
Transient attention degrades perceived apparent motion

Yaffa Yeshurun

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

Elisabeth Hein

Laboratoire Psychologie de la Perception, Université Paris Descartes, Sorbonne Paris Cité, Paris, France; and CNRS UMR 8158, Paris, France

Received 19 May 2011, in revised form 4th August 2011

Abstract. Transient spatial attention refers to the automatic selection of a location that is driven by the stimulus rather than a voluntary decision. Apparent motion is an illusory motion created by stationary stimuli that are presented successively at different locations. In this study we explored the effects of transient attention on apparent motion. The motion target presentation was preceded by either valid attentional cues that attract attention to the target location in advance (experiments 1–4), neutral cues that do not indicate a location (experiments 1, 3, and 4), or invalid cues that direct attention to a non-target location (experiment 2). Valid attentional cues usually improve performance in various tasks. Here, however, an attentional impairment was found. Observers' ability to discriminate the direction of motion diminished at the cued location. Analogous results were obtained regardless of cue type: singleton cue (experiment 1), central non-informative cue (experiment 2), or abrupt onset cue (experiment 3). Experiment 4 further demonstrated that reversed apparent motion is less likely with attention. This seemingly counterintuitive attentional degradation of perceived apparent motion is consistent with several recent findings, and together they suggest that transient attention facilitates spatial segregation and temporal integration but impairs spatial integration and temporal segregation.

1 Introduction

Spatial covert attention allows us to selectively attend to the location of relevant information without eye movements to that location. A large body of evidence suggests that spatial attention has two components: a slower component, allocated to a location according to our goals—'sustained attention'; and a faster component, attracted to a location by sudden changes in the display—'transient attention' (eg Jonides 1981). Participants in studies of sustained attention are typically informed regarding the desired attention allocation strategy by verbal instructions or central-informative cues. The manipulation of transient attention typically involves peripheral cues that are presented briefly next to the target prior to its onset, attracting transient attention automatically to the target vicinity. Different effects on behaviour are often found for these two attentional components, suggesting separate attentional mechanisms (eg Briand 1998; Hein et al 2006; Klein 1994; Yeshurun and Carrasco 2008). As will be detailed in the following sections, in this study we explored the effects of transient attention on apparent motion.

When a stimulus is presented briefly at one location and shortly afterwards at another location, a clear perception of motion from the first to the second location may emerge (Wertheimer 1912). This illusory motion is termed apparent motion. Previous studies that examined the effects of attention on (apparent) motion perception employed various experimental paradigms and different manipulations of attention, yielding different results. For instance, several studies (eg Dick et al 1987; Horowitz and Treisman 1994; Ivry and Cohen 1990) employed a visual-search task and inferred the involvement of attentional processes based on the presence of a set-size effect (an increase in response time with increased number of items). They found that the number of items in the

display did not affect search performance with 'short-range' apparent-motion targets (with spatial displacements of less than 1 deg) and concluded that the detection of short-range apparent motion is preattentive. The search for long-range targets was affected by the number of items and therefore led to the conclusion that 'long-range' apparent motion requires attention. Other studies manipulate the voluntary allocation of attention using verbal instructions or volitional cues (eg Chaudhuri 1990; Dobkins and Bosworth 2001; Hock et al 2002; Lankheet and Verstraten 1995; Shiori and Matsumiya 2009; Shulman 1993; Treue and Maunsell 1996; Tsuchiya and Braun 2007). The outcomes of these studies depended on the nature of their attentional instructions and the specific aspect of motion perception studied. Hock et al (2002) instructed their observers to either distribute attention over a broad area or focus it over a narrow region. They found that the narrow focus of attention reduced the formation of global motion patterns but had no reliable effect on local motion perception. These findings led to the conclusion that focusing attention over a narrow region does not affect the activation level of local motion detectors but instead decreases the interaction between detectors. Dobkins and Bosworth (2001) reached a somewhat similar conclusion. They measured coherent motion thresholds under two attentional conditions: with endogenous pre-cues that encouraged the observers to volitionally attend in advance the quadrant with the motion stimulus or without such cues. They found a large reduction in motion thresholds with pre-cues when the motion target appeared simultaneously with other motion distractors and a much smaller, though significant, reduction when the motion target was presented alone. The latter attentional effect was found only for short durations. Based on these findings the authors concluded that the observed reduction in motion thresholds does not reflect perceptual enhancement. Instead, they suggest that, when distractors are present, attention reduces noise, and when there are no distractors attention increases effective processing time by eliminating the time required to orient to the stimulus. Chaudhuri's study (1990), however, led to a different conclusion. He found that the duration of the motion aftereffect was shorter when the observers were instructed to attend to a central letter rather than to the surrounding moving dots, and he therefore concluded that the neural response to motion is weaker without attention. This conclusion is supported by neurophysiological findings demonstrating that activity in motion areas such as MT is reduced when the stimulus is not attended (eg Treue and Maunsell 1996). Finally, some studies even found that verbal attentional instructions can determine the direction of perceived motion (eg Lu and Sperling 1995; Verstraten et al 2000).

Thus, previous studies clearly demonstrate that attention can modulate motion perception, particularly when more complex motion processing is involved (eg global integration of the output of local motion detectors) and when several stimuli are present, but there appear to be large variations in the nature of these modulations, and there is no consensus regarding the mechanisms underlying these attentional effects. These previous studies, however, did not examine transient attention directly (some did not manipulate spatial attention, and others manipulated only the slower volitional component of spatial attention). An exception is a study by Liu et al (2006), which manipulated transient attention, but their main goal was to examine whether transient attention can affect the subjective appearance of motion coherence. The observers, therefore, saw two pairs of moving dot patterns and had to first judge which pattern was more coherent and only then report its motion direction. They found a moving dot pattern appeared more coherent when transient attention was attracted to its location by a peripheral cue and that its motion direction was identified more accurately.

