Differential effects of transient attention on inferred parvocellular and magnocellular processing

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ABSTRACT

The pulsed-pedestal paradigm consists of the simultaneous brief presentation of a test stimulus and luminance pedestals. Processing with this paradigm is thought to be mediated by the parvocellular pathway. The steady-pedestal paradigm consists of the brief presentation of a test stimulus against a continuously presented luminance pedestals. Processing with this paradigm is thought to be mediated by the magnocellular pathway. To test the prediction that transient attention should have a differential effect on performance with these two paradigms, we added to their typical procedures peripheral precues that trigger transient attention. As expected, we have found that the attraction of transient attention to the target location improved performance with the pulsed-pedestal paradigm, but had no reliable effect on performance with the steady-pedestal paradigm. These findings support the hypothesis that transient attention favors parvocellular over magnocellular processing.

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1. Introduction

It is without doubt that both the spatial and temporal aspects of the visual stimulus affect our experience. Understanding how our system processes both aspects is crucial for a comprehensive view of the visual perceptual system. The importance of the selection processes termed attention is also rarely doubted. Indeed, a large body of evidence has demonstrated that paying attention to a specific location of the visual display (i.e., the deployment of spatial attention) improves performance on a wide variety of tasks designed to explore spatial perception (e.g., Posner, 1980; Smith, 2000; for a review see Carrasco, 2011). Much less is known about spatial attention and temporal processes, though recently there is a growing interest in attentional effects on the complementary temporal aspect of perception (e.g., Enns, Brehaut, & Shore, 1999; Shore, Spence, & Klein, 2001; Yeshurun & Marom, 2008). In this study we evaluate a mechanism of transient attention – the more automatic, stimulus-driven component of spatial attention – that can account for attentional effects on both the spatial and temporal aspects of perception. Particularly, we test a possible physiological instantiation of this mechanism. These various effects and the proposed mechanism are described in the following paragraphs.

Several recent studies demonstrate that transient attention can alter temporal processing as it alters spatial processing. Some studies have found an impaired temporal resolution at the attended location suggesting that transient attention degrades temporal segregation. For instance, the automatic orienting of attention impaired detection of brief temporal gaps (Rolke et al., 2008; Yeshurun, 2004; Yeshurun & Levy, 2003), and temporal order judgment (Hein, Rolke, & Ulrich, 2006; Nicol et al., 2009). Moreover, Yeshurun and Hein (2011) recently found that indicating the motion direction of an apparently moving rectangle was less accurate when an attentional cue preceded the presentation of the motion target. In contrast, an attentional improvement was found when the task required long temporal integration. Visser and Enns (2001) combined the missing-dot task with the attentional blink procedure and found that attention afforded information integration over a longer duration.[1] Similarly, Megna, Rocchi, and Baldassi (2012) have demonstrated, using the Classification Images technique, that the deployment of transient attention results in a larger temporal integration window. Furthermore, the perceived duration of brief visual events is prolonged when transient attention is attracted to their location via predictive or non-predictive peripheral cues (Yeshurun & Marom, 2008).

An attentional improvement or impairment has also been found in the spatial domain of perception, depending on whether spatial segregation or integration was required. Unlike the attentional impairment of temporal resolution, transient attention sharpens spatial resolution (e.g., Yeshurun & Carrasco, 1998; for a review see Carrasco & Yeshurun, 2009). For example, performance in both

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[1] Although the attentional blink paradigm does not directly manipulate transient attention, an unpublished experiment conducted in our lab replicated the attentional prolongation of temporal integration with a manipulation of transient attention.

acuity and hyperacuity tasks improved when the target appeared at the attended location (e.g., Carrasco, Williams, & Yeshurun, 2002; Yeshurun & Carrasco, 1999), and deteriorated when the target appeared at the unattended location (Montagna, Pestilli, & Carrasco, 2009). Critically, transient attention enhanced texture segmentation when the texture target appeared at the periphery where the ability to perform fine spatial segregation is limited. Yet when the target appeared at the fovea, where the ability to integrate information across spatial regions is limited, attention impaired performance (e.g., Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2000, 2008). Similarly, precueing transient attention to the target location reduced the critical distance over which flankers crowded the target, suggesting that with transient attention information is integrated over a smaller spatial region (Yeshurun & Rashal, 2010).

These various findings can be explained by an attentional mechanism that takes into account tradeoffs between segregation and integration processes, and between the spatial and temporal aspects of perception. Tradeoffs between the spatial and temporal domains of perception led to the distinction between transient and sustained channels (not to be confused with transient and sustained attention, which refer to the deployment characteristics of the automatic and controlled components of spatial attention). Sustained channels are slower with longer response latency, they seem to prefer slowly moving or stationary stimuli, and they primarily respond to high spatial frequencies. Transient channels are fast, they are particularly sensitive to transient stimulation such as rapid motion or flicker, and they are particularly sensitive to low spatial frequencies (e.g., Breitmeyer & Ganz, 1976; Kulikowski & Tolhurst, 1973; Legge, 1978). In light of this distinction, an attentional mechanism that favors sustained channels over transient channels can account for all the various attentional effects detailed above. Specifically, by facilitating the sustained channels transient attention should prolong the perceived duration (Yeshurun & Marom, 2008), prolong temporal integration (e.g., Megna, Rocchi, & Baldassi, 2012), and improve sensitivity to high spatial frequencies resulting in enhanced spatial resolution (e.g., Carrasco, Loula, & Ho, 2006; Yeshurun & Carrasco, 1999). Yet the inhibition of transient channels, possibly due to inter-channel inhibition (e.g., Breitmeyer, Rudd, & Dunn, 1981), should lead to a decrease in sensitivity to high temporal frequencies and therefore result in impaired temporal resolution (e.g., Yeshurun & Levy, 2003) and degraded motion perception (Yeshurun & Hein, 2011).

