Attention relieves visual crowding: Dissociable effects of peripheral and central cues

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Visual crowding can be reduced when attention is directed to the target by peripheral cues. However, it is unclear whether central cues relieve visual crowding to the same extent as peripheral cues. In this study, we combined the Posner cueing task and the crowding task to investigate the effect of exogenous and endogenous attention on crowding. In Experiment 1, five different stimulus-onset asychronies (SOAs) between the cue and the target and a predictive validity of 100% were adopted. Both attentional cues were shown to significantly reduce the effect of visual crowding, but the peripheral cue was more effective than the central cue. Furthermore, peripheral cues started to relieve visual crowding at the shortest SOA (100 ms), whereas central cues worked only at later SOAs (275 ms or above). When the predictive validity of the cue was decreased to 70% in Experiment 2, similar results to Experiment 1 were found, but the valid cue was less effective in reducing crowding than that in Experiment 1. In Experiment 3, when the predictive validity was decreased to 50%, a valid peripheral cue improved performance but a valid central cue did not, suggesting that endogenous attention but not exogenous attention can be voluntarily controlled when the cues are not predictive of the target's location. These findings collectively suggest that both peripheral and central cues can alleviate crowding, but they differ in terms of strength, time dynamics, and flexibility of voluntary control.

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Introduction

You have probably had the following experience: you want to open an App on your smartphone but notice that you cannot find it quickly, or you accidentally click on a wrong one. This is largely caused by visual crowding, a phenomenon that refers to the detrimental effect of nearby items (in this case, other Apps) on target identification (Bouma, 1970). The phenomenon of crowding is ubiquitous, which occurs not only between low-level features (e.g., Levi & Carney, 2009), but also between complex objects (e.g., Farzin, Rivera, & Whitney, 2009). Crowding is thought to be the primary limiting factor for reading speed (e.g., Pelli et al., 2007) and a fundamental limit on object recognition in the visual periphery (Levi, 2008; Whitney & Levi, 2011). Reducing crowding therefore can be extremely beneficial.

One way to reduce crowding is by means of enhancing attentional resolution. According to the attentional resolution model (He, Intriligator, & Cavanagh, 1996; Intriligator & Cavanagh, 2001), visual crowding is caused by the low resolution of spatial attention, which restricts target representation to conscious awareness, at a stage beyond the primary visual cortex. He et al. (1996) provided several pieces of evidence to support this model. For instance, they showed that the target had been processed by the

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primary visual cortex when crowding occurs. They also discovered that crowding, like attentional resolution, was stronger in the upper than the lower visual field, despite that V1 devoted approximately the same amount of area to representing the upper and lower visual fields. Therefore crowding sets a bottleneck in the late visual cortex, preventing the target from being identified. The attentional resolution model suggests that attention plays a crucial role in visual crowding, which has been supported by a growing body of empirical evidence (e.g., TKacz-Domb & Yeshurun, 2017).

First, pre-cueing attention to the target's location largely diminishes crowding (Freeman & Pelli, 2007; Kewan-Khalayly, Migó, & Yashar, 2022; Scolari & Awl, 2019; Scolari, Kohnen, Barton, & Awh, 2007; Yeshurun & Rashal, 2010; TKacz-Domb & Yeshurun, 2017). For instance, in one study, the target—a letter T—was presented in several orientations, either in isolation or with two flankers, and participants were asked to judge the orientation of the target. It was shown that crowding was significantly relieved and the critical distance of crowding was dramatically reduced if an attentional cue was provided to inform participants where the target was about to appear before its onset (Yeshurun & Rashal, 2010). Similar findings have been reported in people with attentional deficits including developmental dyslexia (Bertoni, Franceschin, Ronconi, Gori, & Facoetti, 2019; Callens, Whitney, Tops, & Brysbaert, 2013; Joo, White, Strodtman, & Yeatman, 2018; see Gori & Facoetti, 2015, for a review) and autism spectrum disorder (Grubb et al., 2013). For instance, Grubb et al. showed that exogenous attention reduced the magnitude and critical distance of crowding in people with autism spectrum disorder to a level that was comparable to that of typically-developing control participants.