Here we focus on the effects of transient attention on our ability to discriminate the direction of apparent motion, when this motion involves local luminance changes over short distances (less than 1 deg), only a single stimulus is present, and there is

no need for motion integration (pooling of local motion signals across space). Can transient attention affect motion discrimination under these conditions and, if so, what is the nature of this effect? One possible prediction regarding the effect of transient attention on apparent motion stems from several recent studies that investigated the effects of transient spatial attention on various temporal processes. Some of these studies suggest that transient attention degrades the temporal resolution at the attended location (eg Hein et al 2006; Nicol et al 2009; Rolke et al 2008; Yeshurun and Levy 2003). For instance, observers' ability to indicate whether a target was flickering or continuous was diminished when a peripheral cue allowed them to attend in advance to the target location (Rolke et al 2008; Yeshurun 2004; Yeshurun and Levy 2003). Similarly, when participants were asked to discriminate the temporal order of two dots, their discrimination performance was impaired by an automatic orienting of attention to the dots location (Hein et al 2006; Nicol et al 2009). Furthermore, Yeshurun and Marom (2008) have shown that the perceived duration of brief visual events is prolonged when transient attention is attracted to their location; Visser and Enns (2001) have found that the duration of visible persistence is shortened under limited attentional resources; and Rolke et al (2006) demonstrated that attracting transient attention to the target location slowed down observers' response to the offset of the target. These various findings are consistent with the hypothesis that transient attention prolongs the internal response to the attended stimulus (eg Yeshurun and Marom 2008). Thus, according to this hypothesis, the internal activation elicited by the attended stimulus is longer and has a slower decay in comparison to the activation elicited by a non-attended stimulus. Critically, such an attentional prolongation of the response reduces temporal sensitivity, as events occurring at different points in time may be integrated into a single event. This predicts that transient attention should diminish perceived apparent motion.

This study was designed to test this prediction. However, testing the effects of transient attention with motion tasks could not merely involve the abrupt onset peripheral cues, typically used to orient transient attention. An abrupt onset, occurring shortly before target onset in an adjacent location, may modify motion perception through some local interactions between the cue and the target. To rule out this possibility, in experiment 1 we employed a singleton cue and in experiment 2 we employed a central non-informative cue. Experiment 3 used an onset cue to test whether the findings of these experiments are unique to these less-common cues. Finally, experiment 4 employed a reversed apparent-motion paradigm to further test the hypothesis that transient attention prolongs the activity at the attended location.

2 Experiment 1

The motion target in this experiment was a rectangle composed of small dots. Following the rectangle's initial presentation, it was shifted slightly upward or downward, appearing to move up or down, respectively. The observers had to indicate the direction of motion. The singleton cue included one red bar appearing above the rectangle's location and five green bars appearing above the other possible locations (figure 1a). The single red bar is considered a colour-singleton capable of attracting attention to its location (eg Theeuwes 1991). The neutral cue included six green bars appearing above all possible locations. Because the only difference between the singleton and neutral cues is the colour of the bar above the rectangle, they should both lead to the same local interactions, if at all (Yeshurun and Marom 2008).

In light of the recent studies described above (eg Hein et al 2006; Rolke et al 2006, 2008; Visser and Enns 2001; Yeshurun 2004; Yeshurun and Levy 2003; Yeshurun and Marom 2008) we expected attention to diminish the perceived apparent motion. That is, we expected observers' ability to indicate the direction of motion to be worse when the singleton cue attracted attention to the target location.

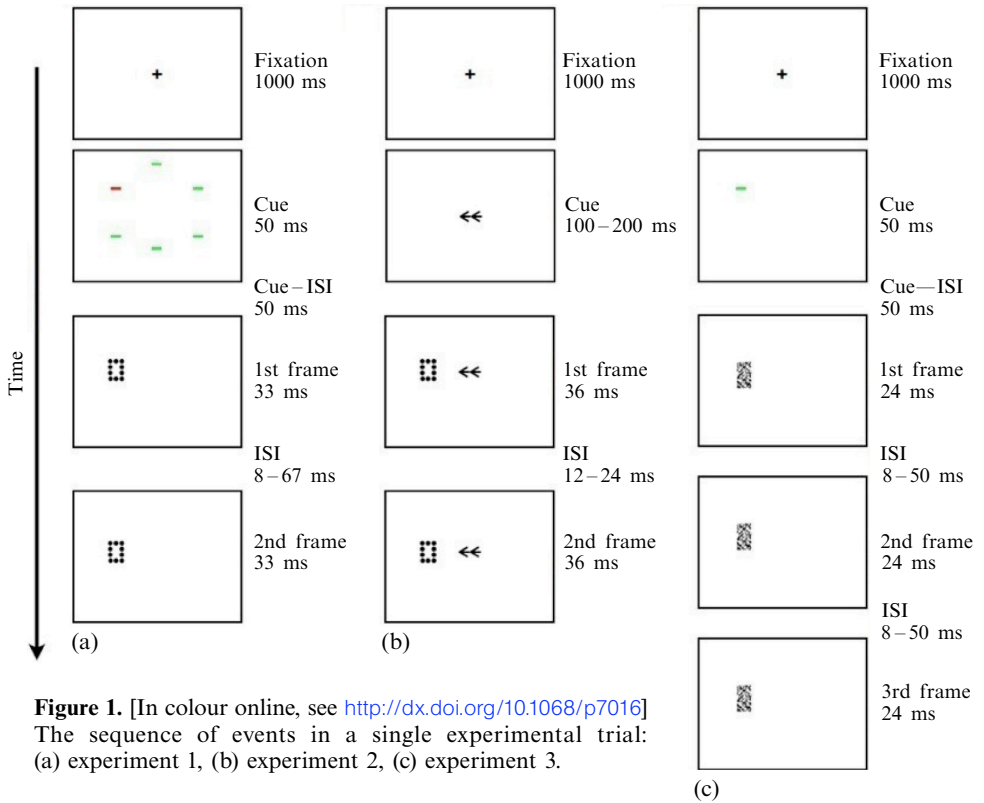


Figure 1. [In colour online, see <http://dx.doi.org/10.1068/p7016>] The sequence of events in a single experimental trial: (a) experiment 1, (b) experiment 2, (c) experiment 3.

2.1 Method

2.1.1 Participants. Five naive observers, from the University of Haifa, with normal or corrected-to-normal vision participated in experiment 1.

2.1.2 Stimuli and apparatus. The stimuli were presented on a 21-inch monitor of a Power-Mac G4 computer (resolution: 1280×1024 pixels, 85 Hz). The target was a $3 \text{ deg} \times 2 \text{ deg}$ rectangle composed of 5×3 small black dots displayed on a grey background, appearing in one of six possible locations each at 4° of eccentricity (figure 1a). The neutral cue included six $0.2 \text{ deg} \times 1 \text{ deg}$ green bars each appearing 1.75° above the centre of one of the possible locations. The singleton cue was identical to the neutral cue apart for the bar above the rectangle location, which was equal-luminance red (CIE coordinates: red, $0.59x$, $0.35y$; green, $0.27x$, $0.59y$).

