1, observers performance deteriorated as target eccentricity increased [$F(4, 60) = 23.10$, $p \leq 0.0001$; Fig. 3a] and as the ISI decreased [$F(2, 30) = 21.63$, $p \leq 0.0001$; Fig.

3b]. However, as predicted, once isoluminant stimuli were used the difference between the cueing conditions was only marginally significant [$F(1, 15) = 3.07$, $p = 0.1$; Fig. 3a and b]. As in Experiment 1, only the ISI * eccentricity interaction was statistically significant [$F(8, 120) = 3.29$, $p \leq 0.002$] and it indicated that the differences between the different ISIs were more pronounced at near eccentricities (Fig. 3c). No speed-accuracy tradeoffs were found.

Finally, the analysis of response bias revealed a marginally significant difference between the cueing conditions [$F(1, 15) = 3.1$, $p = 0.099$]. Observers adopted a slightly liberal criterion in the neutral condition [$c = -0.2$; $t = 3.44$, $df = 15$, $p \leq 0.005$] and a neutral criterion in the cued condition [$c = -0.006$; $t = 0.74$, $df = 15$, $p = 0.5$]. As in Experiment 1, a significant effect of target eccentricity and ISI emerged. Observers adopted a more liberal criterion as target eccentricity increased and as the ISI was longer [eccentricity: $F(4, 60) = 48$, $p \leq 0.0001$; ISI: $F(2, 30) = 12.24$, $p \leq 0.0001$].

2.2. Experiment 2b

2.2.1. Method

Observers: 16 students with normal or corrected to normal vision, who did not participate in the previous experiments and were naive as to the purpose of the study.

Stimuli, apparatus and procedure: The stimuli, apparatus and procedure were similar to the previous experiments except for the following: The target was composed of a red disk appearing on a gray background. On trials with a 'continuous target' the red disk was present throughout target presentation for durations ranging between 34 and 105 ms. On trials with a 'flickering target', the red disk was present for 11, 23, or 34 ms, changed its color to green for 11, 23, or 34 ms, and then turned red again for another 11, 23, or 34 ms, respectively. These red, green, and gray colors were all of equal luminance, based on the minimally distinct

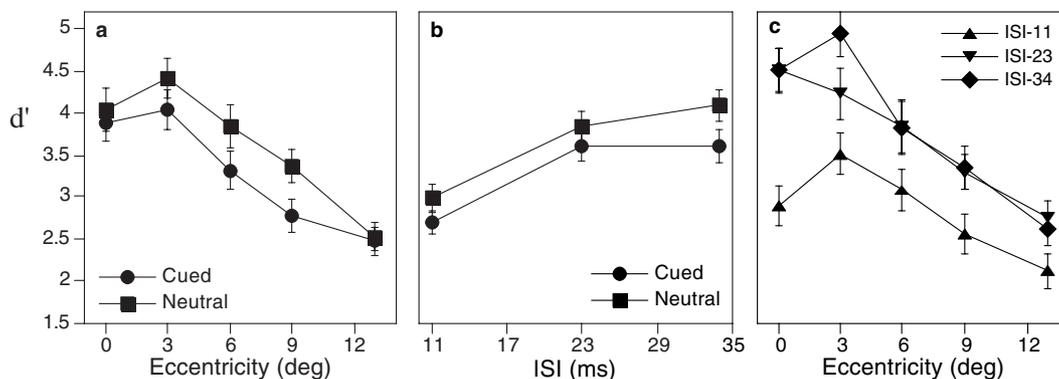


Fig. 3. Observers' performance in Experiment 2a as a function of (a) cueing condition and target eccentricity; (b) cueing condition and ISI; (c) ISI and target eccentricity. Error bars indicate ± 1 s.e.

