Eye of origin guides attention away: An ocular singleton column impairs visual search like a collinear column

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Collinearity and eye of origin were recently discovered to guide attention: Target search is impaired if it is overlapping with a collinear structure (Jingling & Tseng, 2013) but enhanced if the target is an ocular singleton (Zhaoping, 2008). Both are proposed to occur in V1, and we study their interaction here. In our 9 × 9 search display (Experiment 1), all columns consisted of horizontal bars except for one randomly selected column that contained orthogonal bars (collinear distractor). All columns were presented to one eye except for a randomly selected column that was presented to the other eye (ocular distractor). The target could be located on a distractor column (collinear congruent [CC]/ocular congruent [OC]) or not (collinear incongruent [CI]/ocular incongruent [OI]). We expected to find the best search performance for OC + CI targets and the worst search performance for OI + CC targets. The other combinations would depend on the relative strength of collinearity and ocular information in guiding attention. As expected, we observed collinear impairment, but surprisingly, we did not observe any search advantage for OC targets. Our subsequent experiments confirmed that OC search impairment also occurred when color-defined columns (Experiment 2), ocular singletons (Experiments 4 and 5), and noncollinear columns (Experiment 5) were used instead of collinear columns. However, the ocular effect disappeared when paired with luminance-defined columns (Experiments 3A and 3B). Although our results agree well with earlier findings that eye-of-origin information guides attention, they highlight that our previous understanding of search advantage by ocular singleton targets might have been oversimplified.

Introduction

We search in our everyday life; we look for friends in a crowd at a meet-up point, keys on an office desk, and the right kind of vegetables in a grocery store. How do we look for things efficiently in a complex visual scene? Searching deploys attention, both top-down, goal-orientated—by paying attention to relevant features of the items we are looking for—and bottom-up, stimulus-driven attention when our attention is automatically captured by salient items in the array. An item is considered more salient, and thus easier to search for, if it is unique in regard to at least one of its features, for instance, color (e.g., Harris, Becker, & Reminton, 2015; Theeuwes, 1994; Turatto & Galfano, 2000, 2001), orientation (e.g., Müller, Reimann, & Krummenacher, 2003; Nothdurft, 1993), or motion (e.g., Girelli & Luck, 1997; Nothdurft, 1993, 2002), similar to the situation in which we are looking for a red apple among green leaves. This is because our brain takes context into account when computing the bottom-up saliency map: It has been reported that at V1, an early stage in which we process visual information, iso-feature suppression happens such that homogeneous information is suppressed while a unique item in a homogeneous background pops out and gains priority compared to...
an unremarkable item in a homogeneous background or a unique item in a heterogeneous background (e.g., Jones, Grieve, Wang, & Sillito, 2001; Knierim & van Essen, 1992; Wachtler, Sejnowski, & Albright, 2003). Such unintentional capture brings search benefit to items that are either salient themselves or happen to be at a salient location and search impairment to items that are not salient or at a nonsalient location.

Our attention is not only captured by features that we are aware of (e.g., color, orientation, motion direction), but are also guided by information that we are not aware of. One example of such is eye-of-origin information. If different images are presented to our two eyes, and we are asked to report which eye origin information. If different images are presented to our two eyes, and we are asked to report which image is presented to our left or right eye, most likely we do not have any clue (Blake & Cormack, 1979; Enoch, Goldmann, & Sunga, 1969; Martens, Blake, Sloane, & Cormack, 1981; Ono & Barbeito, 1982; Steinbach, Howard, & Ono, 1985). It is also likely that we are unable to identify a target item defined by eye-of-origin information in a visual search task (Wolfe & Franzel, 1988; Zhaoping, 2008). As the information from both eyes converges in V1 (Burkhalter & van Essen, 1986; Hubel & Livingstone, 1987; Hubel & Wiesel, 1968; Zeki, 1978), the eye-of-origin information is not retained for further processing in areas that are higher up in the visual hierarchy and that feed into our conscious perception of the world. Despite being inaccessible to consciousness and top-down attention (e.g., Kimchi, Trainin, & Gopher, 1995), eye-of-origin feature plays a part in bottom-up saliency computation. Zhaoping (2008, 2012) reported a series of experiments in which participants were asked to search for a bar oriented differently from the rest of the distractor bars (an orientation singleton). Participants made fewer errors when the orientation singleton was an ocular singleton (presented to one eye while the rest of the distractor bars were presented to the other eye, dichoptic congruent condition) than when it was not presented to the other eye (dichoptic incongruent condition) or when all stimuli were present to one single eye (monocular baseline). This finding suggests that unique ocular information directs bottom-up attention and benefits visual search. Eye-movement analysis revealed that the ocular singleton captured gaze and thus slowed visual search in the dichoptic incongruent condition (Zhaoping, 2012). This enhanced bottom-up processing of an ocular item is assumed to contribute to iso-ocular suppression at V1: Activity in V1 is more readily suppressed by contextual input presented to the same eye than the other eye (DeAngelis, Freeman, & Ohzawa, 1994; Webb, Dhruv, Solomon, Taiby, & Lennie, 2005). An ocular singleton is thus less suppressed and prioritized during salience computation. Collinear grouping also guides bottom-up attention. Jingling and Tseng (2013) asked participants to search for a tilted bar and report its orientation among a homogenous display of horizontal bars except for one column containing vertical bars orthogonal to the rest of the display (orientation distractor). This collinear structure captures gaze (Jingling, Tang, & Tseng, 2013). However, such gaze capture does not merit search benefit: When the target was located on the salient orientation distractor, search time was longer and accuracy was lower than when the target was located at other columns. This search impairment is exclusive to a collinear (snake-like) but not a noncollinear (ladder-like) orientation distractor (Chow, Jingling, & Tseng, 2013; Jingling & Tseng, 2013). It is also exclusive to an orientation-defined distractor but not to a color-defined or luminance-defined distractor (Jingling, Tseng, & Zhaoping, 2013) and also to a long but not a short distractor (Chow et al., 2013; Jingling & Tseng, 2013). All these properties are consistent with neuronal properties (e.g., collinear facilitation) known to exist in V1. Chow et al. (2013) found that the collinear search impairment effect operates on monococular information, which is consistent with the finding that top-down strategies, such as learning, are unable to counteract the impairment (Tseng & Jingling, 2015) and that the impairment can be induced by collinear distractors that are rendered inaccessible to consciousness (Chow & Tseng, 2015). This collective evidence prompts the conclusion that collinear grouping operates in a bottom-up fashion possibly at V1.