2.1.3 Procedure. Each trial began with 1000 ms of a central fixation cross, followed by 50 ms of the cue. After another 50 ms, the rectangle was displayed for 33 ms. Following a varying interstimulus interval (ISI; 8–67 ms), it appeared 0.25° above or below its initial location for another 33 ms. These durations precluded eye movements before the rectangle's final offset (eg Mayfrank et al 1987). An auditory feedback followed the response. Response was not speeded. On half of the trials the cue was a valid singleton cue, and on the rest of the trials the cue was neutral.

Observers were asked to indicate the direction of motion of the whole rectangle (upward versus downward). Each observer participated in 50 practice trials and 1152 randomised experimental trials, separated into two 1 h sessions performed on separate days.

2.2 Results and discussion

As evident in figure 2a, observers were more accurate in the neutral than the validly cued trials. Indeed, a within-observers two-way ANOVA (cue type \times ISI) indicated that

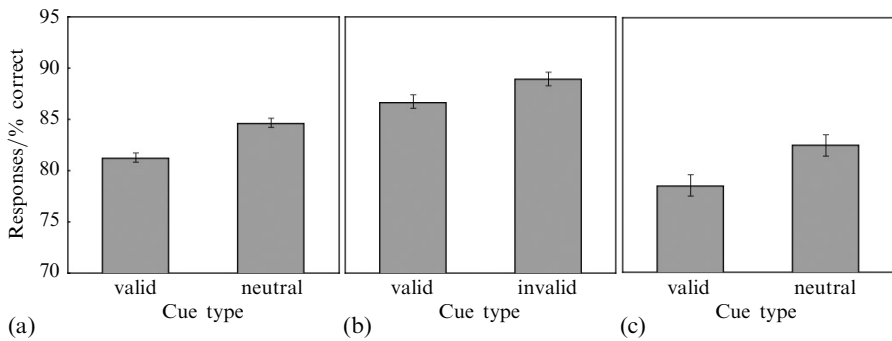


Figure 2. Observers' performance as a function of cueing condition in: (a) experiment 1, (b) experiment 2, (c) experiment 3. Error bars correspond to ± 1 SE.

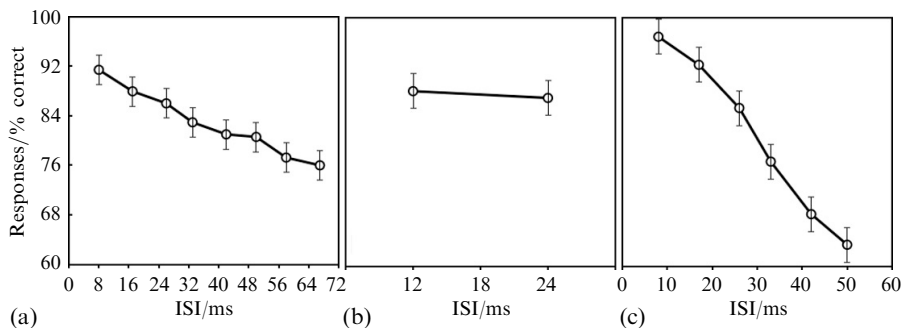


Figure 3. Observers' performance as a function of ISI in: (a) experiment 1, (b) experiment 2, (c) experiment 3. Error bars correspond to ± 1 SE.

the main effect of cueing was significant ($F_{1,4} = 50.14$, $p < 0.002$). The main effect of ISI was also significant ($F_{7,28} = 4.83$, $p < 0.05$)—accuracy decreased as the ISI increased (figure 3a), but the interaction was not significant ($p = 0.31$). A similar analysis was performed on correct reaction time (RT), but none of the effects reached statistical significance ($p > 0.1$). This suggests that there were no speed–accuracy tradeoffs.

One may wonder whether the attentional impairment of motion discrimination found in this experiment is due to the fact that the presentation of the singleton bar above the motion target prior to its presentation created a line-motion illusion (eg Hikosaka et al 1993), biasing the observers to respond 'downward'. However, von Grünau et al (1996) have shown that 200–300 ms are required for a singleton item to generate a line-motion illusion that goes beyond that generated by the other non-singleton items. Given that in this experiment only 100 ms have passed between cue onset and target onset, this alternative explanation is not highly likely. Nevertheless, to ensure that such a line-motion illusion cannot account for our results, we ran an additional analysis testing whether the observers indeed tended to respond 'downward' more often with the singleton cue than with the neutral cue. We found that the frequency of downward responses did not vary significantly between the two cueing conditions ($p > 0.1$). This result indicates that the singleton cue did not bias the observers' response, and therefore the attentional decrement found here cannot be attributed to a line-motion illusion induced by the singleton cue.

In sum, the significant cueing effect suggests that transient attention can affect perceived apparent motion. As predicted, attending the location of the motion target impaired motion-direction discrimination. Importantly, the nature of the singleton cue discounts the possibility that this attentional effect is due to some local interference between the cue and target.

3 Experiment 2

The goal of this experiment was twofold. First, it tested whether the attentional degradation of perceived apparent motion found in experiment 1 can be replicated with a different attentional cue that does not appear in the vicinity of the motion target, and therefore does not elicit any local cue–target interactions. Second, given that the attentional cue in experiment 1 was informative (it indicated the target location with 100% validity), the attentional effect found in experiment 1 may reflect some mixture of volitional and non-volitional attentional effects. This possibility is not highly likely, because the timing between cue onset and target onset in experiment 1 was too short for voluntary allocation of attention (eg Nakayama and Mackeben 1989). Nevertheless, to rule out the involvement of volitional attention, the cue in this experiment was not informative.