The distinction between sustained and transient channels has been linked to the physiological distinction between parvocellular and magnocellular neurons (e.g., Breitmeyer, 1984; Derrington, Krauskopf, & Lennie, 1984; McAnany & Alexander, 2006). Starting as early as the retina, visual cells are divided into two types – parvocellular and magnocellular. These two types of cells project to parallel neural systems in the LGN and the primary visual cortex (V1), and remain somewhat distinct even in their projection to higher visual cortical areas. Parvocellular neurons typically have smaller receptive fields, higher spatial resolution, and they mediate the processing of high spatial frequencies. However, their response duration is longer, their activation decay is slower, and their temporal resolution is low. Magnocellular neurons mediate the processing of low spatial frequencies and high temporal frequencies, they mediate motion perception but are relatively colorblind, and a red diffused light inhibits their activity (e.g., Lee et al., 1990; Lennie, 1993; Livingstone & Hubel, 1984, 1987; Merigan & Maunsell, 1993; Schiller & Logothetis, 1990). Thus, transient channels were linked to magnocellular activity while sustained channels were linked to parvocellular activity.

Given the similarity between these two distinctions, and evidence indicating attentional effects as early as V1 (e.g., Gandhi, Heeger, & Boynton, 1999; Herrmann et al., 2010), one possible

physiological instantiation of the suggested attentional mechanism is a mechanism that favors parvocellular over magnocellular processing (e.g., Yeshurun, 2004; Yeshurun & Levy, 2003). Such an attentional mechanism should have a differential effect on the two neural systems: it should facilitate parvocellular activity but not magnocellular activity. To test this hypothesis this study adopted the steady-pedestal and pulsed-pedestal psychophysical paradigms that were developed to bias processing toward the magnocellular or parvocellular pathway, respectively (e.g., Leonova, Pokorny, & Smith, 2003; McAnany & Alexander, 2006; Pokorny & Smith, 1997). The pulsed-pedestal paradigm consists of the simultaneous brief presentation of a test stimulus and a luminance background field – a pedestal. This paradigm is thought to favor the parvocellular pathway because the abrupt onset of the luminance pedestal causes a large transient response that saturates the magnocellular pathway. The steady-pedestal paradigm consists of the brief presentation of a test stimulus against a continuously presented luminance pedestal (i.e., only the luminance of the test stimulus is changing during the trial). When there is no sudden change in the luminance of the pedestal the briefly presented test stimulus is processed by the magnocellular pathway. Data obtained with these paradigms differ systematically in a manner consistent with previously described spatial and temporal properties of the magnocellular and parvocellular pathways (e.g., Leonova, Pokorny, & Smith, 2003; Smith, Pokorny, & Sun, 2000). For instance, the spatial contrast sensitivity functions (CSFs), obtained using these paradigms, differ substantially in shape (Leonova, Pokorny, & Smith, 2003). The CSF obtained with the steady-pedestal paradigm is typically low-pass, resembling results of previous studies that targeted transient channels or magnocellular activity. The CSF obtained with the pulsed-pedestal paradigm is typically more band-pass, resembling results obtained for sustained channels or parvocellular activity. Moreover, the results of several studies that employed these paradigms to investigate various aspects of normal and impaired vision, are consistent with the assertion that the parvocellular and magnocellular pathways mediate performance with the pulsed- and steady-pedestal paradigms, respectively (see Pokorny, 2011 for a review).

In this study we combined these two paradigms with peripheral precues that attract transient attention. As noted in previous studies (e.g., Pokorny, 2011), an important advantage of these two paradigms is that their test stimulus is identical; only the pre- and post-adaptation displays differ. Thus, combining these paradigms with peripheral precueing allowed, for the first time, a separate examination of the effects of transient attention on performance that is mediated primarily by the parvocellular system or primarily by the magnocellular system, while employing similar experimental conditions. Moreover, with the aid of the two pedestal paradigms we could test the hypothesis that transient attention favors parvocellular over magnocellular processing. This hypothesis predicts that the allocation of transient attention to a specific location should have a differential effect on parvocellular and magnocellular activity. Specifically, this hypothesis predicts that: (a) transient attention should improve performance that is mediated[2] by the parvocellular pathway (i.e., performance measured with the pulsed-pedestal paradigm). (b) Transient attention should have no effect on performance that is mediated by the magnocellular pathway (i.e., performance measured with the steady-pedestal paradigm) if the attentional effects on the transient channels is brought about by inter-channel inhibition as we suggested above. Alternatively, if transient attention directly exerts inhibition on the transient channels it should impair performance that is mediated by magnocellular activity.

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[2] Following previous papers (e.g., Pokorny, 2011) we use the term 'mediation' when the involvement of a neural pathway is inferred based on psychophysical data.