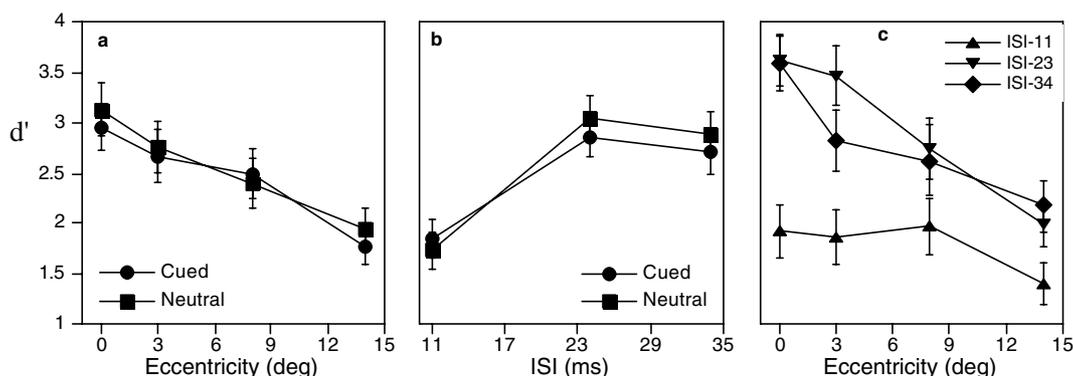


Fig. 4. Observers' performance in Experiment 2b as a function of (a) cueing condition and target eccentricity; (b) cueing condition and ISI; (c) ISI and target eccentricity. Error bars indicate ± 1 s.e.

border method (most frequently chosen CIE coordinates: red— $0.59 x, 0.35 y$; green— $0.27 x, 0.60 y$; gray— $0.31 x, 0.33 y$). The target could appear in one of seven locations with eccentricity ranging between 0° and 14° . The cue in the cued trials was a $1^\circ \times 0.3^\circ$ light gray (84% of maximal brightness) horizontal bar appearing 0.5° above the target location. On the neutral trials two $14^\circ \times 0.3^\circ$ light gray horizontal lines appeared above and below the entire display. Each observer viewed 768 trials presented in a randomized order.

2.2.2. Results

Similar to Experiment 2a, a within-observers three-way ANOVA (cueing*eccentricity*ISI) on accuracy indicated that only the two main effects of eccentricity and ISI were significant [eccentricity: $F(3, 45) = 19.00$, $p \leq 0.0001$; ISI: $F(2, 30) = 6.58$, $p \leq 0.004$; Fig. 4a and b respectively]. In this experiment, however, the attentional disadvantage in temporal resolution was completely eliminated, as there was no significant difference between the two cueing conditions [$F(1, 15) = 1.56$, $p > 0.2$; Fig. 4a and b]. Like before, only the ISI*eccentricity interaction was significant [$F(6, 90) =$

4.7 , $p \leq 0.0003$] and it indicated that the performance decrement as a function of eccentricity was more pronounced for the longer ISI's (Fig. 4c).

Interestingly, the RT analysis revealed a slight attentional benefit that was practically significant [$F(1, 15) = 4.52$, $p = 0.0505$]. However, given there was only a 7 ms difference between the cueing conditions this effect is rather small (cued mean RT = 573 ms; neutral mean RT = 580 ms). No other RT effects were significant.

Similar to Experiment 2a, observers adopted a more liberal criterion as target eccentricity increased and as the ISI was longer [eccentricity: $F(4, 60) = 23.61$, $p \leq 0.0001$; ISI: $F(2, 30) = 32.61$, $p \leq 0.0001$], but there was no significant effect of attentional precueing on response bias.

2.3. Discussion

The goal of Experiments 2a and 2b was to directly test the hypothesis that the attentional decrement in temporal resolution reflects an attentional facilitation of parvo neurons that leads to inhibition of magno neurons. To that end, these experiments employed different

isoluminant stimuli. The prediction was that because the magno system is not sensitive to isoluminant wavelength differences, any effects that are due to magno inhibition elicited by transient attention should be greatly reduced. The findings of both experiments complied with this prediction.