Second, directing attention to flankers changes the pattern of crowding (Mareschal, Morgan, & Solomon, 2010; Petrov & Meleshkevich, 2011a; Petrov & Meleshkevich, 2011b). One diagnostic characteristic of crowding is the radial-tangential anisotropy (Toet & Levi, 1992), which refers to the finding that radially aligned flankers relative to the fixation cross produce a stronger crowding effect than tangentially aligned flankers. To examine how attention modulated the radial-tangential anisotropy of crowding, Mareschal et al. (2010) adopted a dual task in which participants needed to discriminate the orientation of a Gabor surrounded by adjacent flankers in both radial and tangential axes while concurrently performing a spatial frequency task. The crowding effect became stronger when attention was directed to radially aligned flankers by the spatial frequency task, as the weight of radially aligned flankers became heavier when attention was directed to them. Another hallmark

of crowding is the inward-outward asymmetry (Chakravarthi, Rubruck, Kipling, & Clarke, 2021; Levi, 2008), which means that the flanker farther away from the fixation (i.e., the outward flanker) causes a stronger crowding effect than the flanker closer to the fixation (i.e., the inward flanker). Research has shown that the inward-outward asymmetry occurs because attention is usually biased outward of the target, and it disappears when attention is diffused over a large area around the target. When attention is directed inward of the target, the inward flanker produces a stronger crowding effect (Petrov & Meleshkevich, 2011b). Therefore the inward–outward asymmetry of crowding can be altered by the locus of attention (Petrov & Meleshkevich, 2011a; Petrov & Meleshkevich, 2011b).

To summarize, attention modulates the magnitude and pattern of crowding (e.g., Yeshurun & Rashal, 2010; Mareschal et al. 2010). However, these studies have only investigated the influence of exogenous attentional cues on crowding. Very few studies, as far as we know, have explored how endogenous attentional cues affect crowding. Albonico, Martelli, Bricolo, Frasson, and Daini (2018) showed that a small square that appeared at the location of the target and precisely the same size as the target reduced crowding in the visual fovea but not in the periphery. The small square probed the focal component of attention by allowing us to adjust the attentional window size to the size of the target and concentrate attentional resources on it. Although focusing attention can be voluntary and endogenous (Turatto et al., 2000), it is differs from the conventional endogenous attention in that the latter primarily probes the orientation component (which enables us to direct attention to a specific location). The only one study that has yet directly explored the role of endogenous attentional cues in crowding was conducted by Montaser-Kouhsari and Rajimehr (2005). They showed with an orientation-selective adaptation task that adaptation could be increased when observers voluntarily direct their attention to the crowded display. This result demonstrates that endogenous attention can reduce crowding.

Despite that both types of attentional cues improve the attentional resolution of cued positions (Carrasco, 2011; Doallo et al., 2004; Montagna, Pestilli, & Carrasco, 2009; Pestilli & Carrasco, 2005; Posner, 1980), these two types of attention involve different processing mechanisms (e.g., Pinto, Van der Leji, Sligte, Lamme, & Scholte, 2013; for a review, see Anton-Erxleben & Carrasco, 2013). Endogenous attention is a voluntary process driven by goals, whereas exogenous attention is an automatic process triggered by salient events (Keefe & Störmer, 2021; Müller & Rabbitt, 1989). Moreover, endogenous attention is a slow and long-lasting process, and it takes about 300 ms to be allocated, whereas exogenous attention is a rapid, short-lasting process that takes about 100 ms to be deployed (Anton-Erxleben & Carrasco, 2013; Busse, Katzner, & Treue, 2008; Carrasco, 2011; Carrasco & Barbot, 2015; Cheal & Lyon, 1991; Liu, Stevens, & Carrasco, 2007; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). They also have differential effects on humans perceive basic visual information such as contrast (Jigo & Carrasco, 2020), orientation and spatial frequency (Fernandez, Okun & Carrasco, 2022). Because of the distinctive mechanisms, exogenous attention and endogenous attention are differentially influenced by the predictive validity (i.e., the probability of valid trials) (Barbot, Landy, & Carrasco, 2012; Doallo et al., 2004; Giordano, McElree, & Carrasco, 2009). Exogenous attention is unaffected by the predictive validity (i.e., participants would follow exogenous cues regardless of whether they are predictive) (e.g., Giordano et al., 2009), because attention will be automatically drawn to the cued location (Jonides & Yantis, 1988; Keefe & Störmer, 2021; Müller & Rabbitt, 1989), even when participants are aware that the cue is uninformative (Pestilli & Carrasco, 2005; Yeshurun & Rashal, 2010). Endogenous attention, however, depends crucially on the validity (Giordano et al., 2009; Jonides, 1981; Jonides & Yantis, 1988), and participants can flexibly decide to follow the cue or not based on the probability of valid trials (Kinchla, 1980; Müller & Rabbitt, 1989; Sperling & Melchner, 1978).