The commonality between eye-of-origin and collinearity information in bottom-up saliency computation is that they are both monococular and automatic and do not require consciousness with an implied neural site at V1. These similarities suggest that these two features interact with each other during saliency computation. Previous research has addressed how interaction between two features might influence attention allocation. Neurophysiological studies found that conjunctive cells sensitive to combinations of features, for example, color + motion, exist in V1 (e.g., Horwitz & Albright, 2005; Hubel & Wiesel, 1959; Livingstone & Hubel, 1984; Spellmann, Dresp-Langley, & Tseng, 2015; Ts’o & Gilbert, 1988). Psychophysics also revealed an influence of conjunctive tuning of two features on search time (Koene & Zhaoping, 2007; Krummenacher, Müller, & Heller, 2002; Nothdurft, 2000). For example, Koene and Zhaoping (2007) asked participants to search for singletons that were different from distractors with two features (e.g., color + orientation) or one feature only (e.g., color or orientation). They compared participants’ search reaction times (RTs) for double-feature singletons (e.g., color + orientation) against the predicted RTs based on the sum of RTs for single-
feature singletons and found that search times for double-feature singletons were faster than the statistical prediction based on race model for color + orientation and motion + orientation but not color + motion. This suggests that some features are interacted in saliency analysis. However, little is known about whether and how eye-of-origin and collinearity features can interact with each other in V1 and whether such interaction influences the bottom-up saliency map.

To answer these questions, we designed a search paradigm in which a distractor column could be defined by eye of origin (i.e., one column presented to one eye while the other columns are presented to the other eye), collinearity (i.e., the one column is vertically oriented while the rest are horizontally oriented), or both. Search performance for targets located on these distractor columns (ocular congruent [OC] and/or collinear congruent [CC]) was compared against that for targets not located on the distractor singleton columns (ocular incongruent [OI] and/or collinear incongruent [CI]). From previous work, we know that ocular singletons help search whereas collinear singleton columns impair search. When two features were linearly additive, we expected to see best search performance for OC + CI and worst search performance for OI + CC. The other conditions would depend on the relative strength of eye-of-origin and collinearity features: If eye of origin helps more than collinearity impairments, we would expect to see better performance in OC + CC than OI + CI but the opposite if collinearity overrides the effect of eye of origin.

**Experiment 1: Eye of origin versus collinearity**

In this experiment, we quantified and compared the search facilitation/impairment effects by task-irrelevant eye-of-origin (ocularity) and collinearity features in a visual search task.

**Method**

**Participants**

Twenty-three students participated. Two additional participants were excluded because their overall accuracy rate was lower than 70%. All participants had normal or corrected-to-normal visual acuity and were naive about the purpose of the experiment. They signed a consent form and received course credit for participation.

**Stimuli and apparatus**

Participants were shown stimuli programmed by Matlab Psychtoolbox Version 3.0.8 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997) on a CRT monitor (ViewSonic, 21-in., 60 Hz) through a mirror stereoscope. The mirror stereoscope was designed to present each eye with half of the screen display. It was made of a black box, 60 cm deep, 50 cm high, and 55 cm wide with a black divider in the middle, four adjustable mirrors, and an adjustable chin rest. Two mirrors helped to present the image of each half of the screen to each eye while the divider ensured that each eye saw only one half of the screen. The viewing distance from the eye to the mirrors was 71.5 cm. Participants held a keyboard for response collection on their laps.

The stimulus screen was divided into a left and a right part, one for each eye. To promote fusion between the two eyes, we presented two quarters of a black and white circular frame that was 14° in diameter with a 9.06° × 9.06° gray square (7.2 cd/m²) inside to each eye (Figure 1A), such that participants would see a complete circular frame against a gray background only when fusion was complete. In addition to that, at the beginning of each trial, a fusion display that

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Figure 1. Two quarters each were presented to the left and right eyes to promote fusion (A). Additionally, a frame consisting of 9 × 9 “pluses” was presented within the circular frame to enhance fusion (B).
Results and discussion

Trials in which RT was 2 SD above the grand mean (M = 583 ms, SD = 314 ms; 1.91%), and incorrect trials (9.62%) were excluded from the analysis. RT and accuracy data were subjected to a 2 × 2 (target located on ocular distractor column [OC, OI] × target located on collinear distractor column [CC, CI]) repeated-measures ANOVA. Mean RTs for different conditions were plotted in Figure 2A (right panel). As expected from collinear impairment, it took more time to search for CC targets (M = 583 ms) than CI targets (M = 550 ms), \( F(1, 22) = 56.660, MSE = 0.025, p < 0.001 \). We also observed an unexpected impairment from the ocular singleton: It took longer to search for OC targets (M = 575 ms) than OI targets (M = 559 ms), \( F(1, 22) = 10.907, MSE = 0.006, p = 0.003 \). There was no significant interaction, \( F(1, 22) = 2.612, MSE = 0.001, p = 0.120 \).

The accuracy analysis was conducted to test for a possible speed–accuracy trade-off. CC targets (error rate M = 16.4%) were less accurately reported than CI (error rate M = 9.1%), \( F(1, 22) = 18.954, MSE = 0.123, p < 0.001 \). Similarly, OC targets (error rate M = 14.7%) were less accurately reported than OI targets (error rate M = 10.8%), \( F(1, 22) = 9.683, MSE = 0.035, p = 0.005 \). There was no significant interaction, \( F(1, 22) = 2.041, MSE = 0.167, p = 0.085 \). We did not find any evidence of a speed–accuracy trade-off.

