The role of magnocellular signals in oculomotor attentional capture

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While it is known that salient distractors often capture covert and overt attention, it is unclear whether salience signals that stem from magnocellular visual input have a more dominant role in oculomotor capture than those that result from parvocellular input. Because of the direct anatomical connections between the magnocellular pathway and the superior colliculus, salience signals generated from the magnocellular pathway may produce greater oculomotor capture than those from the parvocellular pathway, which could be potentially harder to overcome with "top-down," goal-directed guidance. Although previous research has addressed this with regard to magnocellular transients, in the current research, we investigated whether a static singleton distractor defined along a dimension visible to the magnocellular pathway would also produce enhanced oculomotor capture. In two experiments, we addressed this possibility by comparing a parvo-biased singleton condition, in which the distractor was defined by isoluminant chromatic color contrast, with a magno + parvo singleton condition, in which the distractor also differed in luminance from the surrounding objects. In both experiments, magno + parvo singletons elicited faster eye movements than parvo-only singletons, presumably reflecting faster information transmission in the magnocellular pathway, but magno + parvo singletons were not significantly more likely to produce oculomotor capture. Thus, although magnocellular salience signals are available more rapidly, they have no sizable advantage over parvocellular salience signals in controlling oculomotor orienting when all stimuli have a common onset.

Keywords: attention, eye movements, search, visual cognition

Citation: Leonard, C. J., & Luck, S. J. (2011). The role of magnocellular signals in oculomotor attentional capture. *Journal of Vision, 11*(13):11, 1–12, http://www.journalofvision.org/content/11/13/11, doi:10.1167/11.13.11.

Introduction

The amount of visual input at the retina far exceeds the representational capacity of the visual system, making it necessary to allocate attention to a subset of the incoming visual input (Luck, Girelli, McDermott, & Ford, 1997). Efficient allocation of attention to task-relevant targets can be disrupted when salient distractors capture covert attention (Jonides & Yantis, 1988; Theeuwes, 1994), especially when observers search for a target based on its "bottom-up" salience rather than its specific visual features (Bacon & Egeth, 1994). Certain types of salient stimuli such as luminance transients and motion onsets have been associated with large and potentially insurmountable attentional capture effects (Abrams & Christ, 2003; Girelli & Luck, 1997). These types of stimuli are also likely to activate the magnocellular visual stream, whereas many stimuli that produce weaker capture (i.e., shape singletons) tend to primarily activate the parvocellular visual stream.[1]

Differences in selectivity and anatomical connectivity between the magnocellular and parvocellular streams could potentially produce differences in attentional capture. Early in the thalamocortical visual pathway, these streams are distinct, originating from different retinal ganglion cells and projecting to separate layers of the lateral geniculate nucleus (Livingstone & Hubel, 1988; Schiller, Logothetis, & Charles, 1991). Neurons in early visual areas that are dominated by magnocellular input are highly sensitive to changes in luminance and insensitive to isoluminant color differences, whereas those that are innervated by parvocellular input are sensitive to isoluminant chromatic differences but are significantly slower to reach the cortex (Nowak, Munk, Girard, & Bullier, 1995). While these inputs are separated early in processing, they become integrated in the extrastriate cortex, enabling behavior that clearly takes into consideration both types of visual input. However, magnocellular signals dominate feedforward inputs into the dorsal stream, which plays a key role in the control of spatial orienting (Corbetta & Shulman, 2002; Yantis et al., 2002). The magnocellular system also provides the dominant input to the superior colliculus (SC), a midbrain region that plays a role in covert attention (Lovejoy & Krauzlis, 2010) and ultimately enables the production of saccadic

doi: 10.1167/11.13.11 Received June 20, 2011; published November 10, 2011 ISSN 1534-7362

eye movements (Rodieck & Watanabe, 1993; White & Munoz, 2011; Wurtz & Albano, 1980).

Consistent with these anatomical connections, strong overt oculomotor capture has been observed for task-irrelevant sudden onset stimuli that create a luminance transient that presumably activates the magnocellular system (Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). However, isoluminant singletons that selectively activate the parvocellular system are also capable of leading to both covert attentional capture and oculomotor capture (Snowden, 2002; Theeuwes, De Vries, & Godijn, 2003; Wu & Remington, 2003). Although signals from both the magnocellular and parvocellular pathways can capture attention and influence oculomotor activity, they may operate through different circuits and therefore produce different patterns of capture.

Previous studies have often addressed this question by examining the automaticity of capture by a transient stimulus, such as an onset (Irwin, Colcombe, Kramer, & Hahn, 2000; Theeuwes, 1994; Yantis & Jonides, 1984). The onset of a distractor object slowed search despite the fact that it could never be the target. Subsequently, Theeuwes (1995) showed that the onset of a new object led to oculomotor capture only if it was not isoluminant with the objects already on the screen. Furthermore, Irwin et al. (2000) found significant overt distraction by a luminance increment of an existing distractor, suggesting that changes likely to activate the subcortical magnocellular pathway may also gain strong attentional priority. While these previous studies examined unique transient changes, in the current study, we used a static manipulation of magnocellular involvement in which all objects had common onset. The irrelevant singleton distractor was either defined along a dimension able to be processed by the magnocellular stream (luminance) or one that was not (isoluminant color). In doing so, our study avoids the new object benefit that stems from transient onsets (e.g., Boot, Kramer, & Peterson, 2005; Yantis & Hillstrom, 1994) and asks whether the role of the magnocellular pathway in attentional capture extends beyond onsets to static salience signals. This is an important issue, because a new static input to the retina occurs after every saccadic eye movement, producing the simultaneous onset of signals into the magnocellular and parvocellular pathways. Given that saccades occur 2–4 times per second during natural scene viewing (Henderson, 2008), simultaneous onsets are presumably much more common than the sudden appearance of an isolated object during a period of fixation. Thus, it is important to know whether the role of the magnocellular system in attention capture is limited to the appearance of new objects.