2. Experiment 1

This experiment evaluated the hypothesis that transient attention has a differential effect on performance when it is mediated by the parvocellular or magnocellular pathway. To that end, we combined peripheral onset cues, considered to capture transient attention in a stimulus-driven, "automatic" manner (e.g., Cheal & Lyon, 1991; Giordano, McElree, & Carrasco, 2009; Jonides, 1981; Müller & Rabbitt, 1989), with the pulsed- and steady-pedestal paradigms. Four square pedestals were presented simultaneously on a uniform background during each trial. The target was a 2 cpd Gabor patch. We chose this spatial frequency because Leonova, Pokorny, and Smith (2003) have shown that with 2 cpd the results are consistent with the assertion that the parvocellular and magnocellular pathways mediate performance with the pulsed- and steady-pedestal paradigms, respectively. The target was presented at the center of one of the four pedestals in one of two temporal intervals. The task was to indicate which interval included the target (2IFC – two interval forced choice). In the critical interval (i.e., the interval that included the target) of the pulsed-pedestal paradigm the pedestals and the target were presented simultaneously for a brief duration (Fig. 1a). As mentioned above, it is believed that the rapid onset and offset of the relatively large pedestals generate a strong transient signal that drives the magnocellular system towards saturation. This ensures that the processing in this paradigm is biased towards parvocellular processing. In the other interval of this paradigm, only the four pedestals were presented. In the steady-pedestal paradigm, the four pedestals were present throughout the trial, and in the critical interval the target was presented for a brief duration at the center of one of the pedestals (Fig. 1b). In this case, it is believed that the more sensitive magnocellular pathway mediates the processing of the target.

With both paradigms a cue preceded each of the temporal intervals. In the cued condition, a peripheral cue – a small disk – appeared next to the target location in the critical interval, and in

one of the other three possible locations on the other interval. In the neutral condition, four small disks appeared in both intervals, each disk appeared next to one of the possible target locations. A similar multi-element neutral cue was employed successfully in previous studies, which demonstrated comparable attentional effects with multi-element and single-element neutral cues (e.g., Carrasco, Williams, & Yeshurun, 2002; Talgar, Pelli, & Carrasco, 2004; Yeshurun, 2004). Importantly, because with this multi-element neutral cue a disk appeared next to the target in both cueing conditions, it ensured that the local information around the target was identical in the cued and neutral conditions. The only difference was that with the peripheral cue observers could focus attention in advance on the target's location, as only one location was marked by this cue. Thus, if performance differences between the cueing conditions are found, they are not mediated by any local interactions between the disk and the target. Moreover, because a cue was present in both intervals the cueing manipulation did not provide information regarding the correct response, ensuring attention-related response biases are avoided.

In light of the attention-related studies described above on the spatial domain (e.g., Carrasco & Yeshurun, 2009; Yeshurun & Carrasco, 1998, 1999, 2000) and the temporal domain (e.g., Rolke et al., 2008; Yeshurun & Hein, 2011; Yeshurun & Marom, 2008), and the distinction between the transient and sustained channels of visual perception (e.g., Breitmeyer & Ganz, 1976; Kulikowski & Tolhurst, 1973; Legge, 1978), we expected the attraction of transient attention to the target location to improve performance with the pulsed-pedestal paradigm, but not with the steady-pedestal paradigm.

2.1. Method

2.1.1. Participants

Eighteen naive observers, from the University of Haifa, with normal or corrected to normal vision participated in Experiment 1.
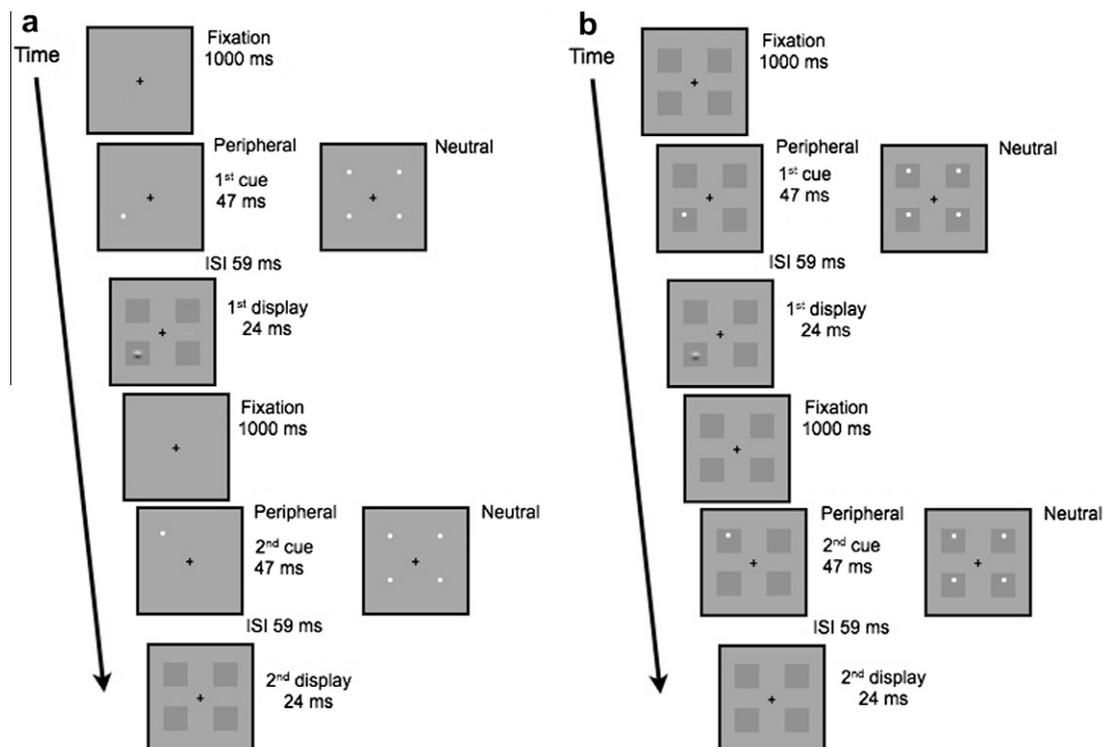