Given the discrepancies between endogenous and exogenous attention, as well as the dearth of investigations on how endogenous attentional cues affect crowding, the present study attempted to examine the potential differences in effects of endogenous and exogenous attentional cues on crowding. To this end, we combined the Posner cueing task and the visual crowding task. Because endogenous and exogenous attentional cues have different temporal dynamics (e.g., Dugué, Merriam, Heeger, & Carrasco, 2020), several stimulus-onset asychronies (SOAs) were used to investigate the differences between their effects. Also, three levels of predictive validity, from 100% predictive to unpredictive, were used to examine whether the effects of endogenous and exogenous attention in crowding were differentially modulated by it. We hypothesized that both types of attentional cues could significantly relieve visual crowding, but that the peripherally presented exogenous cue would be more effective and would take effect earlier than the centrally presented endogenous cue. We also hypothesized that the effect of endogenous attention on crowding would be affected by the predictive validity and that the effect would not occur when the central cue was not predictive of target's location, whereas the effect of peripheral cue would be independent of the predictive validity.

Experiment 1

Method

Participants

Forty-eight undergraduate students (34 females, mean age = 20.12 years old) took part in the experiment. All participants had normal or corrected-to-normal vision, and none of them knew the purpose of the experiment. The experiment was approved by the Review Board of School of Psychology, Jiangxi Normal University, and informed consent was obtained from participants before the experiment. Participants received a monetary payment or extra credits after the experiment.

Stimuli

The target stimulus was a capital letter T, either upright or inverted, and flankers were capital Hs that could be upright or 90° tilted. The letters subtended a visual angle of $0.9^{\circ} \times 0.9^{\circ}$ and were presented in Sloan font. Sloan letters were chosen because they are commonly used for visual acuity test. Target and flankers were tangentially distributed relative to the fixation cross and were presented on a gray background. The center-to-center distance between letters was 1.5° .

A black dot with a diameter of 0.35° served as the peripheral cue. To avoid a masking effect, the cue was located 1° closer to fixation than the target, following Yeshurun and Rashal (2010). An arrow (1° in length) positioned in the center of the screen served as the central cue. The mask stimuli were three windowpane-shaped patterns that were created by superimposing the letter H and upright and inverted Ts.

Design and procedure

This experiment was a 2 (crowding condition: crowded vs. uncrowded) \times 3 (cue type: peripheral cue vs. central cue vs. no cue) \times 5 (SOA: 100 ms vs. 175 ms vs. 275 ms vs. 400 ms vs. 550 ms) within-subject design. The crowding condition was manipulated in two blocks of 480 trials, with their order being counterbalanced among subjects. It took about 50 minutes to complete the entire experiment.

At the beginning of each trial, a fixation cross was presented in the center of the screen for 400 to 1200 ms, and participants were required to keep looking at the fixation throughout the experiment. This was followed by a cue for 50 ms. After a 50 ms, 125 ms, 225 ms, 350 ms, or 500 ms interstimulus interval, the target and two flankers (crowded condition) or the



Figure 1. The procedure of Experiment 1.

target alone (uncrowded condition) was presented at an eccentricity of 9° above, below, left, or right of the fixation for 60 ms. The orientations of the target and flankers were randomized between trials. The letters were then replaced by three masks that appeared for 200 ms. Immediately after the offset of the masks, a blank screen appeared, and participants were required to determine whether the target was upright or inverted as accurately as possible within 4000 ms. After the response, a blank screen was presented for 500 ms, and the next trial was started (see Figure 1). Participants were required to take a five-minute break between blocks.