Particularly, this experiment employed a central arrow pointing to the left or right. Because the target appeared at either side with equal probability, independently of the side indicated by the arrow, this cue was non-informative. In contrast to traditional research that did not find any effect of non-predictive central arrow cues (Jonides 1981), more recent studies have shown that this kind of non-informative central cue can orient attention (Hommel et al 2001; Ristic et al 2002; Ristic and Kingstone 2006; Tipples 2002, 2008). Moreover, these non-informative central cues seem to orient attention in a reflexive way similar to traditional peripheral abrupt onset cues rather than a volitional way, as they were shown to orient attention quickly and even when participants were explicitly told about the non-informative nature of the cues (eg Ristic et al 2002; Tipples 2002). In addition, Hein and colleagues (2006) have shown that such central non-informative arrow cues, like abrupt onset cues (eg Yeshurun and Levy 2003), decreased the temporal resolution at the attended location. Specifically, observers' ability to judge the temporal order of a pair of dots was poorer when the dots appeared at the location indicated by the arrow. Interestingly, when the same central arrow was informative, it improved temporal-order judgments, suggesting that informative and non-informative central arrow cues trigger different mechanisms of attention and that non-informative central cues have similar effects as abrupt onset cues. Note that, although for central cues the key factor determining whether sustained or transient attention is triggered seems to be the informativeness of the cue, this is not the case with peripheral cues. With the latter, similar results were found whether the cue was informative or not (eg Rolke et al 2008; Yeshurun and Marom 2008; Yeshurun and Rashal 2010).

This experiment employed exactly the same apparent motion task as in experiment 1. The attentional cue, however, was a central non-informative double arrow that does not appear in the vicinity of the motion target, and therefore any attentional effects found here could not be due to any local interference between the cue and the target. Moreover, because the cue does not predict the target location, it does not encourage the observers to volitionally allocate attention to the target location. If the negative attentional effect on perceived motion found in the previous experiment does not depend on the specific cue employed there or on the involvement of volitional attentional processes, it should be replicated here. Specifically, given the results of experiment 1, we expected motion discrimination to be less accurate when the central arrow pointed at the target location rather than at the opposite location.

3.1 Method

3.1.1 *Participants.* Six naive observers with normal or corrected-to-normal vision, from Penn State University, participated in this experiment; none of them participated in the previous experiment.

3.1.2 *Stimuli and apparatus.* The stimuli were presented on a 17-inch monitor of an IBM compatible PC (resolution: 1024 × 768 pixels, 85 Hz). Eye movements of the left

eye were recorded with a video-based eye tracker (ViewPoint EyeTracker®, Arrington Research, Inc) with a sampling rate of 30 Hz. The target and background were the same as in experiment 1. The rectangle could appear 4° either to the left or to the right of fixation. The cue was a black central double arrowhead (figure 1b), pointing to the right or to the left. Each arrowhead subtended 0.8 deg × 0.6 deg, and the distance between the arrowheads' centres was 0.8 deg (leaving a gap of 0.2 deg between them).

3.1.3 Procedure. Each trial started with a fixation cross. After 1000 ms the fixation cross was replaced by the central cue, and after a variable cue–target stimulus-onset-asynchrony (SOA) of either 100 or 200 ms the rectangle was presented randomly to the left or right of the cue (the cue did not predict the target location). On valid trials the target appeared at the side indicated by the arrows, and on invalid trials the target appeared on the opposite side. The rectangle appeared for 36 ms and after 12 or 24 ms (ISI) it re-appeared 0.25° above or below its initial position for another 36 ms. As in experiment 1, the task was to indicate the rectangle's motion direction. Each observer participated in at least 32 practice trials and in 640 randomised experimental trials, separated into 2 sessions.

Trials on which eye movements occurred outside a 2 deg region around the fixation between 500 ms prior to cue onset and target offset were discarded and repeated later during the block. Participants got feedback at the end of a trial whenever they lost fixation or gave a wrong response.

3.2 Results and discussion

A three-way within-observers ANOVA (cue validity × SOA × ISI) revealed a significant cueing effect ($F_{1,5} = 9.41$, $p < 0.05$). Similar to experiment 1, observers were more accurate in the invalid than validly cued trials (figure 2b). The effect of ISI was not significant (figure 3b), nor were the interactions. RT analysis indicated that there were no speed–accuracy tradeoffs, as none of the effects reached statistical significance ($p > 0.1$).

These findings support the results of the preceding experiment and strengthen the conclusion that attention can affect perceived apparent motion, in particular by impairing the ability to discriminate the direction of motion. The use of a non-informative central cue rules out alternative explanations, especially that of local cue–target interference, as the distance between the cue and the target was identical in valid and invalid trials.

The similarity of the effects found in this experiment compared to experiment 1 that used a peripheral singleton cue further suggests that non-informative central arrows, in contrast to informative central arrows, trigger the transient attentional system. Moreover, it suggests that the attentional degradation of perceived apparent motion that was found in experiment 1 does not depend on the involvement of volitional attentional processes, because in this experiment the cue was not informative and the participants had no incentive to volitionally attend the cued location.

4 Experiment 3

The first two experiments of this study did not employ an abrupt onset cue that is commonly used to trigger transient attention. This was done to preclude local interactions between the cue and target as alternative explanation of the outcomes. One might wonder, however, whether the findings that direction discrimination is poorer at the cued location is unique to the special cues employed in these experiments. To test this possibility, in this experiment we measured direction discrimination with a typical onset cue. The attentional cue was a single horizontal bar indicating the rectangle's initial location (figure 1c). Given that the effects of transient attention on apparent motion were demonstrated in the previous experiments when local interactions were controlled for, such interactions were not a central concern in this experiment. Still, we employed two measures to minimise their effect on the outcomes.

First, the neutral cue was similar to that of experiment 1—six small bars. Because each bar appeared above one of the possible target locations, the local information around the rectangle was identical in both cueing conditions. The only difference was that with the peripheral cue observers could focus attention in advance on the rectangle's location, as only one location was marked by the cue. Thus, if cueing effects are found, they are not mediated by the bar's mere presence, because a bar appeared above the rectangle in both cueing conditions. Second, the motion target in this experiment included a random placement of dots within the rectangle. The rectangle's location was fixed. Only the dots were shifted within the frame of the rectangle. Hence, the rectangle itself did not appear to move. Only the dots were perceived as moving within the rectangular frame. This reduced the possibility of perceiving local motion between the cue and the target.

This motion stimulus also served to rule out another alternative explanation. The motion target of experiments 1 and 2 was composed of a relatively small number of dots and observers might have used positional cues rather than motion to infer motion direction (Nakayama 1985). This would imply that the impaired performance in the validly cued condition might reflect a diminished ability to apprehend and utilise fine positional relations rather than diminished motion perception. Such alternative explanation is questioned by the finding that transient attention improves the ability to judge fine positional relations when assessed directly with Vernier targets and similar attentional cues (Yeshurun and Carrasco 1999). Nonetheless, the motion stimulus employed in this experiment explored whether attention will degrade performance even with apparent motion stimuli that render positional cues inadequate.