To directly compare the attentional effects with luminance (Experiment 1) and isoluminance (Experiments 2a and 2b) stimuli, the three data sets are combined in Fig. 5. As can be seen, most of the observers who performed the task with luminance stimuli fall below the equal-performance diagonal (i.e., demonstrating higher neutral than cued d' values), whereas most of the observers who viewed isoluminance stimuli fall along the diagonal. In addition, the difference in d' between the cued and neutral conditions was calculated for the different experiments. As can be seen in Fig. 6, the attentional disadvantage in temporal resolution, found in Experiment 1, was reduced by half in Experiment 2a, even though everything, apart for the isoluminant stimuli, was equal to Experiment 1, including the number of participants. This difference was even further reduced in Experiment 2b. A pooled t -test performed on this difference measurement combined from all three experiments indicated that the attentional disadvantage was indeed significantly greater with luminance stimuli than with isoluminant stimuli [$t = 2.66$, $df = 46$, $p \leq 0.005$].³

The finding that a marginally significant attentional decrement emerged in Experiment 2a, rather than a complete elimination of the attentional effect, might be due to the fact that a perfect isoluminosity is very hard to attain (e.g., Cavanagh, Edelson, & Heard, 1992; Kindlmann, Reinhard, & Creem, 2002), and was most likely not attained here, as there was no correction for chromatic aberration and the target was presented in different retinal locations, known to differ in their exact point of isoluminosity (e.g., Livingstone & Hubel, 1987; Mullen, 1991; Wyszecki & Stiles, 1982). It is very likely, then, that there was a slight luminance modulation present in the stimuli, resulting in a modest contribution of magno processing to performance in this experiment. The marginal attentional effect found in Experiment 2a might reflect an attentional inhibition of this modest magno contribution.

Because the employment of isoluminant stimuli cannot completely isolate the functions of the parvo and magno systems (e.g., Leonards & Singer, 1997; Shapley, 1990) an alternative method was employed in Experi-

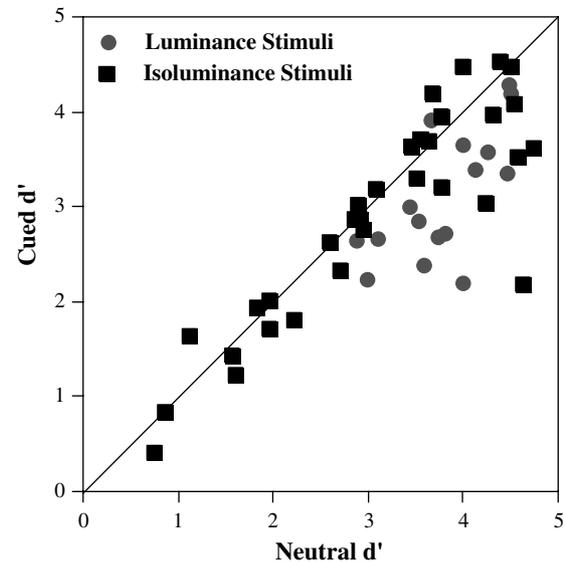


Fig. 5. Observers' performance in the cued condition as a function of performance in the neutral condition for each observer of Experiment 1 (luminance stimuli), and Experiments 2a,b (isoluminance stimuli).

ment 3, to supply converging evidence in support of the 'parvo facilitation—magno inhibition' hypothesis.

3. Experiment 3

The goal of this experiment, like that of Experiments 2a and 2b, was to test the hypothesis that the attentional decrement in temporal resolution is caused by an attentional facilitation of parvocellular neurons leading to inhibition of magnocellular neurons. To achieve this goal, Experiment 3 relied on the finding that the activation of magnocellular neurons is suppressed when diffused red light falls on the surround of their receptive fields (e.g., Kruger, 1977; Livingstone & Hubel, 1984; Schiller & Malpeli, 1978; Van Essen, 1985). Likewise, several previous psychophysical studies have shown that diffused red light impairs perceptual aspects considered to be closely related to the functioning of the magno system (e.g., Breitmeyer & Breier, 1994; Breitmeyer & Williams, 1990; Chase, Ashourzadeh, Kelly, Monfette, & Kinsey, 2003; Edwards, Hogben, Clark, & Pratt, 1996; Michimata, Okubo, & Mugishima, 1999; Pammer & Lovegrove, 2001). For example, Breitmeyer and Williams (1990) compared the quality of the perceived apparent motion and the magnitude of metacontrast masking effects with red, green, or neutral background. They found that with red background the quality of apparent motion and the magnitude of metacontrast masking effects were greatly reduced compare to the other backgrounds. Similarly, Michimata et al. (1999) found that red background impairs the perception of a global visual pattern considered to rely on processing of