These results suggest that there is an overall worsening of performance (i.e., increased error rate and lengthened RT) when a target overlaps with the collinear or ocular distractor. The impairment by the collinear distractor replicates previous research (Chow et al., 2013; Chow & Tseng, 2015; Jingling & Tseng, 2013; Jingling et al., 2013). However, the impairment by the ocular distractor is contrary to our prediction based on earlier findings by Zhaoping (2008). To further understand the effect of the ocular distractor and whether it applies to other visual features known to influence the allocation of attention during our search task, we replaced the collinear distractor with distractors defined by color contrast (Experiment 2) and by luminance contrast (Experiment 3A).

### Experiment 2: Eye of origin versus color

In this experiment, we contrasted the effects of an ocular distractor with a color distracter on search performance.

### Method

#### Participants

Twenty students who did not participate in Experiment 1 participated in this experiment. Four additional participants were excluded because their overall accuracy rate was lower than 70%. All participants had normal or corrected-to-normal...
visual acuity and gave written consent to participate in this experiment.

**Stimuli, apparatus, and procedure**

All stimuli, apparatus, and procedure were the same as in Experiment 1 except that, instead of presenting 9 × 9 horizontal white bars on either side of the search display, there were 9 × 9 vertical green bars (22.7 cd/m²). Also, instead of having one column of bars oriented orthogonally to the others, one column was in red (22.4 cd/m²) and defined as the *color* distractor (color congruent [CoC], color incongruent [CoI]; Figure 2B). A black background was used to enhance

Figure 2. Stimuli and results of (A) Experiment 1 (eye of origin vs. collinearity), (B) Experiment 2 (eye of origin vs. color), (C) Experiment 3A, and (D) Experiment 3B (eye of origin vs. luminance). Error bars indicate the standard error of mean (SEM). **p < 0.01, ***p < 0.001.
Results and discussion

Trials in which the RT was 2 SD above the grand mean ($M = 529$ ms, $SD = 829$ ms; 2.8%) and incorrect trials (13.1%) were excluded from the analysis. Subsequent RT data and accuracy data were subjected to a $2 \times 2$ (target located on ocular distractor column [OC, OI] $\times$ target located on color distractor column [CoC, CoI]) repeated-measures ANOVA. Mean RTs for different conditions were plotted in Figure 2B (right panel). Again, OC targets required a longer search time ($M = 647$ ms) than OI targets ($M = 621$ ms), $F(1, 19) = 16.332$, $MSE = 0.014$, $p = 0.001$. The main effect of target overlapping with color distractor is insignificant, $F(1, 19) = 0.445$, $MSE = 0.001$, $p = 0.513$; so is the interaction effect, $F(1, 19) = 1.131$, $MSE < 0.001$, $p = 0.301$.

The accuracy analysis showed that participants also made more errors with OC targets ($M = 17.3\%$) than OI targets ($M = 12.5\%$), $F(1, 19) = 14.239$, $MSE = 0.044$, $p = 0.001$. There was no difference between accuracy of overlapping targets and nonoverlapping targets with color as a distractor, $F(1, 19) = 0.102$, $MSE < 0.001$, $p = 0.753$. The interaction was not significant, $F(1, 19) = 0.285$, $MSE = 0.001$, $p = 0.600$. We did not find evidence of a speed–accuracy trade-off.

There is an overall worsening of performance (i.e., reduced accuracy and lengthened RT) when the target is located on an ocular singleton distractor column but not a color distractor column. We replicated the impairment by the ocular singleton column in Experiment 1. The null effect from the color distractor is consistent with previous research showing that a color-defined collinear structure did not enhance or reduce target search in a binocular display (Jingling et al., 2013).

Experiment 3A: Eye of origin versus luminance

In this experiment, we contrasted the effects of an ocular distractor column with a luminance distractor column on search performance.

Method

Participants

The same 24 participants from Experiment 2 served as observers in this experiment. Four were excluded because their overall accuracy rate was lower than 70%, yielding a final sample of 20 participants. They had normal or corrected-to-normal visual acuity and gave written consent to participate in this experiment.

Stimuli, apparatus, and procedure

All stimuli, apparatus, and procedure were the same as in Experiment 1 except that, instead of having $9 \times 9$ white horizontal bars in the search display, $9 \times 9$ dark gray vertical bars ($14.5$ cd/m$^2$) were placed against a gray background ($7.2$ cd/m$^2$; Figure 2C). Among those nine columns, one column of vertical bars was in white ($28.2$ cd/m$^2$), which yielded the highest luminance; it was defined as the luminance distractor (luminance congruent [LC], luminance incongruent [LI]).

Results and discussion

Trials in which RT was 2 SD above the grand mean ($M = 601$ ms, $SD = 411$ ms; 1.36%) and incorrect trials (14.7%) were excluded from RT analysis. Subsequent RT data and accuracy data were respectively submitted to a $2 \times 2$ (target located on ocular distractor column [OC, OI] $\times$ target located on luminance distractor column [LC, LI]) repeated-measures ANOVA. Mean RTs for different conditions were plotted in Figure 2C (right panel). A luminance-defined column, although task-irrelevant, helped target search: It was easier to search for LC targets ($M = 574$ ms) than LI targets ($M = 574$ ms), $F(1, 19) = 29.779$, $MSE = 0.016$, $p < 0.001$. OC targets ($M = 563$ ms), surprisingly, did not differ from OI targets ($M = 557$ ms), $F(1, 19) = 1.579$, $MSE = 0.001$, $p = 0.224$. There was no significant interaction, $F(1, 19) = 0.123$, $MSE < 0.001$, $p = 0.730$.