4.1 Method

4.1.1 *Participants.* Six naive observers, from the University of Haifa, with normal or corrected-to-normal vision participated in this experiment; none participated in the other experiments.

4.1.2 *Stimuli and apparatus.* The stimuli were presented with the same apparatus as in experiment 1. The target included about 300 dots that were randomly placed within a 4.8 deg \times 2.5 deg rectangle region. Each dot was approximately 0.2 deg, and had one of 5 grey values chosen randomly from the full luminance range of the monitor. The neutral cue was identical to that of experiment 1, and the onset cue was a bar identical to a single bar of the neutral cue presented above the target location.

4.1.3 *Procedure.* The procedure was similar to that used in experiment 1, apart for the following. There were three 24 ms target presentations, separated by a varying ISI (8–50 ms). The first and last presentations were identical. In the middle presentation the dots were displaced 0.25 deg vertically or horizontally. Dots that would have been displaced outside the rectangle region were wrapped around. This elicited a vertical (up–down–up or down–up–down) or horizontal (left–right–left or right–left–right) apparent motion. On half of the trials the cue was a valid onset cue, and on the rest of the trials the cue was neutral.

Observers were asked to indicate whether the dots moved vertically or horizontally. Note that the observers were not required to discriminate between the two types of vertical motion or between the two types of horizontal motion, but only between the two more general motion directions: vertical versus horizontal. Each observer participated in 50 practice trials and 1728 randomised experimental trials, separated into three 1 h sessions performed on separate days.

4.2 Results and discussion

As evident in figure 2c, observers were again more accurate in the neutral than the validly cued trials. The within-observers two-way ANOVA (cue type \times ISI) indicated that the main effect of cueing was significant ($F_{1,5} = 12.52$, $p < 0.02$). The main effect

of ISI was also significant ($F_{5,25} = 42.39$, $p < 0.0001$); accuracy decreased as the ISI increased (figure 3c), but the interaction was not significant ($p = 0.24$). A similar RT analysis revealed a significant effect of ISI ($F_{5,25} = 4.10$, $p < 0.01$); RT increased as the ISI increased. None of the other effects reached statistical significance. Hence, as in the previous experiments, there were no speed–accuracy tradeoffs.

These findings show that the degradation of perceived apparent motion is found even when the motion target did not include helpful positional cues, suggesting that the attentional degradation of performance does not reflect poorer ability to judge fine positional relations. Moreover, a similar attentional degradation of motion perception was found even when transient attention was attracted to the target location by the typical abrupt onset cue. This suggests that the findings of experiments 1 and 2 are not unique to the cues employed in these experiments. The fact that similar attentional effects can be found with these various cue types is in line with previous findings. Specifically, both onset and singleton cues prolonged the perceived duration of the cued stimulus (Yeshurun and Marom 2008), and both onset-peripheral and central non-informative cues degraded temporal resolution at the cued location (Hein et al 2006; Yeshurun and Levy 2003).

5 Experiment 4

As we have mentioned in the introduction, one possible way in which attention can degrade motion perception is by modifying the temporal characteristics of the response at the cued location. If transient attention prolongs the internal response to attended information (eg Enns et al 1999; Mattes and Ulrich 1998; Yeshurun and Marom 2008), resulting in a response that has a more sustained nature (with longer activation and slower decay), it could lead to a degradation of motion perception, as was found in experiments 1–3, and also a degradation of temporal resolution, as was previously found (eg Hein et al 2006; Yeshurun and Levy 2003). To test this account for the attentional degradation of perceived motion, this experiment employed the reversed apparent motion phenomenon. When two gratings with a phase difference are presented successively to the same location, the perceived direction of motion depends on the ISI between presentations. For short ISIs the perceived direction follows the ‘short-path’, but for long ISIs motion perception follows the reversed ‘long-path’ (eg Pantle and Turano 1992; Strout et al 1994; Takeuchi and DeValois 1997). For example, for gratings with a 90° phase difference, the ‘short-path’ corresponds to a 90° displacement and the ‘long-path’ corresponds to a 270° displacement (figure 4a). This finding of reversed motion has been attributed to the transient, biphasic nature of the temporal response in the system mediating motion perception. In support of this view it has been shown that, when the spatial frequency of the gratings was high, either longer ISIs were required to elicit reversed motion or it never occurred (eg Takeuchi and DeValois 1997). This is because high spatial frequencies are mainly processed by the parvocellular system, which typically has a more sustained, monophasic temporal response (eg DeValois and Cottaris 1998). In light of these findings, if transient attention leads to a more sustained temporal response, then, when the target location is attended, longer ISIs would be needed to reverse the perceived motion direction or the perceived direction will not reverse.

5.1 Method

5.1.1 *Participants.* Eight naive observers, from the University of Haifa, with normal or corrected-to-normal vision participated in this experiment; none participated in the other experiments.

5.1.2 *Stimuli and apparatus.* The stimuli were presented with the same apparatus as in experiment 1. The reversed motion display included two $0.5 \text{ cycle deg}^{-1}$ gratings with a 90° phase difference. The dimensions of the gratings were $2 \text{ deg} \times 5 \text{ deg}$, and both

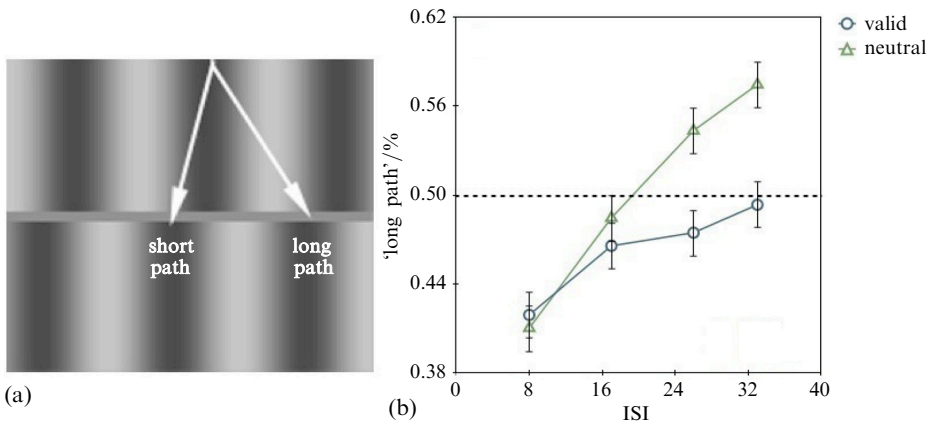


Figure 4. [In colour online.] Experiment 4: (a) The reversed motion display. (b) Percentage of 'long-path' response (reversed motion) as a function of cue type and ISI. The dashed line denotes the 50% 'long-path' report. Error bars correspond to ± 1 SE.

had 50% contrast. The gratings were presented successively to one out of six locations, each at 4° of eccentricity on a mean luminance background. The cues were identical to those used in experiment 3.