In particular, irrelevant singletons that drive direct magnocellular input to the SC and dorsal stream might be expected to produce more overt capture than those that only activate parvocellular projections. In addition, SC-mediated orienting in response to magnocellular signals may be more resistant to "top-down" control than ventral stream-mediated orienting produced by parvocellular signals. We call this the *multiple pathways* hypothesis. An alternative possibility is that both magnocellular and parvocellular signals ultimately pass through a common circuit to produce attentional orienting, and the pattern of orienting will, therefore, be the same as long as the signals are equally strong. We call this the *converging signals* hypothesis. (This hypothesis is also consistent with multiple circuits being involved in controlling orienting, as long as these circuits are equally affected by magnocellular and parvocellular inputs.) According to this hypothesis, magnocellular signals may reach the oculomotor system faster than parvocellular signals (owing to the greater speed of the magnocellular pathway), but the relative occurrence of overt capture and the automaticity of this capture will be equivalent for magnocellular and parvocellular salience signals.

To test these hypotheses, we compared a singleton that was designed to preferentially activate the parvocellular system with a singleton that was designed to additionally recruit the magnocellular system. Specifically, we tracked eye movements during an "additional singleton" paradigm in which observers search for a target shape that is unique on a particular feature dimension in a field of homogeneous distractors (i.e., a single circle among diamonds or a single diamond among circles). The task included trials with (a) no salient singleton distractor, (b) an isoluminant singleton designed to preferentially activate the parvocellular system (a *parvo-biased singleton*), or (c) a luminance singleton designed to activate both the magnocellular and parvocellular systems (a *magno + parvo singleton*).[2]

When comparing the orienting produced by two different stimuli, it is necessary to account for differences in salience. That is, a red object among green objects may be more salient than a gray object among slightly darker gray objects, whereas a red object among slightly off-red objects might be less salient than a gray object among black objects. Thus, it is not possible to determine whether luminance singletons are more salient *in general* than color singletons because measuring salience requires deciding on a metric that can be used to equate across dimensions. Moreover, *salience* is not easily operationalized, and there is not an independent and unambiguous means of quantifying the salience of a given stimulus (see Fecteau & Munoz, 2006 for further discussion of the term). In the present study, we operationalized salience as the overall effect of the irrelevant singletons on manual reaction time (RT), a measure that has been frequently used to gauge the salience of an irrelevant distractor. We used stimulus parameters that approximately equate the parvo-biased and magno + parvo singletons according to this metric of salience. Thus, the present study asks how the pattern of oculomotor capture varies between parvo-biased and magno + parvo singletons when the overall amount of RT interference is equated. In particular, parvocellular signals may predominantly capture covert attention, whereas magnocellular signals may produce

overt as well as covert capture (via projections into the SC and dorsal stream).

To preview the results, in Experiment 1, we found that magno + parvo singletons produced only slightly and non-significantly more oculomotor capture than parvo-biased singletons. However, when oculomotor capture did occur, saccades to magno + parvo singletons were significantly faster than saccades to the parvo-biased singletons. Experiment 2 tested the role of "top-down" guidance by using a fixed target identity, enabling participants to use feature-based guidance when searching for the target. Oculomotor capture was equivalent for parvo-biased and magno + parvo singletons in this experiment but was substantially weaker than that observed in Experiment 1, indicating that magnocellular and parvocellular salience signals were equally suppressed by the addition of greater goal-directed control. These findings are consistent with the converging signals hypothesis.

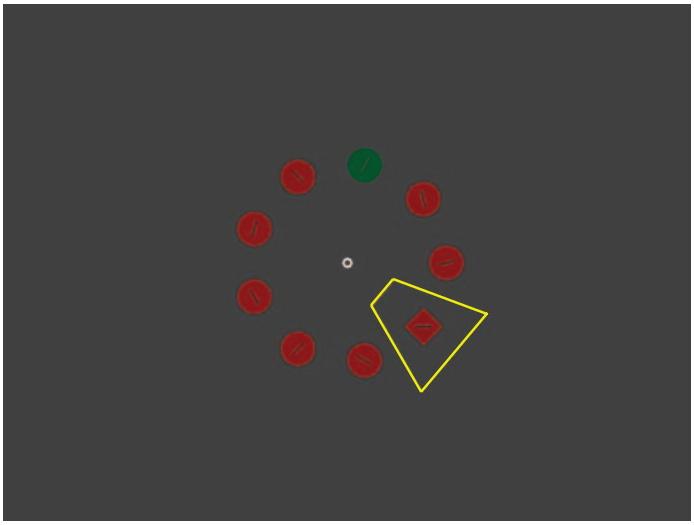

Figure 1. An example of the task display from a trial with a parvo-biased singleton. Overlaid is the outline of the interest area used to define saccades to the target object (note that these were not present during the task).

Experiment 1

Methods

Participants

Twenty-four UC-Davis students between the ages of 18 and 30 participated in exchange for course credit. All observers reported normal or corrected-to-normal vision and intact red–green color vision. Before the task, the point of red–green isoluminance was found for each participant using heterochromatic flicker photometry with stimuli at the same eccentricity as the search display (Mullen, 1991). One participant was excluded from all analyses due to abnormally long mean saccade latencies (greater than 650 ms for all conditions).

Stimuli and procedure

Participants were seated 70 cm from a 53-cm CRT monitor operating at a refresh rate of 60 Hz, with head positioned in a chin-and-forehead rest to reduce motion artifacts. An SR Research Eyelink 1000 desk-mounted system recorded eye position monocularly from the right eye at 2000 Hz.