Results

The average percentage correct in each condition is calculated, and the results are shown in Figure 2. The RT results are also analyzed and shown in Table 1.

A 2 (crowding condition: crowded vs. uncrowded) \times 3 (cue type: peripheral cue vs. central cue vs. no cue) \times 5 (SOA: 100 ms vs. 175 ms vs. 275 ms vs. 400 ms vs. 550 ms) three-way repeated measures analysis

of variance (ANOVA) was conducted on accuracy. The three-way interaction was significant [F(8, 376) =12.79, p < 0.001, $\eta_p^2 = 0.21$]. Further analysis revealed a significant two-way interaction between cue type and SOA in the crowded condition [F(8, 376) = 33.05, p <0.001, $\eta_p^2 = 0.41$]. The percent correct of peripheral cue was higher than central cue and no cue at all SOAs (ps < 0.001), which suggests that the peripheral cue is more effective at relieving crowding than that the central cue. The percent correct of central cue was not significantly better than that of no cue (ps > .05) until the SOA were 275 ms or larger (ps < 0.001), that is, central cues did not alleviate crowding at short SOAs. Moreover, both simple main effects of cue type [F(2, 94) = 173.93, p] $< 0.001, \eta_p^2 = 0.79$] and SOA [F(4, 188) = 103.36, p < 0.001, $\eta_p^2 = 0.69$] were significant. For the uncrowded condition, the two-way interaction between cue type and SOA was also significant [F(8, 376) = 11.71, p < 1000.001, $\eta_p^2 = 0.20$]. The accuracy of central cue was significantly lower than that of no cue at all SOAs (ps < 0.001), except for the SOA of 400 ms (p = 0.17) and 550 ms (p = 0.16), although there was no significant difference between peripheral cue and no cue at any SOA (ps > 0.05), with the exception of 175 ms (p =0.004). The simple main effects of cue type [F(2, 94)]= 27.27, p < 0.001, $\eta_p^2 = 0.37$] and SOA [F(4, 188) = 22.63, p < 0.001, $\eta_p^2 = 0.33$] were also significant.

Significant main effects were revealed for crowding condition [F(1,47) = 396.81, p < 0.001, $\eta_p^2 = 0.89$], cue type [F(2, 94) = 134.05, p < 0.001, $\eta_p^2 = 0.74$], as well as SOA [F(4, 188) = 100.94, p < 0.001, $\eta_p^2 = 0.68$]. Crowding condition by cue type [F(2, 94) = 113.77, p < 0.001, $\eta_p^2 = 0.71$], crowding condition by SOA [F(4, 188) = 49.55, p < 0.001, $\eta_p^2 = 0.51$], as well as SOA by cue type [F(8, 376) = 40.14, p < 0.001, $\eta_p^2 = 0.46$] all showed significant two-way interactions.



Figure 2. Accuracy in Experiment 1, in which predictive validity was 100%. The two panels represent the crowded condition (left panel) and the uncrowded condition (right panel), respectively. The y-axis indicates the proportion of correct orientation discrimination of letter T. The x-axis means different SOAs. Error bars indicate standard errors of the mean. The asterisks indicate the significance relative to the no cue condition. ***p < 0.001, ** p < 0.01.

	Crowded					Uncrowded				
Cue condition	100 (ms)	175 (ms)	275 (ms)	400 (ms)	550 (ms)	100 (ms)	175 (ms)	275 (ms)	400 (ms)	550 (ms)
Peripheral	789	748 [*]	687**	634***	628***	679***	615*	576	526**	527**
Central	685**	628 ^{***}	577***	558 ^{***}	554***	575	516***	504***	514**	515**
No cue	793	810	780	803	782	578	578	579	585	588

Table 1. Response times (ms) in Experiment 1. Notes: The asterisks indicate the significance relative to the no cue condition. ***p < 0.001, **p < 0.01.