Fig. 1. A schematic example of the sequence of events in a single experimental trial: (a) pulsed-pedestal paradigm; (b) steady-pedestal paradigm.

2.1.2. Stimuli and apparatus

The stimuli were presented using MATLAB and the Psychophysics Toolbox extensions (Brainard, 1997) on a 17″ monitor of an IBM compatible PC (resolution: 1024 × 768, 85 Hz). The monitor luminance was calibrated with a Tektronix J18 LumaColori II Photometer. The fixation mark was a 0.3° × 0.3° black cross presented in the center of a uniform gray background (25 cd/m²). Four 5° × 5° square pedestals (12.5 cd/m²) were presented simultaneously on the diagonal meridians with their center at 5° of eccentricity. The target was a 2 cpd Gabor patch (subtending 2°) appearing with equal probability at the center of one of the four pedestals. Following previous studies (e.g., Keri & Benedek, 2007; Leonova, Pokorny, & Smith, 2003; McAnany & Alexander, 2006), the contrast C of the Gabor patch was defined as:

$$C = (L_{max} - L_p)/L_p \qquad (1)$$

where L_{max} is the maximum luminance of the Gabor patch, and L_p is the luminance of the pedestal on which it is presented. Because the goal of this study is to demonstrate a differential effect of attention on performance with the two pedestal paradigms, there was no need to employ several contrast levels and measure thresholds. Results that demonstrate a differential attentional effect on accuracy suffice to achieve this goal. Hence, we only employed a single contrast level, but adjusted this contrast level for each participant during the practice phase to ensure performance is above chance but below ceiling. In order to keep the experimental conditions of the two paradigms as similar as possible we employed the same contrast level in both paradigms (mean contrast: 0.107, range: 0.09–0.20).

The peripheral cue was presented on half of the trials – the cued trials, and it was composed of a small white disk (50 cd/m²) with a diameter of 0.3°. The peripheral cue appeared 0.5° above the target in the critical interval (2.5° above the center of the pedestal on which the target appeared), and in a corresponding location of one of the other three pedestals in the other interval. The neutral cue was presented on the other half of the trials – the neutral trials, and it was composed of four disks, each identical to the disk of the peripheral cue.

2.1.3. Procedure

In the pulsed-pedestal paradigm each trial included two temporal intervals. Each interval began with 1000 ms of a central fixation cross followed by 47 ms of the cue. After another 59 ms, the four pedestals were displayed for 24 ms (Fig. 1a). These durations ensured that the effects of the peripheral cue are optimal (e.g., Nakayama & Mackeben, 1989), but also precluded eye movements between the onset of the cue and the offset of the target (e.g., Mayfrank, Kimmig, & Fischer, 1987). On half of the trials the target was presented together with the pedestals of the first interval, and on the other half of the trials the target was presented together with the pedestals of the second interval. The task was to indicate which interval included the target. The response was not speeded and it was followed by an auditory feedback. The procedure of the steady-pedestal paradigm was identical to that of the pulsed-pedestal paradigm apart for the fact that the pedestals were presented throughout the trial (Fig. 1b).

The participants performed two experimental sessions, one for each paradigm. Each session contained 384 trials (i.e., a total of 768 experimental trials), and was preceded by 30 s of adaptation to the surround with the pulsed-pedestal paradigm or to the pedestals and surround with the steady-pedestal paradigm (e.g., McAnany & Alexander, 2006). Prior to the beginning of each session the participants performed 48 practice trials. The order of the sessions was randomized.

2.2. Results and discussion

A within-observers two-way ANOVA (cue type × paradigm) was performed on the accuracy of target detection. This analysis revealed a significant main effect of paradigm ($F(1,17) = 56.73$, $p < 0.0001$). The participants were more accurate with the steady-pedestal than the pulsed-pedestal paradigm. This finding is not surprising given sensitivity differences between the parvocellular and magnocellular pathways. Several previous studies demonstrated that the magnocellular pathway is more sensitive than the parvocellular pathway, particularly with stimuli of low spatial frequency (e.g., Alexander et al., 2001; Kaplan & Shapley, 1986; Smith, Sun, & Pokorny, 2001). Because we have employed, for a given observer, the same contrast level in both paradigms, the more sensitive magnocellular system should lead to a more accurate performance. Thus, the fact that performance was more accurate with the steady-pedestal paradigm further supports the claim that performance in this paradigm is mediated by magnocellular processing. The main effect of cue type was also significant ($F(1,17) = 5.09$, $p < 0.05$): performance was more accurate in the cued than neutral trials. Most importantly, the cue type × paradigm interaction was significant ($F(1,17) = 5.2$, $p < 0.05$). As can be seen in Fig. 2, the effect of cue type – higher accuracy in the cued than the neutral trials – was only present with the pulsed-pedestal paradigm. No effect of the attentional manipulation was found with the steady-pedestal paradigm. Least-significant-differences (LSD) post hoc analyses further confirmed that the difference in accuracy between the cued and neutral trials was highly significant ($p < 0.001$) with the pulsed-pedestal paradigm but not with the steady-pedestal paradigm ($p = 0.462$). Thus, assuming we can infer magnocellular and parvocellular activity based on performance in the steady- and pulsed-pedestal paradigms, respectively, we can conclude that transient attention facilitated parvocellular activity but not magnocellular activity.