As illustrated in Figure 1, the stimulus arrays consisted of 9 filled shapes (diameter of 0.9°), equally spaced around a notional circle with an eccentricity of 3.6°. The target was defined as the unique shape: It was equally likely to be a single diamond among circles or a single circle among diamonds, forcing the adoption of a singleton detection mode that leads to strong attentional capture effects (Bacon & Egeth, 1994). A line (vertical or horizontal for the target and randomly tilted to the right or left of vertical for distractors) was cut out of each object to reveal the gray background (3.7 cd/m^2, x = 0.30, y = 0.32). All of the objects with the exception of the irrelevant singleton were filled with red (3.8 cd/m^2, x = 0.66, y = 0.35). The magno + parvo singleton distractor was also red but was much lower in luminance than the other objects (0.5 cd/m^2, x = 0.37, y = 0.41); the parvo-biased singleton was green, with a luminance set to be perceptually isoluminant to the non-singleton red objects (with an average luminance of 3.6 cd/m^2 across participants). Thus, all of the items were isoluminant with each other and with the background, except that the magno + parvo singleton was defined by having a lower luminance than the other non-singleton objects and the background. We used lower rather than higher luminance for the magno + parvo singleton because we wanted to stress the existence of luminance contrast rather than intensity per se. That is, something that is more intense than the background might capture attention because of a higher level cognitive bias toward high intensity, not because the more intense object is visible to the magno system (which can detect both luminance increments and luminance decrements).

The fixation point appeared at the beginning of each trial. After the participant maintained fixation for 500 ms within 0.5° of this point, the search display appeared and remained until a response was made. Observers pressed the left or right trigger button on a gamepad to indicate whether the line inside the target shape was vertical or horizontal, respectively. A blank intertrial interval of 1200–1500 ms was interposed between the response and the appearance of the fixation point for the next trial.

Each observer received 432 trials, 144 with no singleton distractor, 144 with a parvo-biased distractor, and 144 with a magno + parvo distractor (randomly intermixed). The target was equally likely to appear at any of the 9 locations, and the singleton distractor was equally

likely to appear at any of the other 8 locations. The data were collapsed across the location of the target and the irrelevant singleton for all analyses. Participants were informed that the singleton distractor would never be the target. With the exception of maintaining fixation to initiate each trial, participants were not given any instructions regarding eye movements. Those who asked were told that they could make eye movements but that it was not required. Ten trials of practice preceded the experiment.

Analysis

The onset of a saccade was defined using a minimum eye velocity threshold of 30°/s and a minimum eye acceleration threshold of 9500°/s. Wedge-shaped interest areas were used to classify saccade-landing position. Each wedge encompassed 40° of arc and subtended 1.8° both inward and outward from the center of the object (see Figure 1 for an example of an interest area). Mean accuracy on the task was 95%, and trials with manual response errors were excluded. Trials on which observers completed the task without making an eye movement, which were rare, were excluded from all analyses. Trials were also excluded if the manual RT was more than 3 standard deviations greater than that participant's mean. In total, 10% of trials were excluded.

Results

Manual reaction time

As shown in Figure 2, the mean manual RT was slowed approximately equally by the presence of the parvo-biased singleton (1155 ms) and the magno + parvo singleton (1153 ms) relative to no singleton distractor trials (1083 ms). An ANOVA including the three trial types (parvo-biased, magno + parvo, and no singleton distractor) revealed a significant difference among trials types, $F(2, 44) = 24.9$, $p < 0.001$. Planned comparisons between singleton and no singleton distractor trials confirmed that mean RT was significantly slowed for both the parvo-biased singleton, $t(22) = 5.8$, $p < 0.001$, and the magno + parvo singleton, $t(22) = 5.5$, $p < 0.001$. RTs did not differ between the parvo-biased and magno + parvo singletons, $t(22) = 0.27$, $p = 0.78$. It should be stressed that the non-significant difference in manual RT between the parvo-biased and magno + parvo stimuli does not reflect a broader equivalence between these two types of singletons, because the stimulus parameters used to create the parvo-biased and magno + parvo singletons were designed to make them equally salient (in terms of RT capture effects). It does, however, make it possible to compare the patterns of oculomotor capture produced by parvo-biased and magno + parvo singletons that are equated on this measure of salience.

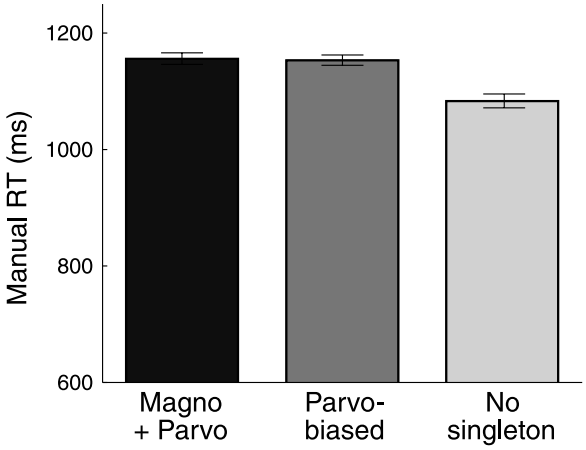

Figure 2. Mean manual reaction time for the manual response in Experiment 1 as a function of singleton type. Error bars here and in subsequent figures depict within-subjects confidence intervals (Morey, 2008).

Overall frequency of eye movements

Although overt selection was not required of observers, saccades were made on over 95% of trials (and the remaining trials were excluded from all analyses). In addition, the target interest area was fixated prior to the behavioral response on 84% of trials. Thus, it is likely that the orienting of attention in our paradigm involves overt as well as covert attention.

First saccade destination

As can be seen in Figure 3A, the first saccade was less likely to visit the target when a singleton distractor was present. The first saccade went to the target on 39.2% of no singleton distractor trials, on 31.8% of parvo-biased singleton trials, and on 30.2% of magno + parvo singleton trials. An ANOVA with trial type (parvo-biased, magno + parvo, and no singleton distractor) as a factor confirmed this, $F(2, 44) = 13.4$, $p < 0.001$. Follow-up comparisons showed that no singleton distractor trials differed from both parvo-biased singleton trials, $t(22) = 4.2$, $p < 0.001$, and magno + parvo singleton trials, $t(22) = 3.9$, $p < 0.001$, with no difference between the parvo-biased and magno + parvo singleton trials, $t(22) = 1.2$, $p = 0.23$. Thus, parvo-biased and magno + parvo singletons produced approximately equivalent disruption of the observers' ability to direct the first saccade to the target.