³ Because d' values were relatively high the analysis was redone excluding 9 observers whose averaged d' was equal or higher than 4. Like before, the attentional disadvantage was significantly greater with luminance stimuli than with isoluminant stimuli [$t = 2.93$, $df = 37$, $p \leq 0.005$].

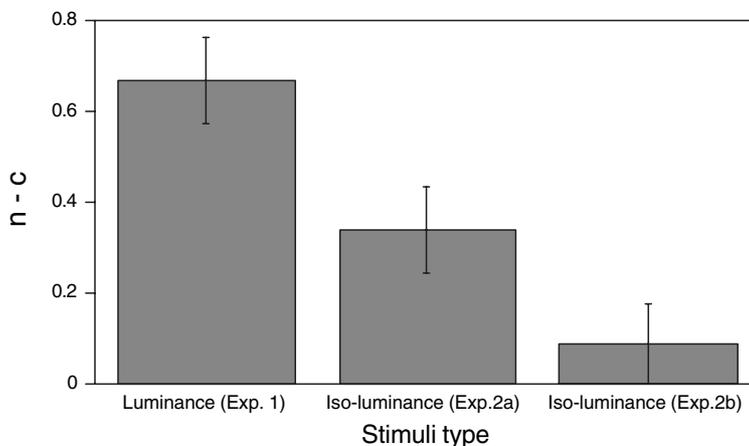


Fig. 6. The difference in d' between the cued and neutral conditions (n-c) for the different experiments. Error bars indicate ± 1 s.e.

low spatial frequencies. In addition, several studies have shown that flicker sensitivity is reduced when the flickering target is presented on a red background (e.g., Eisner & MacLeod, 1981; Pokorny, Smith, Lee, & Yeh, 1999; Stromeyer, Cole, & Kronauer, 1987).

If a red background indeed inhibits the activity of the magno system, then when a red background is used with the original temporal resolution task, performance should be primarily mediated by the parvo system, and should not be greatly affected by any parvo-magno inhibitory processes. The hypothesis that transient attention favors parvocellular over magnocellular neurons predicts, therefore, that with red background the attentional decrement should be greatly reduced.

3.1. Method

Observers: 22 students with normal or corrected to normal vision, who did not participate in the previous experiments and were naive as to the purpose of the study.

Stimuli and apparatus: The stimuli and apparatus, were similar to Experiment 1 except for the following: (a) There were two background conditions—gray and red. In the gray background condition the target color was gray (60% of maximal monitor brightness) and the background color was a darker gray (20% of maximal monitor brightness). In the red background condition the target color was red (CIE coordinates—0.63 x, 0.35 y; with brightness set at 60%) and the background color was a darker red (brightness set at 20%). To further simulate the effect of a diffused red light the monitor's tonal balance was adjusted to maximize red and minimize green and blue. With this adjustment the display looked similar to the way it would look when viewed through a light red filter. These were the only differences between the two background conditions. (b) The cue in the cued trials was a $1^\circ \times 0.3^\circ$ green horizontal bar appearing 0.5° above the target location. In the neutral

trials, two $14^\circ \times 0.3^\circ$ green horizontal lines appeared above and below the entire display.

Procedure: The procedure was similar to Experiment 1 except for the following: (a) Each of the two disks in the 'flickering target' trials was presented for 11 ms and the single disk in the 'continuous target' trials was presented for a duration ranging from 34 to 58 ms. (b) Each observer participated in two sessions, one for each background condition. Each session included 840 trials for a total of 1680 trials. The order of the sessions was counterbalanced and the order of trials within a session was randomized.