Participants made fewer errors with LC targets ($M = 8.3\%$) than LI targets ($M = 14.7\%$), $F(1, 19) = 49.454$, $MSE = 0.082$, $p < 0.001$. Error rate of targets overlapping with the ocular distractor did not differ from that of nonoverlapping targets, $F(1, 19) = 2.095$, $MSE = 0.002$, $p = 0.164$. There was no interaction, $F(1, 19) = 0.887$, $MSE = 0.001$, $p = 0.358$. We did not find evidence for a speed–accuracy trade-off.

This suggests that there is a facilitation effect (i.e., improved accuracy and shortened RT) when the target is overlapping with a luminance distractor, consistent with previous literature showing that a luminance-defined collinear structure facilitates target search in a binocular display (Jingling et al., 2013). Interestingly, the impairment effect by ocular distractor disappeared. We found that the RT in Experiment 3A was much shorter than in Experiments 1 and 2. Conceivably, this is a ceiling effect, which might mask the ocularity effect. To test this hypothesis, we conducted an additional experiment to address this concern.
Experiment 3B: Eye of origin versus luminance (four levels)

The absence of ocular impairment in Experiment 3A prompted us to conduct a further examination by manipulating the luminance contrast of the search display to increase its task difficulty. We varied the luminance contrast between the distractor and background bars to provide a total of four contrast levels.

Method

Participants

A separate group of 25 participants served as observers in this experiment. Nine participants were excluded because their overall accuracy rate was lower than 70%. They had normal or corrected-to-normal visual acuity and gave written consent to participate in this experiment.

Stimuli, apparatus, and procedure

All stimuli, apparatus, and procedure were the same as in Experiment 3A except that the luminance distractor had one of the following four brightness levels: 0.4 (15.7 cd/m²), 0.6 (20.6 cd/m²), 0.8 (22.3 cd/m²), or 1 (24.7 cd/m²) against a gray background (7.2 cd/m²) while background bars were fixed at 0.3 (14.5 cd/m²) same as before (Figure 2D). The contrast between the luminance-defined distractor and other bars allowed us to manipulate the relative difficulty: The lowest luminance contrast had the least salience and was thus most difficult to capture attention. The number of trials was quadrupled compared to that in Experiment 3A.

Results and discussion

Trials in which RT was $2\, SD$ above the grand mean of this experiment ($M = 656$ ms, $SD = 450$ ms; 2.02%) and incorrect trials (12.3%) were excluded from RT analysis. Subsequent RT data and accuracy data were submitted to a $2 \times 2 \times 4$ within-subject factor (target located on the ocular distractor column [OC, OI] × target located on the luminance distractor column [LC, LI] × brightness level [0.4, 0.6, 0.8, 1]) repeated-measures ANOVA.

We confirmed the luminance facilitative effect. Participants searched for LC targets ($M = 589$ ms) more quickly than LI targets ($M = 622$ ms), $F(1, 15) = 31.023$, $MSE = 0.069$, $p < 0.001$. Search time for OC targets ($M = 610$ ms) was not different from that of OI targets ($M = 601$ ms), $F(1, 15) = 3.141$, $MSE = 0.005$, $p = 0.097$ (Figure 2D, right panel). There was no significant interaction between ocularity and luminance, $F(1, 15) = 0.53$, $MSE < 0.001$, $p = 0.821$. There was a significant interaction between luminance and contrast levels, $F(3, 45) = 5.353$, $MSE = 0.008$, $p = 0.003$. Post hoc analysis revealed that the difference between LC and LI was significant at brightness levels of 0.6, 0.8, and 1 (Holm-adjusted $ps < 0.008$) but not significant when the contrast was the lowest (Holm-adjusted $p = 0.847$). The interaction between ocularity and contrast levels was not significant, $F(3, 45) = 1.202$, $MSE = 0.002$, $p = 0.320$. Planned post hoc analysis did not find a difference between OC and OI targets for any contrast level (Holm-adjusted $ps > 0.180$).

Participants made fewer errors with LC targets ($M = 8.8\%$) than LI targets ($M = 13.8\%$), $F(1, 15) = 11.872$, $MSE = 0.163$, $p = 0.004$. No difference in error rates was found between OC and OI targets, $F(1, 15) = 2.096$, $MSE = 0.010$, $p = 0.168$. There was no interaction between ocularity and luminance, $F(1, 15) = 0.065$, $MSE < 0.001$, $p = 0.802$, nor between luminance and contrast levels, $F(3, 45) = 1.066$, $MSE = 0.004$, $p = 0.373$, nor between ocularity and contrast levels, $F(3, 45) = 0.704$, $MSE = 0.001$, $p = 0.555$. We did not find evidence for a speed–accuracy trade-off.

The current experiment confirmed the findings of luminance facilitation and null effect of ocular distractor in Experiment 3A despite its being controlled for level of difficulty, such that the general RT matched more closely with that of other experiments.

Experiment 4: Contrasting ocular singleton and ocular column in vertical displays

Our consistent observation of ocular disadvantage is intriguing when it is compared to the ocular advantage reported by Zhaoping (2008, 2012). There are several possible differences between the two series of studies that can account for the difference between search effects. First, ocular length differed. Our ocular distractor in Experiments 1, 2, 3A, and 3B was a column of bars whereas in Zhaoping (2008, 2012) the ocular distractor was one bar (a singleton) presented to one eye while the rest of the background bars were presented to the other eye. Second, the orientation of the bars differed. Our display was composed of vertical bars, and the display of Zhaoping (2008, 2012) was either composed of horizontal bars or horizontal bars tilted $\pm 20^\circ$–25°. In the next two experiments, we examined whether these two possibilities might account for the differences found. In Experiment 4, we introduced an ocular singleton (one item presented to
one eye, similar to that in Zhaoping, 2008, 2012) and contrasted the effect with an ocular column (a column of items presented to one eye). In Experiment 5, we introduced horizontal display to examine the orientation effect. Additionally, we also introduced a monocular and binocular baseline to help us disentangle whether the impairment in ocular search was rooted at OC impairment or OI facilitation compared to the baseline or both.