When a singleton distractor was present, the first saccade went to the parvo-biased singleton on 15.5% of trials and to the magno + parvo singleton on 19.5% of trials (Figure 3B), a marginally significant difference, $t(22) = 1.82$, $p = 0.08$. To confirm that the irrelevant singletons did, in fact, produce oculomotor capture, these results were compared to the percentage of saccades that went to other non-salient distractor locations on singleton-present

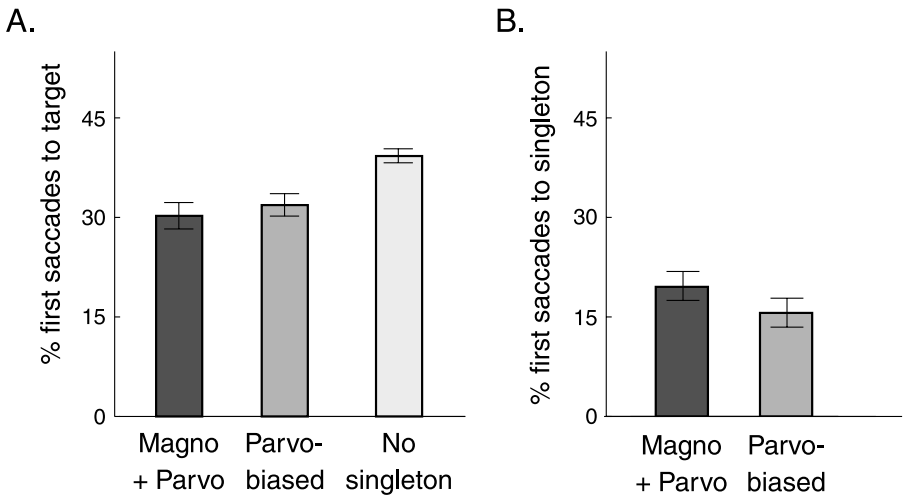

Figure 3. (A) The percentage of trials in each condition on which the first saccade landed at the target in Experiment 1. (B) The percentage of trials in each condition on which the first saccade landed at the irrelevant singleton distractor in Experiment 1.

trials. The first saccade went to any given non-singleton, non-target object on 4.4% of trials with a parvo-biased singleton and on 4.5% of trials with a magno + parvo singleton, which was significantly fewer than to the singleton location (parvo-biased: $t(22) = 4.1$, $p < 0.001$; magno + parvo: $t(22) = 4.7$, $p < 0.001$).[3]

First saccade latency

We next measured saccade latency for trials on which the first saccade went to either the target or the salient distractor (Figure 4). The saccadic RT to the target was 334 ms in the no singleton distractor condition, 342 ms in the parvo-biased distractor condition, and 340 ms in the magno + parvo distractor condition. These differences were not significant in a one-way ANOVA, $F(2, 44) = 0.53$ $p = 0.59$.

Saccades to the parvo-biased singleton had a mean latency of 262 ms, which was significantly slower than the mean latency of 239 ms for those eye movements to the magno + parvo singleton, $t(22) = 2.9$, $p = 0.008$. Saccades to both the parvo-biased and magno + parvo singletons

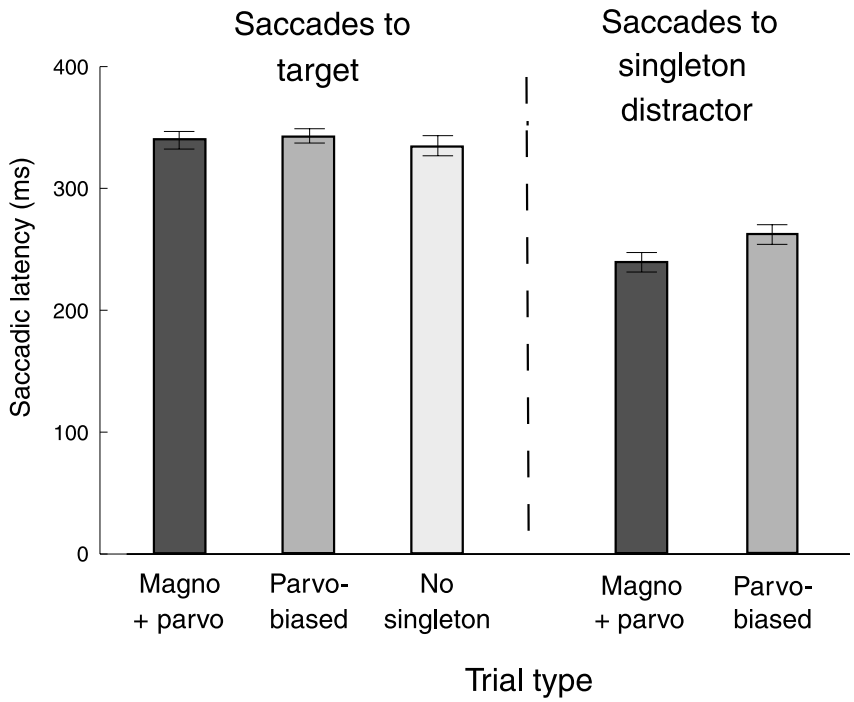

Figure 4. The latency of first saccades (ms) to the target and irrelevant singleton distractor across the different singleton conditions in Experiment 1.

were faster than those that went to the target on the corresponding singleton-present trials (parvo-biased: $t(22) = 7.1$, $p < 0.001$); magno + parvo: $t(22) = 5.9$, $p < 0.001$).