3.2. Results and discussion

As predicted by the 'parvo facilitation-magno inhibition' hypothesis, the difference between the cueing conditions was statistically significant only with the gray background [$\mu(\text{neutral } d' - \text{cued } d') = 0.20$; $t = 2.29$, $df = 21$, $p \leq 0.016$]. Once a red background was used this difference was no longer significant [$\mu(\text{neutral } d' - \text{cued } d') = 0.08$; $t = 0.85$, $df = 21$, $p = 0.2$]. With both backgrounds this difference did not vary significantly as a function of target eccentricity, ISI, or their interaction.

RT analysis revealed a tradeoff between accuracy and RT for the 11 ms ISI of the gray background condition. The analysis was, therefore, redone with the data of 11 ms ISI excluded, but the pattern of results did not change. The difference between the cueing conditions was still significant with the gray background [$\mu(\text{neutral } d' - \text{cued } d') = 0.22$; $t = 2.4$, $df = 21$, $p \leq 0.013$], but not with the red background [$\mu(\text{neutral } d' - \text{cued } d') = 0.05$; $t = 0.37$, $df = 21$, $p = 0.36$]. No other speed accuracy tradeoffs were found.

With both backgrounds observers adopted a mildly conservative criterion in the cued condition [Red: $c = 0.095$; Gray: $c = 0.268$] and a neutral criterion in the neutral condition [Red: $c = 0.057$; Gray: $c = 0.084$]. This difference in response bias between the two cueing

conditions was significantly more pronounced with the gray background [$t = 3.1$, $df = 21$, $p \leq 0.005$].

Given that a red background inhibits magnocellular neurons, the finding that the attentional decrement in temporal resolution did not reach statistical significance with a red background, supports the hypothesis that attention favors parvocellular over magnocellular neurons.

4. General discussion

We have shown, in the past, that transient attention lowers temporal resolution at the attended location (Yeshurun & Levy, 2003a). Experiment 1 of the present study replicated this finding, but with a 'multi-bar' neutral cue ensuring that the local information is identical in both cueing conditions, hence, ruling out local temporal interference as a possible account of the results. A possible attentional mechanism that can account for this attentional decrement in temporal resolution is a mechanism that selectively facilitates parvocellular neurons at the attended location, which in turn leads to inhibition of magnocellular neurons at the same location. Experiments 2a, 2b, and Experiment 3 tested this hypothesis directly by isolating, at least partially, the functions of the magno and parvo systems. Specifically, the displays of these experiments were designed to mainly activate the parvo system, so that the contribution of the magno system to performance will be relatively small. This way, any parvo-magno inhibitory processes that might be elicited by transient attention should only have a minor effect on performance and the attentional decrement in temporal resolution should be greatly reduced. To test this hypothesis Experiments 2a and 2b exploited the fact that the magno system is relatively colorblind and therefore does not contribute considerably to the processing of isoluminant stimuli, and Experiment 3 utilized the finding that diffused red light inhibits the activity of magnocellular neurons. The expected reduction in the attentional impairment of temporal resolution was found in all three experiments.

Several different mechanisms have been suggested, previously, to account for attentional effects found with attentional precues. One explanation, for example, suggests that the attentional precue encourages observers to adopt a more liberal decisional criterion or to assign more weight to information extracted from the cued location (e.g., Kinchla, 1980; Kinchla, Chen, & Evert, 1995; Shaw, 1984). Another explanation attributes attentional effects to an efficient reduction of decisional noise. The precue allows observers to monitor only the relevant location(s) instead of all possible locations, thus, reducing the statistical noise introduced at these non-relevant locations (e.g., Cohn & Lasley,

1974; Graham, Kramer, & Haber, 1985; Morgan, Ward, & Castet, 1998; Palmer, 1994; Shiu & Pashler, 1994; Sperling & Doshier, 1986). A related interpretation of precueing effects is based on a paradigm, in which the target and distractor are embedded in varying amounts of external noise. It was suggested that attentional effects with peripheral precues and low-noise displays may reflect stimulus enhancement, whereas attentional effects with central cues and high-noise displays reflect external noise exclusion (Doshier & Lu, 2000; Lu & Doshier, 2000). Yet another alternative is that attention modulates perceptual discriminability by decreasing the variance in the perceived quality of the relevant information (Prinzmetal, Amiri, Allen, & Edwards, 1998; Prinzmetal et al., 1997). These and other models of visual attention (e.g., Duncan & Humphreys, 1992; Graham, 1989; Wolfe, 1994) could not account for the finding the attention degrades temporal resolution, because they predict that attention always helps and never hinders performance.