One may wonder, however, whether the lack of attentional effect with the steady-pedestal paradigm is merely due to the relatively high accuracy level obtained in this condition, rather than a differential attentional effect on the two pathways. In this experiment we have used the same contrast level for both paradigms in order to keep the experimental conditions as similar as possible. This resulted in significantly higher accuracy in the steady- than pulsed-pedestal paradigm, and as mentioned above this outcome is expected given the assumption that the more sensitive magnocellular pathway mediates performance in the steady-pedestal
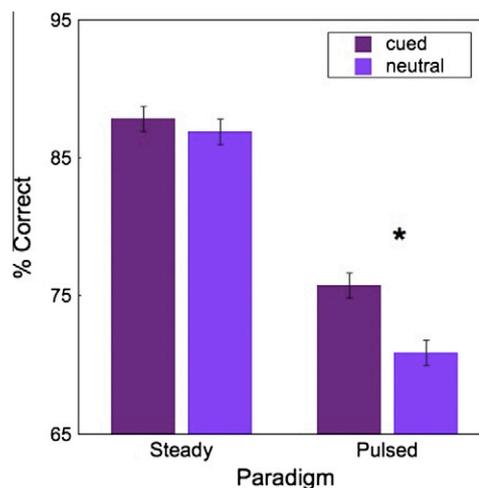

Fig. 2. Observers' accuracy in Experiment 1 as a function of paradigm and cueing condition. Error bars correspond to 1 SE; the symbol '*' indicates a significant difference between the two cueing conditions.

paradigm. Is this difference in overall accuracy between the two paradigms the cause of the differential attentional effect? We note that given an overall accuracy level of 87% in the steady-pedestal paradigm, there was still room for improvement. Furthermore, precueing effects with peripheral cues were previously found even with higher accuracy levels than those attained with the steady-pedestal paradigm (Carrasco, Penpeci-Talgar, & Eckstein, 2000). Nevertheless, to rule out this possibility we performed Experiment 2.

Finally, there is one methodological difference between the two pedestal paradigms that requires further discussion. Unlike the steady-pedestal paradigm, in which the pedestals were present throughout the trial, in the pulsed-pedestal paradigm the pedestals appeared shortly after the cue. Given this close proximity in time, the onset of the pedestals may have masked the cue, resulting in reduced cueing effect. Importantly, this methodological difference cannot account for the differential attentional effect found in this experiment because such backward masking was only possible in the pulsed-paradigm. Hence, if backward masking between the pedestals and the cue indeed occurred it only served to reduce the attentional effect in the pulsed-pedestal paradigm, and could not account for the fact that an attentional effect was not found in the steady-pedestal paradigm.

To sum, as expected a differential attentional effect emerged for the different paradigms. Specifically, a significant cueing effect was found with the pulsed-pedestal paradigm but not with the steady-pedestal paradigm, in accordance with the hypothesis that transient attention facilitates parvocellular or sustained channels but not magnocellular or transient channels.

3. Experiment 2

This experiment evaluated whether the differential attentional effect found with the two paradigms of Experiment 1 was due to the difference in their overall performance. More specifically, this experiment was designed to rule out the possibility that an attentional effect was found with the pulsed-pedestal paradigm but not with the steady-pedestal paradigm because accuracy in the latter was much higher than in the former. To that end, this experiment was identical to Experiment 1 apart for the fact that the contrast level was adjusted separately for each paradigm to keep performance level at about 80–85% in both paradigms. If the differential attentional effect found in the previous experiment was not merely due to differences in overall performance it should be replicated here. Hence, although we expected similar overall accuracy in both paradigms, we also expected to find an attentional improvement with the pulsed-pedestal paradigm but not with the steady-pedestal paradigm.

3.1. Method

3.1.1. Participants

Twenty-one naive observers, from the University of Haifa, with normal or corrected to normal vision participated in this experiment; none of them participated in Experiment 1.

3.1.2. Stimuli, apparatus, and procedure

All aspects of the stimuli and procedure were similar to Experiment 1 expect that the contrast level was adjusted separately for each paradigm and each participant in an attempt to keep performance level in both paradigms around 80–85%.

3.2. Results and discussion

As in Experiment 1, a within-observers two-way ANOVA (cue type × paradigm) was performed on the accuracy data of Experiment 2. Unlike Experiment 1, in this experiment there was no significant main effect of paradigm ($F < 1$), indicating that we were successful in keeping similar performance level in the two paradigms. This lack of overall accuracy difference between the paradigms was established by employing a lower contrast with the steady- than pulsed-pedestal paradigm (steady-pedestal: mean contrast 0.075, range 0.04–0.12; pulsed-pedestal: mean contrast 0.096, range 0.07–0.16). The fact that performance in the steady-pedestal paradigm was similar to that in the pulsed-pedestal paradigm even though the contrast level in this paradigm was significantly lower ($t(20) = 3.8$, $p < 0.001$) provides further support to the assertion that performance with the steady-pedestal paradigm is mediated by the more sensitive magnocellular neural system while performance in the pulsed-pedestal paradigm is mediated by the parvocellular neural system.