Manual reaction time contingent on first saccade destination

We analyzed the manual RT when the first saccade went to the target to see if there was a covert effect of the singleton distractor. When the eyes went directly to the target, there was a mean RT of 996 ms for the magno + parvo singleton trials, 973 ms for the parvo-biased singleton trials, and 969 ms for the no distractor trials. However, there was no significant effect of trial type, $F(2, 44) = 2.04$, $p = 0.14$. When the eyes went directly to the singleton distractor, the RTs were 1266 ms for the magno + parvo trials and 1296 ms for the parvo-biased trials, with no significant difference between them, $t(22) = 0.92$, $p = 0.37$. Manual RT was significantly slowed when the eyes went directly to the singleton distractor compared to when they went directly to the target on singleton-present trials (averaged over singleton type), $t(22) = 11.7$, $p < 0.001$.

Discussion

Given the dominance of magnocellular inputs to the dorsal stream and SC, one might expect singletons that can be easily detected by the magnocellular system to elicit more oculomotor orienting than singletons that cannot easily be detected by this system and primarily activate the parvocellular system. However, we found that the parvo-biased singletons elicited significant oculomotor capture, with only a small and non-significant trend toward a greater probability of oculomotor capture by the magno + parvo singletons. The only significant difference was that eye movements toward the magno + parvo singletons were generated more quickly than eye movements toward the parvo-biased singleton. This speed difference is consistent with evidence that luminance information is available to neurons in the superior colliculus before chromatic information (White & Munoz, 2011), likely reflecting the faster transmission of information along the magnocellular pathway (Nowak et al., 1995; Schmolesky et al., 1998).

Experiment 2

Experiment 2 served two interrelated purposes. First, it tested whether magnocellular salience signals are less influenced by "top-down" control than parvocellular salience signals. Second, it tested a potential explanation for the lack of large differences in oculomotor capture between the parvo-biased and magno + parvo singletons in Experiment 1. Observers in Experiment 1 were searching for a target that was defined as a unique shape and were unable to predict whether it would be a circle among diamonds or a diamond among circles. Previous research has shown that this design leads observers to search specifically for feature discontinuities (i.e., "singleton detection mode"), and this produces strong capture of attention by feature discontinuities along task-irrelevant dimensions (Bacon & Egeth, 1994; Leber & Egeth, 2006). Because it encourages singleton detection, the use of this design in Experiment 1 may have led to a ceiling effect on oculomotor capture by irrelevant singletons. That is, even if magnocellular signals cause task-independent, automatic oculomotor capture, they may produce no more capture than parvocellular signals under conditions that encourage strategic orienting to all singletons. To test whether magnocellular salience signals lead to more automatic oculomotor orienting than parvocellular salience signals, it is necessary to create conditions in which observers are not motivated to strategically orient to the irrelevant singletons. This was accomplished in Experiment 2, in which the task was changed so that observers could use a specific feature value rather than the mere presence of feature discontinuities to find the target. If magno + parvo singletons elicit oculomotor orienting more automatically than parvo-only singletons, then this should be visible in the present experiment. If, in contrast, goal-directed, feature-based guidance can modulate orienting to both magnocellular and parvocellular salience signals, then very little oculomotor orienting should be observed for either the parvo-biased or magno + parvo singletons.

Methods

Twenty new participants from the same population were recruited for Experiment 2. The stimuli, procedure, and analyses were identical to those of Experiment 1, with one exception. Whereas the target in Experiment 1 was simply defined as a shape singleton (unpredictably a circle among diamonds or a diamond among circles), the target in Experiment 2 was defined as a specific, consistent shape. For half of the subjects, the target was always a diamond among circles, and for the other half, it was always a circle among diamonds. As before, heterochromatic flicker photometry was used to create a perceptually isoluminant singleton, which had an average luminance of 4.2 cd/m^2 across participants.

As in Experiment 1, performance was highly accurate (94%). A total of 9% of trials were excluded from further analysis because of erroneous responses, slow responses, or a lack of eye movements. One observer made no saccades to the parvo-biased singleton over the course of the experiment, making it impossible to recover a mean latency for this condition. This person was therefore excluded from all latency analyses. Rerunning the other

analyses without this observer's data did not change the results in any way.

Results

Manual reaction time

The mean manual RT was 860 ms for the parvo-biased singleton condition, 851 ms for the magno + parvo singleton condition, and 826 ms for the no singleton distractor trials (see Figure 5). An ANOVA revealed a significant effect of singleton condition on RT, $F(2, 38) = 9.94$, $p < 0.001$. Subsequent planned comparisons between singleton distractor and no singleton distractor trials found that manual RT was still slowed by the presence of a parvo-biased singleton distractor, $t(19) = 3.6$, $p = 0.003$, or the presence of a magno + parvo singleton, $t(19) = 5.5$, $p < 0.002$. However, once again, there was no significant difference in manual RT between the parvo-biased and magno + parvo singleton conditions, $t(19) = 1.2$, $p = 0.24$. Overall, the magnitude of the capture effect on manual RT was reduced from approximately 70 ms in Experiment 1 to 25 ms in Experiment 2.

To verify that the use of a consistent target identity led observers to use a more efficient attentional set, an ANOVA was conducted with factors levels of trial type (parvo-biased, magno + parvo, and no singleton distractor) and experiment. There was a significant main effect of experiment, $F(1, 41) = 23.8$, $p < 0.001$. There was also a significant effect of trial type, $F(2, 82) = 32.4$, $p < 0.001$, which was modulated by a significant interaction with experiment, $F(1, 82) = 5.5$, $p = 0.006$. Consistent with the results of Leonard and Egeth (2008) that top-down guidance can speed singleton search, the ability to use a specific feature to guide search led to faster manual RTs on no singleton distractor trials in Experiment 2 compared to Experiment 1, $t(41) = 4.6$, $p < 0.001$. These results support the assertion that the small change in procedure between experiments led to significantly greater feature-based guidance in Experiment 2.