5.1.3 Procedure. The procedure was similar to that used in experiment 1 apart for the following. Each trial began with a central fixation cross, followed by a cue (50 ms). After another 50 ms, the first grating was displayed for 58 ms. Following a varying ISI (8–34 ms), the second grating was displayed for another 58 ms. On half of the trials the cue was a valid onset cue and on the rest of the trials the cue was neutral. Observers were asked to indicate their perceived direction of motion (leftward or rightward), and each viewed 30 practice trials and 864 randomised experimental trials in a single 1 h session.

5.2 Results and discussion

A two-way within-observers ANOVA (cue type \times ISI) was performed on the percentage of 'long-path' response. This analysis revealed a significant effect of ISI ($F_{3,21} = 12.32$, $p < 0.0001$); the percentage of 'long-path' response increased as the ISI increased, in accordance with previous demonstrations of increased reversed motion reports with longer ISI (eg Pantle and Turano 1992; Strout et al 1994; Takeuchi and DeValois 1997). A significant cueing effect was also found ($F_{1,7} = 8.33$, $p < 0.05$); as expected, 'long-path' responses were significantly less frequent in the valid than neutral condition. Most importantly, a significant cue type \times ISI interaction emerged ($F_{3,21} = 4.85$, $p < 0.05$; figure 4b): the increase in reversed motion report as a function of the ISI was shallower with the valid than with the neutral cue. In fact, with the valid cue, all of the tested ISIs produced less than 50% 'long-path' reports. Hence, similar to increasing the spatial frequency of the stimuli (eg Takeuchi and DeValois 1997), directing transient attention to the target location decreased the frequency of perceived reversed motion, suggesting that the allocation of transient attention results in a more sustained temporal response, in the same way as a manipulation of spatial frequency.

6 General discussion

This study demonstrates that transient attention can affect perceived apparent motion. Specifically, focusing attention on the target location diminished the ability to discriminate the direction of motion. This attentional degradation of perceived apparent motion seems quite robust. It was highly consistent across observers (figure 5) and was found for the two different types of stimuli employed here: a rectangle composed of a

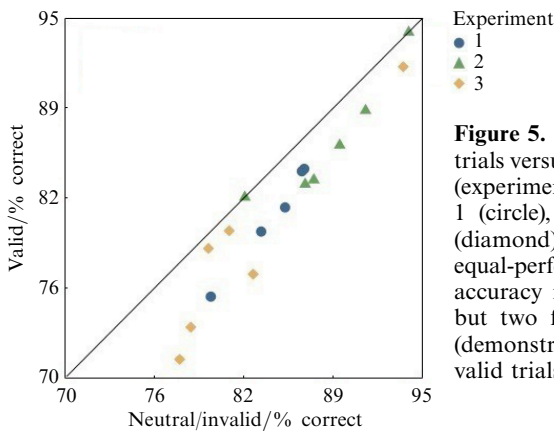


Figure 5. [In colour online.] Performance in the valid trials versus the neutral (experiments 1 and 3) or invalid (experiment 2) trials for each observer of experiment 1 (circle), experiment 2 (triangle), and experiment 3 (diamond). None of the observers fall above the equal-performance diagonal (none demonstrated higher accuracy in valid than neutral/invalid trials), and all but two fall below the equal-performance diagonal (demonstrating higher accuracy in neutral/invalid than valid trials).

relatively small number of dots that move up or down (experiments 1–2), as well as a large number of dots that moved vertically or horizontally within a stationary frame (experiment 3). Furthermore, the attentional degradation was found with different kinds of attentional cues: singleton cues (experiment 1), non-informative central arrows (experiment 2), and abrupt onset cues (experiment 3), all triggering transient attention. The fact that the pattern of results was similar for such highly different attentional cues and stimuli suggests that these findings are not due to some artifact related to the specific cue or stimulus employed, but rather to the allocation of transient attention to the target location.

The finding that attention degrades motion perception may seem counterintuitive, as most models of spatial attention would not predict an attentional impairment. For instance, noise reduction models suggest that attention reduces internal or external noise (eg Palmer 1994). This predicts attentional improvement with significant noise levels, or in effect when noise levels are negligible (as was the case in this study). It was also recently shown that transient attention enhances the contrast-sensitivity function and increases apparent contrast (Carrasco et al 2000, 2004). However, a mere increment in contrast cannot account for the attentional degradation of perceived motion. Given the brief stimuli durations, the range of ISIs, and the relatively high contrast used in this study, a mere contrast increase should either improve motion perception or have no effect on it (eg Johnston and Wright 1985; Shioiri et al 2002). Thus, although previously suggested models are certainly relevant for other attentional effects, they cannot account for the attentional impairment found here.

One possible way in which attention can impair our ability to discriminate motion direction is by modifying the temporal characteristics of the internal response elicited by the stimulus presented at the cued location. If the response at the cued location has a more sustained nature (eg longer activation with slower decay), this could lead to a degradation of motion perception. Such an attentional mechanism could also account for the findings that attention degrades temporal resolution (eg Hein et al 2006; Yeshurun 2004; Yeshurun and Levy 2003), prolongs temporal integration (Visser and Enns 2001), and prolongs perceived duration (eg Enns et al 1999; Rolke et al 2006; Yeshurun and Marom 2008). Hence, although an attentional disadvantage may seem counterintuitive, it is predictable and consistent with several previous findings. In addition, an attentional disadvantage seems less counterintuitive when one considers the tradeoff between segregation and integration of information. The opposing nature of these two processes suggests that a mechanism enhancing one should degrade the other. Indeed, transient attention helps performance when tasks such as spatial gap detection require fine spatial segregation (eg Yeshurun and Carrasco 1999; Yeshurun and Levy 2003), or when tasks

such as typical visible persistence tasks require integration across time (Visser and Enns 2001). Yet, when there is a need for spatial integration, as is the case with some texture-segmentation tasks (eg Yeshurun and Carrasco 1998, 2000, 2008), or fine temporal segregation, as with flicker-detection tasks (Rolke et al 2008; Yeshurun 2004; Yeshurun and Levy 2003) and the apparent motion tasks employed here, attention degrades performance.