The main effect of cue type also did not reach statistical significance ($p = 0.14$), but the cue type × paradigm interaction was significant ($F(1,20) = 4.58$, $p < 0.05$). Similar to Experiment 1, an attentional effect emerged with the pulsed-pedestal paradigm but not with the steady-pedestal paradigm (Fig. 3). LSD post hoc analyses further confirmed that the observers were significantly more accurate in the cued than neutral trials with the pulsed-pedestal paradigm ($p < 0.01$), but there was no such significant difference with the steady-pedestal paradigm ($p = 0.61$). Thus, the finding of selective attentional effect on inferred parvocellular activity was replicated even when overall performance was similar in the two paradigms.

To further support the claim that the difference in overall performance is not the cause for the differential effect of attention we combined the data of Experiments 1 and 2. We conducted a 3-way ANOVA on this combined data with the variable of experiment as a between participants factor and the variables of cue type and paradigm as within participants factors. If the differential effect of attention is merely due to the difference in overall performance a 3-way interaction (experiment × cue type × paradigm) should emerge because differences in overall performance were only found in Experiment 1. However, the results of this analysis do not follow this prediction. Although a highly significant 2-way interaction between cue type and paradigm emerged ($F(1,37) = 9.98$, $p < 0.005$), confirming that an attentional facilitation is only found with the pulsed-pedestal paradigm, the 3-way interaction was not significant ($F < 1$). Thus, the presence of differences in overall performance did not affect the nature of the attentional effect in the two paradigms. A
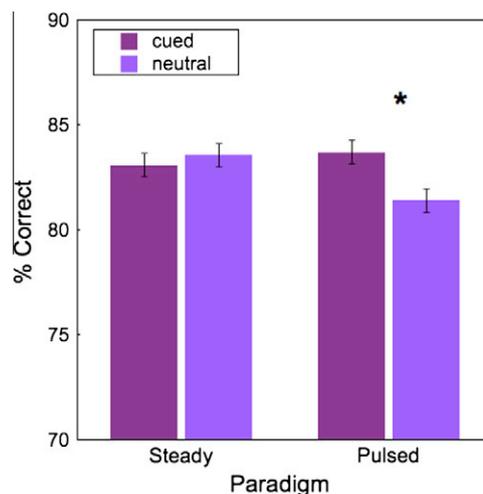

Fig. 3. Observers' accuracy in Experiment 2 as a function of paradigm and cueing condition. Error bars correspond to 1 SE; the symbol '*' indicates a significant difference between the two cueing conditions.

differential effect of attention was found regardless of whether or not overall performance in the two paradigms varied.

To sum, the results of these various analyses rule out the possibility that the differential attentional effect found for the two paradigms in Experiment 1 is a mere outcome of differences in overall performance. Instead, they strengthen the conclusion that transient attention has a beneficial effect on parvocellular activity but not on magnocellular activity.

4. General discussion

This study was motivated by several recent findings suggesting that the allocation of transient attention to the task-relevant location results in performance that has similar characteristics to performance that is mediated by the sustained channels of visual perception. For instance, it has been suggested that the sustained channels are responsible for the processing of high spatial frequency information and therefore demonstrate high spatial resolution, they have longer integration time and longer response latency than transient channels, but their temporal resolution is low and they seem to prefer slowly moving or stationary stimuli. In contrast, transient channels have lower spatial resolution than sustained channels but they can integrate information over a larger spatial area, they have high temporal resolution and they respond well to rapid motion (e.g., Breitmeyer & Ganz, 1976; Kulikowski & Tolhurst, 1973). Like sustained channels, when transient attention is allocated to a location, performance has a higher spatial resolution, information is integrated over a longer time, and stimuli appear to have a longer duration. Moreover, attracting transient attention results in lower temporal resolution and degraded motion discrimination (e.g., Hein, Rolke, & Ulrich, 2006; Megna et al., 2012; Rolke et al., 2008; Yeshurun, 2004; Yeshurun & Hein, 2011; Yeshurun & Marom, 2008). This resemblance suggests that transient attention favors sustained over transient channels. In other words, an attentional mechanism that facilitates the activity of the sustained channels but not that of the transient channels can account for all the attentional effects mentioned above. Furthermore, given the common view that the parvocellular and magnocellular neuronal systems are the neural correlates of the sustained and transient channels, respectively (e.g., Breitmeyer, 1984; Livingstone & Hubel, 1987, 1988; McAnany & Alexander, 2006), the resemblance above suggests that such an attentional mechanism should have a facilitatory effect on parvocellular activity but not on magnocellular activity.

In this study we tested and supported this hypothesis by demonstrating that transient attention has a differential effect on performance in the pulsed-pedestal and steady-pedestal paradigms, assumed to bias processing towards the parvocellular and magnocellular pathways, respectively. In particular, we have shown that focusing attention on the target location improved accuracy with the former but not with the latter. This differential effect of attention was found both when the target was identical in the two paradigms (Experiment 1) and when performance in the two paradigms was equalized (Experiment 2). Moreover, this pattern of results was consistent for the majority of our participants. As evident in Fig. 4, most of the participants show a positive attentional effect with the pulsed-pedestal paradigm (i.e., their data point falls above the equal-performance diagonal), but with the steady-pedestal paradigm there is no consistent effect of attention.