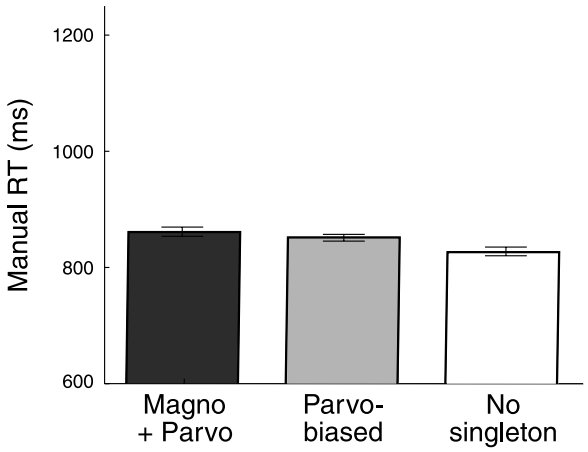

Figure 5. Mean manual reaction time for the manual response in Experiment 2 as a function of singleton type.

The question of particular interest was whether attentional capture would be less suppressed by the additional "top-down" guidance for magno + parvo singletons than for parvo-biased singletons. The lack of a difference in manual RT between these two types of singletons in both experiments suggests that capture was reduced equivalently for both singleton types in Experiment 2. To test this more directly, a follow-up ANOVA was conducted with singleton type (parvo-biased and magno + parvo) and experiment as factors. As in the previous analysis, there was a significant effect of experiment because RTs were significantly faster when feature-based guidance was available, $F(1,41) = 25.7$, $p < 0.001$. However, no significant effect of singleton type ($F(1, 41) = 0.92$, $p = 0.35$) or interaction between singleton type and experiment was found ($F(1, 41) = 0.29$, $p = 0.6$). This provides additional evidence that attentional capture is equally influenced by "top-down" control for parvo-biased and magno + parvo singletons.

Overall frequency of eye movements

Although overt selection was not required of observers, saccades were made on 96% of trials (and the remaining trials were excluded from all analyses). In addition, the target interest area was fixated prior to the behavioral response on 81% of trials.

First saccade destination

As can be seen in Figure 6A, the first saccade went to the target on 49.9% of trials in the no singleton distractor condition, 44.3% in the parvo-biased singleton distractor condition, and 43% in the magno + parvo singleton distractor condition. An ANOVA found an effect of condition on the likelihood of the first saccade landing at the target, $F(2, 44) = 10.0$, $p < 0.001$. Post-hoc comparisons revealed that the presence of an irrelevant singleton significantly reduced the likelihood of the first saccade landing at the target in the parvo-biased condition, $t(19) = 3.2$, $p < 0.005$, as well as the magno + parvo singleton condition, $t(19) = 4.3$, $p < 0.001$. However, once again, there was no difference in this reduction of first saccades to the target between the parvo-biased and magno + parvo singleton conditions, $t(19) = 0.82$, $p = 0.42$. An ANOVA including experiment as a factor found that significantly more first saccades went to the target in Experiment 2 than in Experiment 1, $F(1, 41) = 6.7$, $p = 0.01$, and this effect did not interact with condition, $F(2, 82) = 0.4$, $p = 0.7$.

Figure 6B shows the frequency of first saccades to the irrelevant singleton. The first saccade went to a parvo-biased singleton on 9.8% of trials and to the magno + parvo singleton on 10.4%. This difference in the likelihood of

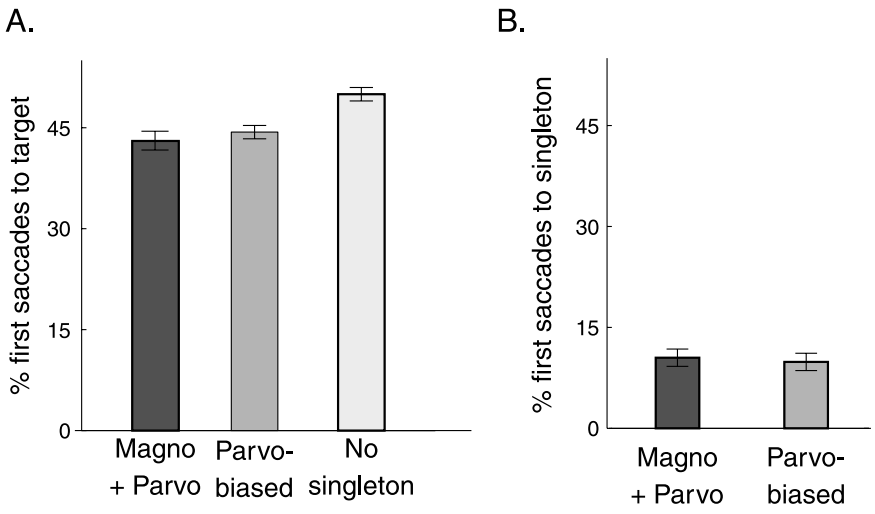

Figure 6. (A) The percentage of trials in each condition on which the first saccade landed at the target in Experiment 2. (B) The percentage of trials in each condition on which the first saccade landed at the irrelevant singleton distractor in Experiment 2.

visiting the parvo-biased singleton versus the magno + parvo singleton was not significant, $t(19) = 0.41$, $p = 0.68$. A significant amount of oculomotor capture still remained in comparison to the baseline level of saccades that went to other non-salient distractor locations on singleton-present trials (parvo-biased: 2.8%, $t(19) = 2.7$, $p = 0.01$; magno + parvo: 3.8%, $t(19) = 5.4$, $p < 0.001$). An ANOVA including experiment as a factor confirmed that significantly fewer first saccades went to the singleton distractor in Experiment 2, $F(1, 41) = 5.4$, $p = 0.03$, there was no overall difference for magno + parvo and parvo-biased singletons, $F(1, 41) = 1.9$, $p = 0.17$, and there was no interaction of singleton type and experiment, $F(1, 41) = 1.0$, $p = 0.32$.