A possible implementation of an attentional mechanism that facilitates spatial segregation and temporal integration but impairs spatial integration and temporal segregation is a mechanism that favours parvocellular over magnocellular activity (Yeshurun 2004; Yeshurun and Levy 2003). 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. Many studies (eg Maunsell et al 1990; Merigan and Maunsell 1993; Schiller and Logothetis 1990) have shown that magnocellular neurons have a higher temporal resolution than parvocellular neurons, and they mediate motion perception, but they are relatively colourblind and a red diffused light inhibits their activity. Parvocellular neurons have higher spatial resolution than magnocellular neurons, longer response duration, slower decay, and longer temporal integration (ie a more sustained response). In view of these findings and evidence of attentional effects as early as V1 (eg Gandhi et al 1999), an attentional mechanism that facilitates parvocellular activity but inhibits magnocellular activity can account for the present results (attentional degradation of the perceived apparent motion), and the attentional effects mentioned above (degradation of temporal resolution, prolongation of temporal integration, prolongation of perceived duration, and enhancement of spatial resolution). The hypothesis that transient attention favours parvocellular over magnocellular activity is further supported by the findings that the attentional decrement in temporal resolution is greatly reduced when isoluminant stimuli or a red background are used (Yeshurun 2004), because 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–magnocellular inhibitory effects elicited by attention. Finally, the hypothesis that the allocation of transient attention to the target location results in a more sustained temporal response, possibly via facilitation of parvocellular activity, is also supported by the outcomes of experiment 4. Previous studies have found fewer reports of reversed apparent motion with gratings of high spatial-frequency, whose processing is mediated by the parvocellular system (eg Takeuchi and 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 (eg DeValois and Cottaris 1998). Hence, if the allocation of transient attention results in a more parvo-like sustained activity, reversed apparent motion should be less likely when a valid cue attracts attention to the target location. This was indeed the pattern of results in experiment 4. Further research is required to test the viability of this hypothesis and contrast it with other possible implementations of the suggested attentional mechanism.

To conclude, this study demonstrates that transient attention can affect perceived apparent motion. In particular, our ability to discriminate the direction of motion is diminished with transient attention. These and other attentional effects support the hypothesis that transient attention leads to a more sustained temporal response, possibly by favouring parvocellular over magnocellular activity.

Acknowledgments. We would like to thank Cathleen Moore for supporting Elisabeth Hein while collecting some of the data reported here, and two anonymous reviewers for their valuable comments on an earlier draft of this paper. This study was supported by The Israel Science Foundation grants (no 925/01-1 and no 748/05) to Yaffa Yeshurun.

References

- Briand K A, 1998 "Feature integration and spatial attention: More evidence of a dissociation between endogenous and exogenous orienting" *Journal of Experimental Psychology: Human Perception and Performance* **24** 1243–1256
- Carrasco M, Ling S, Read S, 2004 "Attention alters appearance" *Nature Neuroscience* **7** 308–313
- Carrasco M, Penpeci-Talgar C, Eckstein M, 2000 "Spatial covert attention increases contrast sensitivity along the CSF: Support for signal enhancement" *Vision Research* **40** 1203–1215
- Chaudhuri A, 1990 "Modulation of the motion aftereffect by selective attention" *Nature* **344** 60–62
- DeValois R L, Cottaris N P, 1998 "Inputs to directionally selective simple cells in macaque striate cortex" *Proceedings of the National Academy of Sciences of the USA* **95** 14488–14493
- Dick M, Ullman S, Sagı D, 1987 "Parallel and serial processes in motion detection" *Science* **237** 400–402
- Dobkins K R, Bosworth R G, 2001 "Effects of set-size and spatial selective attention on motion processing" *Vision Research* **41** 1501–1517
- Enns J T, Brehaut J C, Shore D I, 1999 "The duration of a brief event in the mind's eye" *Journal of General Psychology* **126** 335–372
- Gandhi S P, Heeger D J, Boynton G M, 1999 "Spatial attention affects brain activity in human primary visual cortex" *Proceedings of the National Academy of Sciences of the USA* **96** 3314–3319
- Grünau M von, Dubé S, Kwas M, 1996 "Two contributions to motion induction: Are preattentive erect and facilitation due to attentional capture" *Vision Research* **36** 2447–2457
- Hein E, Rolke B, Ulrich R, 2006 "Visual attention and temporal discrimination: Differential effects of automatic and voluntary cueing" *Visual Cognition* **13** 29–50
- Hikosaka O, Miyauchi S, Shimojo S, 1993 "Focal visual attention produces illusory temporal order and motion sensation" *Vision Research* **33** 1219–1240
- Hock H S, Park C L, Schöner G, 2002 "Self-organized pattern formation: experimental dissection of motion detection and motion integration by variation of attentional spread" *Vision Research* **42** 991–1003
- Hommel B, Pratt J, Colzato L, Godijn R, 2001 "Symbolic control of visual attention" *Psychological Science* **12** 360–365
- Horowitz T, Treisman A, 1994 "Attention and apparent motion" *Spatial Vision* **8** 193–219
- Ivry R, Cohen A, 1990 "Dissociation of short- and long-range apparent motion in visual search" *Journal of Experimental Psychology: Human Perception and Performance* **16** 317–331
- Johnston A, Wright M J, 1985 "Lower threshold of motion for gratings as a function of eccentricity and contrast" *Vision Research* **25** 179–185
- Jonides J, 1981 "Voluntary vs. automatic control over the mind's eye's movement", in *Attention and Performance IX* Eds J B Long, A D Baddeley (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 187–204
- Klein R M, 1994 "Perceptual-motor expectancies interact with covert visual orienting under conditions of endogenous but not exogenous control" *Canadian Journal of Experimental Psychology* **48** 167–181
- Lankheet M J M, Verstraten F A J, 1995 "Attentional modulation of adaptation to two-component transparent motion" *Vision Research* **35** 1401–1412
- Liu T, Fuller S, Carrasco M, 2006 "Attention alters the appearance of motion coherence" *Psychonomic Bulletin & Review* **13** 1091–1096
- Lu Z L, Sperling G, 1995 "Attention-generated apparent motion" *Nature* **377** 237–239
- Mattes S, Ulrich R, 1998 "Directed attention prolongs the perceived duration of a brief stimulus" *Perception & Psychophysics* **60** 1305–1317
- Maunsell J H R, Nealey T A, DePriest D D, 1990 "Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey" *Journal of Neuroscience* **10** 3323–3334
- Mayfrank L, Kimmig H, Fischer B, 1987 "The role of attention in the preparation of visually guided saccadic eye movements in man", in *Eye Movements: From Physiology to Cognition* Eds J K O'Regan, A Levy-Schoen (New York: North-Holland) pp 37–45
- Merigan W H, Maunsell J H R, 1993 "How parallel are the primate visual pathways?" *Annual Review of Neuroscience* **16** 369–402
- Nakayama K, 1985 "Biological image motion processing: A review" *Vision Research* **25** 625–660
- Nakayama K, Mackeben M, 1989 "Sustained and transient components of focal visual attention" *Vision Research* **29** 1631–1646
- Nicol J R, Watter S, Gray K, Shore D I, 2009 "Object-based perception mediates the effect of exogenous attention on temporal resolution" *Visual Cognition* **17** 555–573
- Palmer J, 1994 "Set-size effects in visual search: The effect of attention is independent of the stimulus for simple tasks" *Vision Research* **34** 1703–1721