Method

Participants

Fifteen participants served as observers in this experiment. No participants were excluded because of an overall accuracy rate lower than 70%. They had normal or corrected-to-normal vision and gave consent to participate in this experiment.

Stimuli, apparatus, and procedure

All stimuli, apparatus, and procedure were the same as in Experiment 1 except that the display consisted of vertical bars without any horizontal bars and there were no distractors defined by collinearity, color, or luminance (Figure 3A). In half of the trials, the entire display was presented either to one eye (monocular baseline [MB]) or to both eyes (binocular baseline [BB]) in a random order, which gave us a baseline of search accuracy and RT for a target placed in a homogenous display without any ocular component. In the other half of the trials, one center item (ocular length 1) or one entire column (ocular length 9) from one of the five possible columns was presented randomly to one eye while the rest were presented to the other. In all trials, the target appeared randomly in one of the five possible locations, such that in 20% of the dichoptic trials the target was overlapping with the ocular distractor singleton/column (OC), and in 80%, the target was nonoverlapping with the ocular distractor singleton/column (OI).

Results and discussion

Trials in which RT was 2 SD above the grand mean of this experiment ($M = 529$ ms, $SD = 203$ ms; 2.37%) and incorrect trials (3.72%) were excluded from analysis. Subsequent mean RT and error rate data were plotted in Figure 3C. The mean RT and error rate for the MB condition was 508 ms ($SD = 48$ ms) and 4.2% ($SE = 2.7$%), and that for the BB condition was 500 ms ($SD = 45$ ms) and 2.3% ($SE = 1.9$%). RT data and accuracy data of the dichoptic trials were respectively subjected to a $2 \times 2$ (target located on ocular distractor column [OC, OI] × ocular distractor length [1, 9]) repeated-measures ANOVA. The RT of OC targets (531 ms) was significantly longer than that of OI targets (511 ms), $F(1, 14) = 14.802$, $MSE = 0.006$,
p = 0.002. This was not due to a speed–accuracy trade-off as the error rate of OC targets (7.6%) was also significantly higher than that of OI targets (3.3%), F(1, 14) = 15.378, MSE = 0.027, p = 0.002. The effect of ocular distractor length on RT was not significant, F(1, 14) = 3.698, MSE = 0.001, p = 0.075, nor was the interaction between ocularity and distractor length, F(1, 14) = 2.877, MSE = 0.001, p = 0.112. The effect of ocular distractor length on error rate was significant, F(1, 14) = 5.14, MSE = 0.006, p = 0.04, suggesting that the error rate with length 1 (6.5%) was higher than that of length 9 (4.5%). However, the interaction between ocularity and distractor length on error rate was not significant, F(1, 14) = 0.356, MSE = 0.001, p = 0.56.

We also collapsed data across ocular distractor length and checked whether RT and error rate were different between conditions using repeated-measures, one-way ANOVA of a factor (MB, BB, OC, OI). The effect of condition on RT was significant, F(3, 42) = 23.781, MSE = 0.002, p < 0.001. Post hoc analysis revealed that regardless of distractor length, OC targets (M = 530 ms) took significantly longer to search than OI targets in the dichoptic display (M = 511 ms; Bonferroni-adjusted p = 0.011). This impairment effect comes from the impairment of OC targets as RT was significantly longer than that of MB (M = 508 ms; Bonferroni-adjusted p < 0.001) and that of BB (M = 500 ms; Bonferroni-adjusted p < 0.001), and RT of OI targets was not significantly faster than MB (Bonferroni-adjusted p = 1.000); instead, it was significantly slower than BB (Bonferroni-adjusted p = 0.004). RT of BB was marginally faster than MB (Bonferroni-adjusted p = 0.058).

There was also a significant difference between the four conditions in terms of error rate, F(3, 42) = 11.609, MSE = 0.008, p < 0.001. Regardless of distractor length, participants made more errors with OC targets (M = 7.6%) than OI targets (M = 3.3%; Bonferroni-adjusted p = 0.009), which is similar to that for RT. This effect is likely caused by the impairment due to OC targets compared to BB (M = 2.3%; Bonferroni-adjusted p = 0.003) but not with MB (M = 4.2%; Bonferroni-adjusted p = 0.091) and not facilitation by OI targets compared to MB or BB (Bonferroni-adjusted ps > 0.4). Error rates of MB and BB conditions were not different (Bonferroni-adjusted p = 0.094).

The ocular search impairment appeared across distractor lengths, so our findings rejected this factor as the main reason to account for the difference between our results and those of Zhaoping (2008, 2012). The other possible reason is the difference in orientation of the search displays. In the next experiment, we compared the search effects across ocular distractor lengths in horizontal displays, similar to those used in experiment 1 by Zhaoping (2008).

### Experiment 5: Contrasting ocular singleton and ocular column in a horizontal display

In this experiment, we examined whether ocular singleton and ocular column differ in their effect on search in horizontal displays.

**Method**

**Participants**

A separate group of 16 participants served in this experiment. Five additional participants were excluded because their overall accuracy rate was lower than 70%. They had normal or corrected-to-normal vision and gave consent to participate in this experiment.

**Stimuli, apparatus, and procedure**

Our stimuli, apparatus, and procedure were identical to previous experiments except that there was only a singleton distractor defined by eye of origin: one (distractor length = 1) or a column of horizontal bars (distractor length = 9) was presented to the other side of the display (the ocular distractor) while in the other half of the trials the entire display was presented to one eye only (MB). The ocular distractor columns were independently located at a distance of –3, –1, 0, +1, and +3 columns from the center. The target was gap (0.16") tilted 45° clockwise or counterclockwise from vertical placed on an element bar. Its location was at the middle row of –3, –1, 0, +1, or +3 columns from the center, such that target location could fall onto one of the following locations: OC or OI (Figure 3B).