The hypothesis that transient attention favors parvocellular over magnocellular neurons, however, is consistent with the hindered temporal resolution at the attended location, and it seems to withstand the tests performed here on temporal resolution. Interestingly, it can also account for a range of attentional effects found previously. First, as detailed above, this hypothesis can account for our previous finding that transient attention enhances spatial resolution (e.g., Yeshurun & Carrasco, 1998, 1999, 2000), as parvocellular neurons indeed have higher spatial resolution and their facilitation should result in attentional enhancement of spatial resolution. Second, it can account for the finding that attention prolongs perceived duration (e.g., Enns, Brehaut, & Shore, 1999; Mattes & Ulrich, 1998; Tse, Intriligator, Cavanagh, & Rivest, 1997). Tse et al. (1997) flashed a series of standard disks of constant duration. One of the disks differed from the other in its motion, color, or size, and observers were asked to judge whether the odd disk lasted for a longer or shorter duration than the other standard disks. They found that odd items were judged to last longer than standard items of the same duration. Based on the assumption that attention is attracted to the odd item, they concluded that attention prolongs the perceived duration. Similarly, Mattes and Ulrich (1998) and Enns et al. (1999) used central cues to direct sustained attention to the target location, and found that attended targets were judged as present for a longer duration than unattended targets. Finally, we recently used peripheral cues to direct transient attention to the target location and found similar attentional prolongation of the perceived duration (Yeshurun, Levy, & Marom, 2002). Because parvocellular neurons are typically active for a longer duration than magnocellular neurons and are characterized by a slower decay (e.g., Merigan & Maunsell, 1993; Schiller & Logothetis, 1990),

an attentional facilitation of parvocellular neuron should indeed result in a prolonged perceived duration.

The prolonged activation of parvocellular neurons and their slower decay also means longer temporal integration, and because the duration of visible persistence reflects the duration of temporal integration, an attentional mechanism that favors parvocellular over magnocellular neurons should prolong the duration of visible persistence. This, in fact, was recently found either with the attentional blink paradigm (Visser & Enns, 2001) or with peripheral precueing (Yeshurun et al., 2002). In both cases, a task that requires temporal integration was used, and the length of visible persistence was measured. Both studies found significantly longer visible persistence with attention.

An attentional facilitation of parvocellular neurons, which in turn inhibits magnocellular neurons could also account for the finding that attention reduces metacontrast masking (e.g., Enns & Di Lollo, 1997; Ramachandran & Cobb, 1995). Metacontrast masking is a type of backward masking occurring between spatially separated stimuli. It was suggested that at least some of the metacontrast masking effects are 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). In this case, the attentional facilitation of parvocellular neurons should reduce the impact of such magnocellular inhibition, and therefore reduce metacontrast effects. Enns and Di Lollo (1997) measured the magnitude of metacontrast masking as a function of set-size (1 vs. 3 targets). They found that the magnitude of metacontrast masking was greatly reduced in the single item condition in which observers could attend the target location. Likewise, Ramachandran and Cobb (1995) presented a row of disks flanked by a column of squares. One of the disks served as the target and the squares served as the metacontrast mask. They found less metacontrast masking when observers attended the row of disks than when they attended the column of squares.

In addition, because the magno system is, presumably, the main system responsible for the processing of motion, attentional processes that inhibit magno activation due to parvo facilitation, should impair motion perception. We are currently carrying out a series of experiments that test this prediction with apparent motion displays. Data collected thus far is consistent with this prediction—the quality of the perceived apparent motion is lowered with transient attention (Yeshurun & Levy, 2003b).