- Pantle A, Turano K, 1992 "Visual resolution of motion ambiguity with periodic luminance- and contrast-domain stimuli" *Vision Research* **32** 2093–2106
- Ristic J, Friesen C K, Kingstone A, 2002 "Are eyes special? It depends on how you look at it" *Psychonomic Bulletin & Review* **9** 507–513
- Ristic J, Kingstone A, 2006 "Attention to arrows: Pointing to a new direction" *Quarterly Journal of Experimental Psychology* **59** 1921–1930
- Rolke B, Dinkelbach A, Hein E, Ulrich R, 2008 "Does attention impair temporal discrimination? Examining non-attentional accounts" *Psychological Research* **72** 49–60
- Rolke B, Ulrich R, Bausenhardt K M, 2006 "Attention delays perceived stimulus offset" *Vision Research* **46** 2926–2933
- Schiller P H, Logothetis N K, 1990 "The color-opponent and broad-band channels in the primate visual system" *Trends in Neuroscience* **13** 392–398
- Shioiri S, Ito S, Sakurai K, Yaguchi H, 2002 "Detection of relative and uniform motion" *Journal of the Optical Society of America A* **19** 2169–2179
- Shioiri S, Matsumiya K, 2009 "Motion mechanisms with different spatiotemporal characteristics identified by an MAE technique with superimposed gratings" *Journal of Vision* **9**(5):30, 1–15
- Shulman G L, 1993 "Attentional effects on adaptation of rotary motion in the plane" *Perception* **22** 947–961
- Strout J J, Pantle A, Mills S L, 1994 "An energy model of interframe interval effects in single-step apparent motion" *Vision Research* **34** 3223–3240
- Takeuchi T, DeValois K K, 1997 "Motion-reversal reveals two motion mechanisms functioning in scotopic vision" *Vision Research* **37** 745–755
- Theeuwes J, 1991 "Cross-dimensional perceptual selectivity" *Perception & Psychophysics* **50** 184–193
- Tipples J, 2002 "Eye gaze is not unique: Automatic orienting in response to uninformative arrows" *Psychonomic Bulletin & Review* **9** 314–318
- Tipples J, 2008 "Orienting to counterpredictive gaze and arrow cues" *Perception & Psychophysics* **70** 77–87
- Treue S, Maunsell J H R, 1996 "Attentional modulation of visual motion processing in cortical areas MT and MST" *Nature* **382** 539–541
- Tsuchiya N, Braun J, 2007 "Contrast threshold for component motion with full and poor attention" *Journal of Vision* **7**(3):1, 1–15
- Verstraten F A J, Cavanagh P, Labianca A, 2000 "Limits of attentive tracking reveal temporal properties of attention" *Vision Research* **40** 3651–3664
- Visser T A W, Enns J E, 2001 "The role of attention in temporal integration" *Perception* **30** 135–145
- Wertheimer M, 1912 "Experimentelle Studien über das Sehen von Bewegung" *Zeitschrift für Psychologie* **61** 161–265 [translated in part in 1961 *Classics in Psychology* Ed. T Shipley (New York: Philosophical Library)]
- Yeshurun Y, 2004 "Isoluminant stimuli and red background attenuate the effects of transient spatial attention on temporal resolution" *Vision Research* **44** 1375–1387
- Yeshurun Y, Carrasco M, 1998 "Attention improves or impairs visual performance by enhancing spatial resolution" *Nature* **396** 72–75
- Yeshurun Y, Carrasco M, 1999 "Spatial attention improves performance in spatial resolution tasks" *Vision Research* **39** 293–305
- Yeshurun Y, Carrasco M, 2000 "The locus of attentional effects in texture segmentation" *Nature Neuroscience* **3** 622–627
- Yeshurun Y, Carrasco M, 2008 "The effects of transient attention on spatial resolution and the size of the attentional cue" *Perception & Psychophysics* **70** 104–113
- Yeshurun Y, Levy L, 2003 "Transient spatial attention degrades temporal resolution" *Psychological Science* **14** 225–231
- Yeshurun Y, Marom G, 2008 "Transient spatial attention and the perceived duration of brief visual events" *Visual Cognition* **16** 826–848
- Yeshurun Y, Rashal E, 2010 "Precueing attention to the target location diminishes crowding and reduces the critical distance" *Journal of Vision* **10**(10):16, 1–12

ISSN 0301-0066 (print)

ISSN 1468-4233 (electronic)

PERCEPTION

VOLUME 40 2011

www.perceptionweb.com

Conditions of use. This article may be downloaded from the Perception website for personal research by members of subscribing organisations. Authors are entitled to distribute their own article (in printed form or by e-mail) to up to 50 people. This PDF may not be placed on any website (or other online distribution system) without permission of the publisher.