**Results and discussion**

Trials in which RT was 2 SD above the grand mean of this experiment (M = 847 ms, SD = 140 ms; 2.6%) and incorrect trials (10.5%) were excluded from RT analysis. Subsequent mean RT and error rate data were plotted in Figure 3D. The mean RT and error rate for the MB condition was 669 ms (SD = 69 ms) and 9.1% (SD = 4.7%). RT data and error rate of dichoptic trials were subjected to a 2 × 2 (target located on the ocular distractor column [OC, OI] × ocular distractor length [1, 9]) repeated-measures ANOVA. The search for OC targets took longer (725 ms) than for OI targets (684 ms), F(1, 15) = 15.236, MSE = 0.027, p = 0.001. This was not due to a speed–accuracy trade-off as the error rate of OC targets (14.4%) was also significantly higher than that of OI targets (10.7%), F(1, 15) = 5.103, MSE = 0.022, p =
There was no significant effect of distractor length, $F(1, 15) = 1.609, \text{MSE} = 0.009, p = 0.224$, nor any interaction, $F(1, 15) = 1.305, \text{MSE} = 0.005, p = 0.271$. Similarly, the effect of ocular distractor length on error rate was not significant, $F(1, 15) = 0.475, \text{MSE} = 0.002, p = 0.475$, nor was the interaction, $F(1, 15) = 0.203, \text{MSE} = 0.001, p = 0.658$.

The data were therefore collapsed across ocular distractor length and reanalyzed with a repeated-measures, one-way ANOVA with two levels (MB, overlap with ocular, nonoverlap with ocular). There was a significant main effect of condition, $F(2, 30) = 10.1, \text{MSE} = 0.013, p < 0.001$. Post hoc analysis revealed that regardless of distractor length, OC targets ($M = 725$ ms) took significantly longer to search than OI targets in the dichoptic display ($M = 684$ ms; Bonferroni-adjusted $p = 0.004$). This impairment effect comes mainly from the impairment of overlapping targets as RT was significantly longer than that of MB ($M = 669$ ms; Bonferroni-adjusted $p = 0.009$), and RT of nonoverlapping targets was not significantly faster than MB, $p = 0.665$.

There was also a significant difference between the three conditions in terms of error rate, $F(2, 30) = 3.993, \text{MSE} = 0.007, p = 0.029$. However, post hoc analysis with Bonferroni adjustment revealed no significant differences between conditions.

We consistently found, from RT and error rate, that an ocular singleton (length = 1) and column (length = 9) impaired observers’ performance in searching for a target in horizontal displays. Our results suggest that search display orientation and number of ocular items did not account for the difference in search effects found in our experiments and in Zhaoping (2008, 2012).

To compare the effect by eye-of-origin feature across experiments, normalization of the search effect is necessary. We computed a search impairment index related to eye-of-origin singleton column (SIocular $[i, j]$), which was the ratio of RT difference between OC and OI targets for each observer $i$ to the mean RT of the experiment $j$ for each distractor condition (Equations 1 and 2). A zero SIocular means that there is no effect. A positive SI reflects search impairment, and a negative SI reflects search facilitation when the target overlaps with the distractor defined by that feature. The more positive or negative the SI index, the larger the effect.

$$SI_{\text{ocular}}(i, j) = \frac{RT_{\text{OC}}(i, j) - RT_{\text{OI}}(i, j)}{RT(i, j)}$$  

(1)

$$\overline{SI}_{\text{ocular}}(i, j) = \frac{\sum_{i=1}^{n} SI_{\text{ocular}}(i, j)}{n}$$  

(2)

Search impairment indices of Experiments 1, 2, 3A, and 3B are plotted in Figure 4A. The SIocular index was subjected to a one-way ANOVA with experiment (Experiment 1, 2, 3A, or 3B) as a between-subjects factor. The effect from experi-
ment was significant, $F(3, 60) = 4.917, MSE = 0.005, p = 0.004$, suggesting the search effect of eye of origin is different in at least two experiments. A post hoc analysis was performed to understand which groups were different. The SI_{ocular} of Experiment 2 (eye of origin vs. color; $M = 4.65\%$) was significantly higher than that of Experiment 3A (eye of origin vs. collinearity; $M = 1.17\%$; Bonferroni-adjusted $p = 0.014$), that of Experiment 3B ($M = 1.38\%$; Bonferroni-adjusted $p = 0.021$), and that of Experiment 1 ($M = 1.92\%$; Bonferroni-adjusted $p = 0.026$). The effect between other experiments was not significantly different (Bonferroni-adjusted $p = 1.000$).

To understand whether the search effect by eye-of-origin information was modulated by distractor length (Experiment 4) and display orientation (Experiment 5), we subjected the search impairment indices of SI_{ocular} for each condition to a $2 \times 2$ ANOVA (1 between-subjects factor: orientation [vertical, horizontal] $\times$ 1 within-subject factor: ocular distractor length [1, 9]). We found no significant effect of distractor length, $F(1, 29) = 0.160, MSE = 0.019, p = 0.160$, or experiment, $F(1, 29) = 1.592, MSE = 0.008, p = 0.217$, nor interaction, $F(1, 29) = 0.103, MSE = 0.001, p = 0.751$.

A similar computation was also performed for the search effect of luminance contrast, thus allowing comparison of the search facilitation by luminance across Experiments 3A and 3B (Equations 3 and 4):

$$SI_{\text{luminance}}(i,j) = \frac{RT_{\text{LC}}(i,j) - RT_{\text{Ll}}(i,j)}{RT(i,j)}$$

$$\overline{SI}_{\text{luminance}}(i,j) = \frac{\sum_{i=1}^{n} SI_{\text{luminance}}(i,j)}{n}$$

The SI_{luminance} index was submitted to an independent samples $t$ test (Experiments 3A, 3B; Figure 4B). There was no significant difference between the luminance facilitation of Experiment 3A ($M = -4.96\%$), 3B ($M = -5.42\%$), $t(30) = 0.152, p = 0.880$.