First saccade latency

Mean saccadic latency is shown in Figure 7 for the first eye movement that went to either the target or salient distractor. The saccadic RT to the target was 278 ms on no singleton distractor trials, 284 ms on parvo-biased distractor trials, and 287 ms on magno + parvo distractor

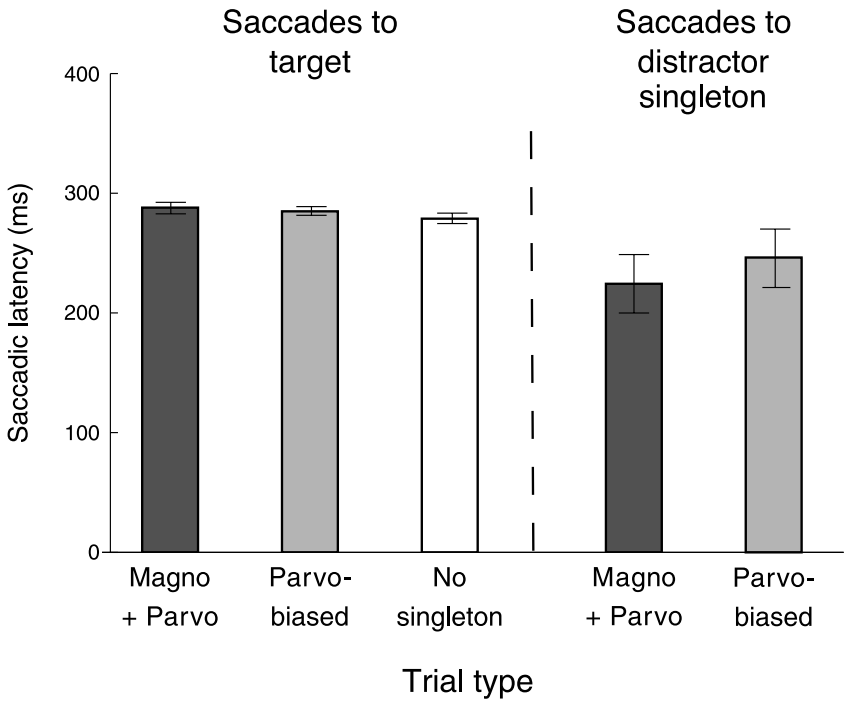

Figure 7. The latency of first saccades (ms) made to the target and to the irrelevant singleton distractor across the different singleton conditions in Experiment 2.

trials. These saccadic RTs were not significantly different from each other in a one-way ANOVA, $F(2, 36) = 1.88$, $p = 0.17$.

Saccades to singleton distractors had a mean latency of 246 ms for parvo-biased singletons and 224 ms for magno + parvo singletons. Once again, eye movements to the parvo-biased and magno + parvo singletons were significantly faster than the eye movements to the target on the corresponding singleton-present trials (parvo-biased: $t(18) = 5.3$, $p < 0.001$; magno + parvo: $t(18) = 2.4$, $p = 0.03$). As in Experiment 1, there was a speed advantage for saccades to the magno + parvo singletons (23 ms in Experiment 1 and 22 ms in Experiment 2). However, this difference did not reach significance in Experiment 2 (likely due to high variance caused by few eye movements to singletons for some observers), $t(18) = 0.92$, $p = 0.37$. When saccade latency to the singleton was entered into an ANOVA with singleton type (parvo-biased and magno + parvo) and experiment as factors, there was no main effect of experiment, $F(1, 40) = 1.2$, $p = 0.27$, nor was there an interaction of singleton type and experiment, $F(1, 40) = 0.01$, $p = 0.966$. However, there was a marginally significant trend across experiments for magno + parvo singletons to produce faster oculomotor capture than parvo-biased singletons, $F(1, 40) = 3.7$, $p = 0.06$.

Manual reaction time contingent on first saccade destination

Once again, there was no covert effect of singleton distractor when the eyes went directly to the target. The mean RT was 785 ms for the magno + parvo singleton trials, 783 ms for the parvo-biased singleton trials, and 770 ms for the no distractor trials, with no significant effect of trial type, $F(2, 38) = 0.89$, $p = 0.42$. When the eyes went directly to the singleton distractor, the RTs were 962 for the magno + parvo trials and 964 ms for the parvo-biased trials, with no significant difference between them, $t(18) = 0.09$, $p = 0.93$. Once again, manual RT was significantly slowed when the eyes went directly to the singleton distractor compared to when they went directly to the target in singleton-present trials (averaged across singleton type), $t(19) = 5.4$, $p < 0.001$.

General discussion

In the current experiments, we directly compared the amount of oculomotor capture produced by a singleton that was biased toward the parvocellular system and a singleton that additionally activated the magnocellular system. Both the magno + parvo singleton and the parvo-biased singleton led to oculomotor capture, replicating previous findings that isoluminant singletons are capable of capturing overt attention even when task-irrelevant (Theeuwes et al., 2003; Wu & Remington, 2003). However, our design goes beyond those results, allowing direct within-block comparison of capture between parvo-biased and magno + parvo singletons to determine whether magnocellular salience signals are more likely to produce oculomotor capture than parvocellular salience.

In Experiment 1, the first saccade was less likely to go to the target when an irrelevant singleton was present, but the likelihood and timing of these target saccades were equivalent for parvo-biased and magno + parvo singletons. The first saccade was slightly more likely to go to the magno + parvo singleton than to the parvo-biased singleton, but this effect did not reach statistical significance. The only significant difference between the two singletons was that, when the first saccade went to the singleton, this saccade was faster for the magno + parvo singleton than for the parvo-biased singleton. This is consistent with the faster propagation of signals in the magnocellular pathway (White & Munoz, 2011), and the hypothesis that both magnocellular and parvocellular salience signals ultimately converge on a common attentional orienting circuit. Thus, these results are consistent with the converging signals hypothesis and provide no evidence for the common pathway hypothesis.