We also conducted paired-samples *t*-tests to compare the cueing effects (the difference between the accuracy of cue condition and no cue condition) of crowded versus uncrowded conditions for both exogenous and endogenous attention. The results showed that the cueing effects of both types of attention were significantly greater in the crowded condition than those in the uncrowded condition at all SOAs (all ps < 0.001). Together, this experiment showed that both peripheral and central attentional cues significantly alleviated the interference of visual crowding, but the exogenous cue reduced crowding to a greater extent and took effect sooner.

Experiment 2

In Experiment 1, the predictive validity of the attentional cue was 100%, that is, the target always appeared at the cued location. Prior research has shown a validity effect (i.e., a valid cue can result in a better performance than an invalid cue) (Posner, 1980; Vossel, Thiel, & Fink, 2006). This effect is contingent on the type of attention and the predictive validity of the cue: whereas exogenous attention is unaffected by probability of valid trials, endogenous attention depends crucially on the probability (e.g., Giordano et al., 2009). In this experiment, we reduced the predictive validity to 70% to test how the effects of the two types of attention in alleviating crowding are differentially affected by it.

Method

Participants

Fifty undergraduate students (34 females, mean age = 18.97 years old) attended the experiment. All participants had normal or corrected-to-normal vision, and none of them knew the purpose of the experiment. The experiment was approved by the Review Board of School of Psychology, Jiangxi Normal University, and informed consent was obtained from participants before the experiment. Participants received a monetary payment or extra credits after the experiment.

Stimuli

The stimuli were identical to Experiment 1 except that the condition of no cue was replaced by neutral cue. The neutral peripheral cue consisted of four black dots with a diameter of 0.35°. It was located 1° closer to fixation than the target and appeared simultaneously in four directions: up, down, left, and right. The neutral central cue were four arrows (1° in length) that pointed up, down, left, and right, positioned at the center of the screen.

Design and procedure

The design was identical to that in Experiment 1 except for the following differences. First, the predictive validity was decreased to 70%. The target would appear in the same position as the cue in 70% of the trials (the valid trials), whereas it would appear in the opposite position showed by the cue in the other 30% of the trials (the invalid trials). Second, a neutral cue condition, rather than a no-cue condition, served as the baseline. The neutral cues always indicated all four possible locations that the target might appear, so they were uninformative of the target's locations. Third, only crowded condition was examined. Fourth, instead of five SOAs, four (100 ms, 200 ms, 400 ms, and 700 ms) were used in this experiment. These changes made this experiment a 2 (cue type: peripheral cue vs. central cue) \times 3 (cue validity: valid vs. invalid vs. neutral) \times 4 (SOA: 100 ms vs. 200 ms vs. 400 ms vs. 700 ms) within-subject design.

The experiment followed the same procedure as Experiment 1. Participants were told explicitly in the instruction that the valid-invalid ratio was 7:3. The cue type was manipulated in blocks, and its order was counterbalanced among participants. Each block contained 440 experimental trials, with each participant completing 880 trials in total.

Results

The average percentage correct in each condition is calculated, and the results are plotted in Figure 3. The RT results are also analyzed and shown in Table 2.

A three-way repeated measures ANOVA was used to examine the main effects and interactions of cue type, cue validity and SOA. The three-way interaction was significant [$F(6, 294) = 2.27, p = 0.01, \eta_p^2 =$ 0.04]. Further analyses showed a significant two-way interaction between the validity of central cue and SOA $[F(6, 294) = 11.11, p < 0.001, \eta_p^2 = 0.19]$. The accuracy of valid central cue was significantly higher than neutral cue when the SOA were 100 ms (p = 0.04), 400 ms (p <0.001), and 700 ms (p < 0.001), but not when the SOA was 200 ms (p = 0.51). The accuracy of invalid central cue was lower than neutral cue for the SOA of 700 ms (p = 0.03), but no significant difference was yielded for other SOAs (ps > 0.05). The accuracy of valid central cue was significantly higher than invalid central cue when the SOAs were 400 ms (p < 0.001) and 700 ms (p< 0.001), but they were not significantly different for