The hypothesis that transient attention favors parvocellular over magnocellular activity is also supported by the findings that the attentional decrement in temporal resolution (i.e., the diminished ability to detect temporal gaps) is greatly reduced when isoluminant stimuli or a red background are used (Yeshurun, 2004). Performance with isoluminant stimuli or a red background is primarily mediated by the parvocellular system, and therefore should not be greatly affected by any parvo-magno inhibitory effects elicited by attention, as was indeed found. Additionally, the hypothesis that the allocation of transient attention to the target location results in a more sustained response, possibly via facilitation of parvocellular activity, is also supported by the recent finding that transient attention decreases the reports of reversed apparent motion (Yeshurun & Hein, 2011). Previous studies have found fewer reports of reversed apparent motion with gratings of high spatial frequency, whose processing is mediated by the parvocellular system (e.g., Takeuchi & DeValois, 1997). This finding was attributed to the fact that the typical temporal response of parvocellular neurons has a more sustained nature than the temporal response of magnocellular neurons (e.g., DeValois & Cottaris, 1998). Hence, if the allocation of transient attention results in a more parvo-like sustained activity, reversed apparent motion should indeed be less likely when a peripheral cue attracts attention to the target location (Yeshurun & Hein, 2011). Thus, the findings of the study reported here are in agreement with these previous studies, but the current study provides the most direct evidence in support of the differential attentional effect on the parvocellular and magnocellular systems because in this study we directly manipulated the involvement of these systems in task performance.

The findings of the current study are also consistent with a recent study (Sewell & Smith, 2011) that examined the effects of attentional peripheral precues (i.e., valid vs. invalid) on detection with and without abrupt onset. A trial of the no-onset condition
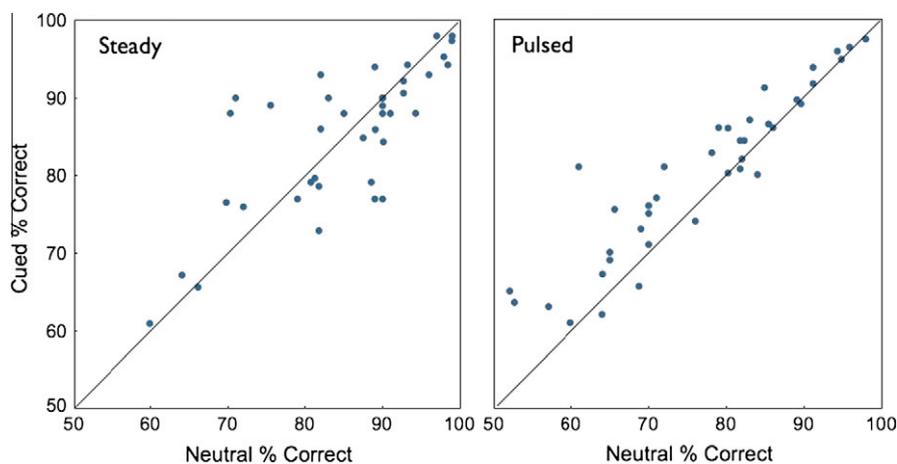

Fig. 4. Performance in the cued vs. neutral trials of each paradigm for each participant of Experiments 1 and 2.

started with four plaids. Three plaids then disappeared and one component of the forth plaid was removed to reveal the target. Thus, there was no unique onset associated with the target, and the offsets of the other plaids created a relatively strong transient noise. Given this strong transient signal, this condition resembles the pulsed-pedestal paradigm. A trial of the onset condition started with four luminance pedestals, and then the target was added on top of one of them. In this condition, a unique onset is associated with the target, and there is no strong transient noise. Hence, this condition resembles the steady-pedestal paradigm. Consistent with our findings, a large cueing effect was found in the no-onset condition, and a much smaller effect was found in the onset condition. Sewell and Smith (2011) did not interpret their results in the context of parvocellular and magnocellular activity. Instead, they suggested that the unique onset of the target in the onset condition allowed the observers to efficiently re-orient attention to the target location even when it was initially misdirected by the invalid cue. This resulted in small differences between the valid and invalid conditions. Such an efficient re-orienting was not possible in the no-onset condition because there was no unique onset.

Could this interpretation also account for our findings? In our study an onset was always associated with the target, but in the pulsed-pedestal paradigm it was not unique. Is it possible, then, that no precueing effect was found with the steady-pedestal paradigm because it allowed an efficient re-orienting of attention to the target even in the neutral condition? A critical assumption required for this interpretation is that there is enough time, between target onset and offset, for the actual action of re-orienting of attention and for the efficient processing involved with the re-allocation of attentional resources. That is, re-orienting of attention can have a considerable effect on performance only if there is enough time for: (a) an initial detection of the unique onset, (b) re-orienting of attention to the location of this onset, and (c) the utilization of the re-allocated resources for efficient processing of the target. Given prior estimation of the time required for the orienting of transient attention (e.g., Bergen & Julesz, 1983; Cheal & Lyon, 1992; Nakayama & Mackeben, 1989; Saarinen & Julesz, 1991) and the fact that the target in our study was only present for 24 ms, this assumption does not seem to hold. Hence, although the interpretation suggested by Sewell and Smith (2011) is certainly viable for their study, it is not a likely account of our findings.