Experiment 2 explored the possibility that magnocellular salience signals lead to more automatic orienting of attention than parvocellular salience signals and also ruled out the possibility that the lack of a significant magnocellular advantage in Experiment 1 may have reflected a ceiling effect due to voluntary orienting to singletons. If the direct inputs from the magnocellular pathway to the SC or dorsal stream produce automatic orienting, whereas parvocellular signals do not produce automatic orienting, then a difference between magnocellular and parvocellular signals should be observed when observers adopt control settings that favor orienting to specific feature values rather than orienting to singletons. This was addressed in Experiment 2, in which observers could find the target by searching for a specific feature value rather than relying on target salience to perform the search. This manipulation clearly increased feature-based guidance, leading to faster target detection, a greater probability that the first saccade was directed to the target, a reduction in RT measures of attention capture, and a reduction in the probability that the first saccade was directed to an irrelevant singleton. However, all of these benefits of greater "top-down" control were observed equally for the magno + parvo and parvo-biased singletons, and there was no evidence of greater residual capture by the magno + parvo singletons. Moreover, the marginally significant trend for more oculomotor capture by magno + parvo singletons than by parvo-biased singletons that was found in Experiment 1 did not approach statistical significance in Experiment 2. Thus, rather than increasing the advantage of magnocellular signals over parvocellular signals, the increased feature guidance in Experiment 2 minimized the small differences that were observed in Experiment 1.

These results are consistent with the converging signals hypothesis, and they also dovetail with prior research showing that "top-down," goal-directed guidance and bottom-up salience influence attentional selection through the same network of cortical areas, including intraparietal sulcus, frontal eye fields, and the SC, with the SC ultimately enabling the production of a saccadic eye movement (see Schall, 2002 for a review). White and Munoz (2011) have shown that faster luminance signals, likely from the magnocellular pathway, are available before chromatic signals reach the final stages of saccade production in the SC. This facilitation in processing speed may explain the current finding that oculomotor capture is faster for singletons containing luminance contrast than for purely chromatic singletons. We should also note that the speed advantage of the magnocellular system could explain the observation of a slightly greater probability of oculomotor capture due to speed–accuracy trade-offs, even if the same circuitry is activated by parvocellular and magnocellular salience signals. However, the non-significant trend for a benefit for magnocellular signals in Experiment 1 no longer approached significance when feature-based guidance signals were available for use in Experiment 2. This is consistent with researching showing that knowledge of the upcoming target feature leads to faster neuronal target discrimination in the frontal eye fields, a region in close communication with the SC (Bichot & Schall, 2002). This type of biasing input from the parvocellular pathway has an important role to play in the competition for oculomotor selection, exerting its influence on the common network of attentional orienting. We cannot, of course, conclude with certainty that magnocellular signals produce exactly the same amount of oculomotor capture as parvocellular signals, because this would require accepting the null hypothesis. However, we can conclude that any advantage for magnocellular signals must be small and that the capture produced by these signals is strongly modulated by top-down control signals.

These findings differ from the results of previous studies in which magnocellular activation was driven primarily by a transient stimulus, such that the irrelevant distractor either appeared or changed after the other objects in the search display had already been presented (Boot et al., 2005; Irwin et al., 2000; Theeuwes, 1995). However, the timing that is required to define this type of distractor stimulus does not allow for the examination of how competition between various types of salience signals proceeds in parallel. Although dynamic visual transients may be able to have more direct control of oculomotor behavior due to activation of the SC, our current results indicate that, under conditions of common onset, singletons defined by a type of contrast detectable by the magnocellular system do not have a strong benefit compared to those that are not. This is important, because each eye movement causes the sudden and simultaneous appearance of an image on the retina, which stimulates both the magnocellular and parvocellular pathways. Consequently, the simultaneous onset of stimuli is the most common occurrence in the natural environment.

In conclusion, the presence of magnocellular salience signals did not produce enhanced oculomotor capture relative to parvocellular salience signals. Instead, salience signals from both pathways seem to operate via the same attentional orienting network, in which information about bottom-up salience and goal-related relevance are integrated to guide shifts of covert and overt attention. Further support for a shared network comes from electrophysiological measures that have shown a commonality in attentional selection for singletons that are biased to activate either magnocellular or parvocellular pathways. Specifically, Girelli and Luck (1997) found that the selection of a motion singleton (largely activating the magnocellular system) and color singleton (activating the parvocellular system) both resulted in an N2pc component, an electrophysiological measure of attentional allocation, with the same time course and scalp topography. Overall, these results speak to a very rapid integration of information across magnocellular and parvocellular inputs that guide a common network of oculomotor selection.

Acknowledgments

We thank our research assistants Kristina Peterson and Mike Maurer who helped collect these data. This work was supported by funding from NIH Grants R01MH076226 and R01MH065034.

Commercial relationships: none.
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Footnotes

[1]Previous psychophysical research has also referred to these as the transient and sustained pathways, which are generally thought of as corresponding to the magnocellular and parvocellular pathways, respectively (Breitmeyer & Williams, 1990). Note that we do not include discussion of the third pathway, originating in the koniocellular layers, which has received considerably less attention in the literature (but see Hendry & Reid, 2000 for a review).

[2]We chose to compare parvocellular activation with combined magnocellular and parvocellular activity rather than with pure magnocellular activity because it would be difficult to design a magnocellular-only stimulus that is similar to the stimuli traditionally used as singleton

distractors. In particular, the magnocellular system is usually isolated by the use of low contrast, low spatial frequency stimuli, and it is difficult to construct discrete, salient singletons from such stimuli. Consequently, the present study asks how the addition of magnocellular activity influences orienting to a salient singleton rather than the orienting that would be produced by pure activation of the magnocellular system. Note, however, that if oculomotor capture is dominated by magnocellular signals, then the capture produced by magno + parvo singletons should be dominated by the magnocellular component of the stimuli, especially given the faster transmission of visual information along the magnocellular pathway.

[3]First fixations that landed on the target, the irrelevant singleton, and the seven non-singleton objects do not add up to 100% because on some trials first fixations landed outside of these interest areas.

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