One might speculate about the possible interaction between different features. For instance, was the ocular impairment more robustly found when the paired feature (e.g., color, collinearity) was weak in influencing attentional allocation? If this is the case, ocular impairment or facilitation is a result of competition between visual feature strengths, and we would expect to see the SI index of ocularity and other visual features (e.g., collinearity, color, luminance) to be negatively correlated. We made such calculation and found that, across experiments, SI of ocularity feature is positively, albeit weakly, correlated with SI of the other feature (collinearity, color, luminance), $r(64) = .253, p = 0.044$ (Figure 5). This positive correlation does not support the hypothesis that ocular impairment is found only when the paired feature is weak.

Another distinct difference in search effects between our study and Zhaoping (2008, 2012) is the eccentricity of targets. Our experiment contained targets at central and peripheral vision ($-3.12^\circ$, $-1.04^\circ$, $0^\circ$, $1.04^\circ$, $+3.12^\circ$ columns from the center) compared to targets of at least $12^\circ$ (Zhaoping, 2008) or $9^\circ$ (Zhaoping, 2012) from center in previous studies. We examine the eccentricity effect on ocularity below. If the strength of ocular facilitation (e.g., Zhaoping, 2008, 2012) is modulated by eccentricity of the target, i.e., limited to eccentric but not central targets, we would see an interaction between the search effect and the position of the target.

For each experiment, RT data and error rate were subjected to a $2 \times 5$ (target located on the ocular distractor column [OC, OI] $\times$ target eccentricity [$-3$, $-1$, 0, $+1$, $+3$]) repeated-measures ANOVA. Across all six experiments, there was no significant interaction between the target being located on the ocular distractor column and target eccentricities on RT, $ps > 0.102$, or on error rate, $ps > 0.125$ (Figure 6) except a marginally significant interaction on error rate in Experiment 2, $F(4, 76) = 2.303, MSE = 0.007, p = 0.066$, with which error rate was higher in OC than OI targets when the target was eccentric ($-3$, $-1$, $+3$ from the center; Holm-adjusted $p < 0.05$) but not when the target was at or close to the center (0, $+1$; Holm-adjusted $ps > 0.122$). This suggests that, in most cases, the search impairment by ocular distractor was consistent across eccentricities. Even in the situation in which ocular search impairment marginally changed depending on how eccentric the target was (Experiment 2), search was impaired at eccentric locations, different

![Figure 5. The relationship between search impairment (SI) index of ocularity and SI of the other paired feature (collinearity, color, or luminance) across experiments.](image-url)
Figure 6. Search time (ms) (A) and accuracy (B) of OC and OI targets across eccentricities and experiments. The error bars’ target eccentricity of zero means that the target was located on the center column; a positive value means that the target was located to the right of the center column, and a negative value means that the target was located to the left of the center column. The difference in search time and accuracy of OC and OI targets did not depend on target eccentricity. Error bars indicate the standard error of mean (SEM).
from the results for eccentric targets by Zhaoping (2008, 2012). However, it should be noted that our most eccentric target (3.12°) was still less than the ones in Zhaoping (2008, 2012) (9° or 12°). It remains possible that a minimum distance of target from center ("eccentricity threshold") is required for the ocular effect to switch.

**General discussion**

Our research started out by seeking answers to how features such as eye of origin and collinearity interact with each other and contribute to bottom-up salience computation through visual search. Unexpectedly, we found an impairment of search performance when the target was located on a distractor column defined by its unique eye of origin. This ocular search impairment was found consistently across experiments regardless of whether eye-of-origin information was paired with collinearity (Experiment 1) or color (Experiment 2), whether the ocular distractor was a one-item singleton item or a nine-bar singleton column (Experiments 4 and 5), whether the search display was vertical (Experiments 1, 2, and 4) or horizontal (Experiment 5), or whether the target was more or less eccentric (see Target eccentricity analysis). Only when the eye-of-origin information was paired with luminance in Experiments 3A and 3B did we not find any ocular search impairment.

**Role of eye-of-origin feature in bottom-up saliency map**

Our findings that eye-of-origin feature is being taken into consideration during salience computation are consistent with those of Zhaoping (2008, 2012). As eye-of-origin information is not retained after V1 in the visual processing hierarchy, our findings support the "V1 hypothesis" postulated by Zhaoping (Li, 2002; Zhaoping, 2005): Bottom-up salience computation occurs at or before V1.

Previous research reported interactions between color and orientation (Koene & Zhaoping, 2007; Krummenacher et al., 2002; Nothdurft, 2000; Töllner, Zehetlsteiner, Krummenacher, & Müller, 2011; Zehetlsteiner, Krummenacher, & Müller, 2009; Zhaoping & May, 2007; Zhaoping & Zhe, 2012) as well as motion and orientation (Koene & Zhaoping, 2007; Nothdurft, 2000). This cannot be fully accounted for by assuming independent processing of each feature. Our study is, to our best knowledge, the first direct examination of the interaction between eye-of-origin contrast and collinearity contour. We found significant main effect but no interaction between the two features on search performance, suggesting that these two prominent features are processed in V1 and are linearly additive. This is in contrast to previous findings, implying that the combination of eye-of-origin contrast and other features might operate in different mechanisms from those of other features.

Despite the consistent implication, the direction of our results (impairment) is different from the facilitatory findings by ocular singletons reported by Zhaoping (2008, 2012). Whereas we have rejected the difference in ocular distractor length, search display orientation, and target eccentricity as factors that could account for the observed differences between studies through our control experiments and analyses, other factors could have contributed to the difference in results. For example, the target used by Zhaoping (2008, 2012) was a tilted bar whereas our target was a small gap in a bar. In the experiments by Zhaoping (2008, 2012) OC targets occurred one third of the time with equal likelihood for OI and monocular targets, and our OC targets only occurred one fifth of the time, appearing less frequently than OI targets. Zhaoping (2008, 2012) used a mask after the 200-ms presentation of search display, and we did not. Zhaoping (2008, 2012) had dots and disks presented to both eyes during the search display presentation for better vergence, and we used crosses presented to both eyes before the search display presentation and a partial ring for binocular fusion during the search display presentation. These are all potential factors to explain the difference in results between the two studies. However, if one or more are critical factors for the search impairment, we should have seen a similar ocular impairment in Experiments 3A and 3B in which these same factors were present. Our Experiments 3A and 3B did not yield ocular search impairment. From this, we speculated that these factors might not be critical for ocular impairment, but further research is needed to reject the aforementioned factors as contributing to ocular impairment.