Clearly, these different attentional effects could be elicited by different attentional mechanisms. For instance, the spatial resolution enhancement could be due to a mere reduction in receptive field size, whereas lengthening of temporal integration may bring about the prolonged duration of visible persistence. In the same

line, the findings of the current study could reflect an attentional mechanism that directly inhibits magnocellular neurons, without facilitation of the parvocellular counterpart. While these different operations may take place independently, a single attentional mechanism that favors parvocellular over magnocellular neurons is the more parsimonious possibility as it can account for all these effects. The need for a mechanism that favors one system on the expense of its counterpart is evident when one considers the tradeoff between segregation and integration of information. Both processes are essential for a successful interpretation of the visual scene. Still, their opposing nature 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. Yet, when there is a need for spatial integration or fine temporal segregation, attention degrades performance.

Selective suppression of the magno system and possible facilitation of the parvo system has also been found during saccades (e.g., Burr & Morrone, 1996; Burr, Morrone, & Ross, 1994; see Ross, Burr, & Morrone, 1996 for a review). For example, when a grating of low spatial frequency was presented during a saccade its detection required a higher contrast than when presented while the eye fixated. In contrast, the detection of a grating of high spatial frequency was not suppressed by the saccade and was even slightly enhanced (Burr, Holt, Johnstone, & Ross, 1982). Moreover, this selective suppression of low frequency information during saccades, found with luminance gratings, disappeared when isoluminant gratings were used (Burr & Morrone, 1996). Further, several studies have suggested a tight coupling of attentional processing and saccades. For instance, it was suggested that an attentional shift to the relevant location typically precedes a saccade to the same location (e.g., Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986), and that attentional processes and eye movements share overlapping brain areas (e.g., Andersen, Bracewell, Barash, Gnadt, & Forgassi, 1990; Brotchie, Andersen, Snyder, & Goodman, 1995; Corbetta, 1998; Kustov & Robinson, 1996). In light of these findings, the resemblance between the effects of transient attention and saccades suppression might indicate that the underlying mechanisms are similar. More research is required to evaluate this hypothesis, but if it is confirmed, it could greatly advance our understanding of both spatial attention and saccade management, as it will allow the integration of the extensive literatures of these two research subjects.

Finally, it is reasonable to assume that an attentional mechanism that facilitates parvocellular neurons is not the only mechanism operating when attention is drawn

to a specific location. Attention consists of multiple independent but interactive systems, and it is very likely that different mechanisms operate when different components of attention are triggered by different experimental paradigms (e.g., peripheral precueing, central precueing, dual task, attentional blink, line-motion illusion). Even within the paradigm of peripheral precueing 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: the precue was not a relevant factor in decision making processes because it always indicated the target location without conveying information about the correct response; only a single target was present at any given moment ensuring that no known sources of added external noise (e.g., distracters, local mask, multiple masks) are present; and the display consisted of a suprathreshold target minimizing the spatial uncertainty associated with stimuli at or near threshold. As was already shown in the past (e.g., Carrasco, Penpeci-Talgar, & Eckstein, 2000; Carrasco, Williams, & Yeshurun, 2002; Yeshurun & Carrasco, 1999), with these conditions the attentional effects must reflect modulations in the representation of the attended information. Specifically, the findings of the present study suggest an attentional mechanism that favors parvocellular over magnocellular neurons. Different attentional mechanisms may be revealed with different experimental conditions. For instance, the addition of non-relevant information to the display, either at the cued location or at other non-relevant locations, might reveal that spatial attention reduces interference from distracters or masking effects (e.g., Morgan et al., 1998; Smith, 2000), and a task that requires temporal-order judgment may reveal an attentional advantage in access to awareness (e.g., Shore, Spence, & Klein, 2001).

In conclusion, this study demonstrated that the attentional decrement in temporal resolution is reduced with isoluminant stimuli or red background. Because isoluminant stimuli and red background ensure that any parvo–magnocellular inhibitory processes will only have a minor effect on performance, these findings enhance our understanding of the attentional mechanisms by providing direct support to the hypothesis that transient attention facilitates parvocellular neurons leading to inhibition of magnocellular neurons at the attended location.

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