An interesting aspect of our data is the fact that there was no significant attentional effect with the steady-pedestal paradigm rather than a negative effect. A negative effect seems as a reasonable outcome given the findings that coupling transient attention with tasks that require high temporal resolution or motion discrimination results in a negative effect of attention (e.g., Hein, Rolke, & Ulrich, 2006; Nicol et al., 2009; Rolke et al., 2008; Yeshurun & Hein, 2011; Yeshurun & Levy, 2003). Because the magnocellular pathway likely mediates these tasks, these findings suggest that attention may have an inhibitory effect on magnocellular activity. They therefore imply that a negative effect may be found with the steady-pedestal paradigm. However, as we suggested before (e.g., Yeshurun, 2004; Yeshurun & Levy, 2003), the inhibitory effect on magnocellular activity may not be due to direct inhibition elicited by the attentional mechanism. Instead, it may be an indirect result of inhibitory interactions between parvocellular and magnocellular channels. Evidence of such inter-channel inhibitory interactions was demonstrated by several studies (e.g., Breitmeyer, Rudd, & Dunn, 1981; Rogowitz, 1983). For instance, Breitmeyer and his colleagues (1981) have employed the target-recovery phenomenon observed with metacontrast masking to demonstrate sustained-on-transient inhibitory interactions. Specifically, they presented the target together with an additional large mask, prior to the presentation of the metacontrast mask. The addition of the large mask increased sustained activity that due to sustained-on-transient inhibition reduced metacontrast masking. Given this sustained-on-transient inhibition, it is possible that transient attention affects directly only the parvocellular pathway, but the attentional enhancement of parvocellular activity ends up inhibiting magnocellular activity via such inter-channel inhibition. When performance is primarily mediated by the magnocellular system, as is the case with the steady-pedestal paradigm, such inter-channel inhibition may only have a negligible effect. Thus, the lack of consistent attentional effect in the steady-pedestal paradigm observed here is in agreement with the possibility of indirect inhibition. Further research is required, however, before this issue can be settled.

An important qualification to keep in mind is that in this study neural activity is inferred based on psychophysical data. Although the psychophysical data obtained with the pedestal paradigms are consistent with activation of a given neural pathway, psychophysical performance is the end-result of processing occurring at various levels. It therefore also reflects the mediation of higher order processes. Additionally, it is reasonable to assume that attention consists of multiple independent but interactive systems. It is very likely, therefore, that several attentional processes take place at the same time, resulting in different outcomes depending on the task at hand and the specific experimental manipulation employed. The findings of our current study support an attentional mechanism that favors parvocellular over magnocellular processing, because such a mechanism is the only attentional mechanism suggested thus far that can predict these results. However, these findings do not preclude the existence of other attentional mechanisms that may emerge under different experimental conditions.

Finally, an attentional mechanism that on some occasions has a detrimental effect on performance may appear counterintuitive. However, given the tradeoffs between spatial and temporal processes, the tradeoffs between integration and segregation processes, and the structure of our visual system, the suggested attentional mechanism is in fact ecologically valid. This is so because the attentional mechanism suggested here is only referring to transient attention – the fast, involuntary component of spatial attention. Mechanisms of involuntary selection are required for unexpected information that appears outside the focus of our conscious interest. Because we typically fixate information at the focus of our interest, such unexpected information typically appears at the periphery of the visual scene. Our perceptual system has to rapidly process this unexpected information to a degree that will allow it to 'decide' whether or not to voluntary allocate further resources to the processing of this information (e.g., whether or not to deploy the controlled attentional mechanisms to its location, and whether or not to make a saccade to this location). In comparison to foveal processing, the processing at the periphery suffers from lower spatial resolution and shorter temporal integration, though its temporal resolution, motion processing, and its ability to integrate information across space are intact (e.g., Rovamo & Virsu, 1979; Swanson, Pan, & Lee, 2008; Wilson, 1980). Hence, transient attention is needed to help the periphery with its weaknesses throughout the initial rapid processing of unexpected information, until a decision is made regarding the allocation of voluntary mechanisms. It is therefore helpful to improve spatial segregation and temporal integration. The impairment of spatial integration and temporal segregation are basically 'side effects' of the improvements of their counterparts due to the above mentioned perceptual tradeoffs, but because peripheral processing is rather proficient in those aspects, their impairment is not considerably damaging. Moreover, if a voluntary allocation of resources follows the rapid initial processing of the unexpected peripheral information, it is likely that this deployment of controlled resources, which are typically more flexible in their operation (e.g., Giordano, McElree, & Carrasco, 2009; Yeshurun, Montagna, &

Carrasco, 2008), will compensate for the brief impairment inflicted by transient attention.

In summary, this study is the first to examine separately the effects of transient attention on inferred parvocellular and magnocellular activity via the employment of peripheral precueing and the pedestal paradigms. This combined manipulation revealed that transient attention improved performance with the pulsed-pedestal paradigm, assumed to be mediated by the parvocellular system, but had no reliable effect on performance with the steady-pedestal paradigm, assumed to be mediated by the magnocellular system. These findings provide further support to the hypothesis that transient attention favors parvocellular over magnocellular processing.

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