the rest of SOAs (ps > 0.05). The simple main effects of cue validity and SOA were significant [F(2, 98) =25.75, p < 0.001, $\eta_p^2 = 0.34$ and F(3, 147) = 20.98, p $< 0.001, \eta_p^2 = 0.30$, respectively]. For the peripheral cue, the two-way interaction between cue validity and SOA was also significant [F(6, 294) = 6.98, p < 0.001, $\eta_{\rm p}^2 = 0.13$]. In all SOAs, the accuracy of valid peripheral cue was better than neutral peripheral cue (ps < 0.001). Identical to Experiment 1, peripheral cues started to alleviate visual crowding at the shortest SOA of 100 ms. The invalid peripheral cue yielded a significantly lower accuracy than neutral peripheral cue when the SOA was 700 ms (p = .002), whereas they did not differ in other SOAs (ps > 0.05). Furthermore, the simple main effects of cue validity $[F(2, 98) = 62.01, p < 0.001, \eta_p^2 = 0.56]$ and SOA [$F(3, 147) = 19.83, p < 0.001, \eta_p^2 = 0.29$] were both significant.

The main effects of cue type $[F(1, 49) = 20.86, p < 0.001, \eta_p^2 = 0.30]$, cue validity $[F(2, 98) = 62.96, p < 0.001, \eta_p^2 = 0.56]$, as well as SOA $[F(3, 147)=40.78, p < 0.001, \eta_p^2 = 0.45]$ were also significant. Cue type by



Figure 3. Accuracy in Experiment 2, in which the predictive validity was 70%. The two panels represent the endogenous attention condition (left panel) and exogenous attention condition (right panel), respectively. Error bars indicate standard errors of the mean. The asterisk indicates the significance relative to the no cue condition. *** p < 0.001, ** p < 0.01, * p < 0.05.

		Cer	ntral		Peripheral				
Cue condition	100 (ms)	200 (ms)	400 (ms)	700 (ms)	100 (ms)	200 (ms)	400 (ms)	700 (ms)	
Experiment 2									
Invalid	879 [*]	835	874*	864*	880	865 [*]	833	861	
Neutral	833	823	817	816	838	825	802	820	
Valid	829	821	762**	761*	761***	751***	710***	701***	
Experiment 3									
Invalid	872	837	853	868	864	858	836	881^*	
Neutral	876	850	857	890	857	844	819	840	
Valid	852	832	791**	841	796 [*]	797**	805	808	

Table 2. Response times (ms) in Experiments 2 and 3. Notes: The asterisks indicate the significance relative to the no cue condition. ***p < 0.001, **p < 0.01, ***p < 0.001.

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The comparison of the benefits of valid peripheral cues and that of the valid central cues showed that peripheral cues were significantly more effective at the SOAs of 150 ms and 300 ms (p < 0.001 and p = 0.019, respectively) and were marginally significantly more effective at the SOAs of 100 ms and 700 ms (p = 0.058and p = 0.073, respectively). Therefore similar results as Experiment 1 were revealed when the predictive validity was reduced to 70%. That is, exogenous attention, as opposed to endogenous attention, was found to be more effective and take effect earlier in alleviating visual crowding. However, when compared to Experiment 1, the facilitation effect caused by the presentation of a valid cue diminished for exogenous attention. We draw this conclusion by comparing the beneficial effects of valid cues on relieving crowding in Experiment 1 with those in Experiment 2 for both peripheral and central cues. The valid peripheral cue in Experiment 1 caused significantly greater benefits than that Experiment 2 at the SOAs of 200 ms and 400 ms (ps < 0.001) with the exception of 100 ms (p = 0.279). The benefits cause by the central cue of Experiment 1, when compared with that of Experiment 2, were smaller at the SOAs of 100 ms (p < 0.001), not significant at the SOAs of 400 ms (p = 0.457), and greater at the SOAs of 400 ms (p =0.011).

With regard to the effect of cue validity, endogenous and exogenous attention showed some differences. Although valid peripheral cues began to alleviate crowding as early as 100 ms, valid central cues did not have a robust effect until 400 ms after cue onset. The invalid cues, central or peripheral, did not relieve crowding. Instead, they even produced a cost—crowding was aggravated—at the SOA of 700 ms.