**Why did ocular singletons not affect search when paired with luminance?**

In an attempt to explain ocular impairment and the lack of ocular impairment when the eye-of-origin feature was paired with luminance contrast, we looked for factor(s) that might have interacted with luminance in a different way than with collinearity or color. Zhaoping (2012) reported an interesting observation, namely, that an eye-of-origin singleton item appeared to contain higher contrast than other items when they were physically identical. Such illusion was much reduced when the luminance of the background bars...
was not uniform. It is unknown whether this illusion from ocular singletons extends to ocular distractor columns. However, if so, the ocular distractor column might appear to have a bigger contrast in our experiments with search displays with uniform luminance (Experiments 1, 2, 4, and 5) and reduced contrast with a nonuniform luminance (Experiments 3A and 3B). As it was not reported in Zhaoping (2012) whether the brightness of ocular singletons was brighter or dimmer than the rest of the search display and whether the direction of effect was consistent across participants, there are some possible consequences. For example, if the ocular distractor column appears brighter than the rest of the search display, it might serve as a salient distractor by luminance contrast (Jingling et al., 2013; Rauschenberger, 2003; Turatto & Galfano, 2000) and facilitate search for OC targets and impair search for OI targets. This possibility is rejected as we never found ocular facilitation in our experiments. If it appears dimmer than the rest of the search display, it is likely to be viewed as a background, which usually receives less attention (Mazza, Turatto, & Umiltà, 2005). If this is the case, performance on OC targets should be worse than on OI targets, consistent with our results. In experiments in which the search display has heterogeneous luminance, such illusion is reduced or removed, which might be why we did not find ocular impairment in Experiments 3A and 3B.

It has been suggested that there are independent processing channels that sum and subtract information across the two eyes (e.g., Cohn & Lasley, 1976; Li & Atick, 1994; May, Zhaoping, & Hibbard, 2012; Yoonessi & Kingdom, 2009), which helps to ensure reduced information redundancy and enhanced efficiency of information transmission. For example, binocular summation is found to be enhanced by adaptation to images that are contrast reversed between two eyes and reduced by adaptation to images that are identical for the two eyes (May et al., 2012). This suggests that the summation and differencing channels can be independently manipulated. Binocular summation is also enhanced when the stimulus has low visual contrast (e.g., Bearse & Freeman, 1994; Moradi & Heeger, 2009; Pardhan, 2003). In our Experiments 3A and 3B, the overall search display had low contrast, which might have promoted binocular summation as opposed to binocular differencing in comparison to other experiments in which the contrast of the search display was high. When the search display from two eyes is summed, the information about the ocular singleton distractor is lost, which might explain why we found a lack of search effect by the ocular distractor in Experiments 3A and 3B. The placement of the target in the dominant eye or not may also interplay with the results. In the current study, we did not take measurement of this factor, and it could be further examined in future study.

Why did ocular singletons impair but not facilitate search?

Ocular information might create a foreground object similar to perceptual grouping of similar features, such as (illusory) luminance contrast and/or eye-of-origin information (Tan & Hsieh, 2013). For example, Tan and Hsieh (2013) used an ambiguous apparent motion display that could lead to the perception of horizontal or vertical motion and presented different parts of the motion quartet to each eye. They found that observers' reports of motion direction were biased depending on which parts were presented to the two eyes: Subjects were more likely to see horizontal motion when the top and bottom halves were presented to different eyes and vertical motions when the left and right halves were presented to different eyes. This suggests that observers preferentially grouped information from the same eye for motion direction perception. Such objecthood formation from perceptual grouping could induce perceptual filling in, the interpolation of background texture to target gap (Spillmann & de Weerd, 2003; Zhaoping & Jingling, 2008), or attention to the global shape as opposed to local elements (Navon, 1977, 2003), which makes local target identification more difficult and impairs task performance (e.g., Yantis & Nakama, 1998; Zhaoping & Jingling, 2008). A similar mechanism was also hypothesized to account for the collinear impairment as a collinear distractor column forms a stronger connection than a noncollinear distractor. This perceptual grouping hypothesis is also a potential answer to why we observed ocular impairment, but Zhaoping (2008, 2012) reported ocular facilitation. Our small gap target might integrate better to the global orientation of the whole column, thus enhancing perceptual grouping more by similarity of orientation than the tilted bar target in Zhaoping (2008, 2012). If this is the case, it suggests that target appearance might modulate the ocular search effect through a perceptual grouping mechanism. It is important to note that such an objecthood formation mechanism might be unique to collinearity, eye of origin, and/or illusory luminance as impairment was not found when the distractor was defined by color or luminance.

Conclusion

As eye of origin is not accessible to consciousness, it has been a much-neglected field of research, and little is known about what it does to attention allocation.
compared to what we know about other features (such as orientation, color, and luminance). Our findings add to the previous research, suggesting that eye-of-origin information may affect attentional allocation and perhaps perceptual grouping. This calls for more research to understand the role of eye of origin on attention allocation to clarify, for example, when the eye of origin produces facilitation or impairment in visual search; to understand whether it is limited to bottom-up processes or whether it participates in top-down mechanisms, such as priming and probability; and, finally, whether it plays a role in other types of attention mechanisms, such as feature- and object-based attention.

**Keywords:** visual search, eye of origin, collinearity, V1

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