Experiment 3

In Experiments 1 and 2, the predictive validity was 100% and 70%, respectively, which were informative of the target's location. In this experiment, we reduced the predictive validity to 50% to determine whether the two forms of uninformative cues had different effects on crowding. Previous studies have found that participants will not follow central cues, but they cannot resist following peripheral cues when the cues are uninformative of target's location (e.g., Giordano et al., 2009). Based on this finding, we predicted that the strength of crowding would be similar in valid, invalid, and neutral central cue conditions and that a valid

peripheral cue would benefit the alleviation of crowding whereas an invalid peripheral cue might be harmful.

Method

Participants

Forty-six undergraduate students (31 females, mean age = 19.23 years old) attended the experiment. All participants had normal or corrected-to-normal vision, and none of them knew the purpose of the experiment. The experiment was approved by the Review Board of School of Psychology, Jiangxi Normal University, and informed consent was obtained from participants before the experiment. Participants received a monetary payment or extra credits after the experiment.

Stimuli

All stimuli were identical to those in Experiment 2.

Design and procedure

The predictive validity was reduced to 50% in this experiment. Otherwise, the design and procedure were the same as in Experiment 2. Each block contained 384 trials, with each participant completing 768 of them.

Results

An ANOVA was performed, as in Experiment 2, and the results are plotted in Figure 4. No significant three-way interaction was found [F(6, 270) = 1.17, p]= 0.38, η_p^2 = 0.02]. The interaction between cue type and cue validity was significant [F(2, 90) = 3.18, p = 0.046, $\eta_p^2 = 0.07$]. The pairwise comparisons between cue validity of endogenous attention did not yield any difference (ps > 0.05). For exogenous attention, the accuracy of valid cues was significantly higher than neutral (p < 0.001) and invalid cues (p = 0.001), whereas the accuracy between invalid and neutral cues was not significantly different (p = 0.99). The two-way interaction of cue validity and SOA was also significant $[F(6, 270) = 2.58, p = 0.02, \eta_p^2 = 0.05]$. The accuracies of valid cues were higher than neutral cues at the SOAs of 200 ms (p = 0.006) and 400 ms (p = 0.002) and 700 ms (p = 0.003). Meanwhile, the valid cues had a higher accuracy than invalid cues at the SOAs of 200 ms (p =0.01) and 400 ms (p = 0.007) and 700 ms (p = 0.002). Other comparisons were not significant. The interaction between cue type and SOA was not significant [F(3, $(135) = 1.50, p = 0.22, \eta_p^2 = 0.03]$. The main effects of cue validity [$F(2, 90) = 12.02, p < 0.001, \eta_p^2 = 0.21$] and SOA [$F(3, 135) = 4.19, p = 0.007, \eta_p^2 = 0.09$] were



Figure 4. Accuracy in Experiment 3, in which the predictive validity was 50%. The two panels represent the endogenous attention condition (left panel) and exogenous attention condition (right panel), respectively. Error bars indicate standard errors of the mean. The asterisk indicates the significance relative to the no cue condition. ** p < 0.01.

significant, but the main effect of cue type was not significant [F(1, 45) = 0.89, p = 0.35, $\eta_p^2 = 0.02$].

In sum, this experiment showed that when the cue was unpredictable of the target's position, the effects of endogenous and exogenous attention on crowding were differently affected by cue validity—the performance did not vary in valid, invalid, and neutral central cue conditions, but a valid peripheral cue enhanced the performance, although an invalid peripheral cue did not harm the alleviation of crowding. This finding suggests that participants can voluntarily control their endogenous attention although they cannot resist following peripheral cues when the cues are uninformative of the target's location, which is in line with previous research (e.g., Giordano et al., 2009).

General discussion

In the present study, we combined the Posner cueing task and the visual crowding task to investigate the effect of peripheral and central cues on visual crowding. Experiment 1 demonstrated that both types of attentional cues relieved visual crowding when they were 100% valid, with the peripheral cue having a stronger impact. In addition, the effects of the two types of cues on crowding showed different temporal dynamics. The peripheral cue started to relieve crowding at the shortest SOA whereas the central cue worked at longer SOAs. Experiment 2 showed that when the predictive validity of the cue was 70%, the effect of valid cues on crowding was significantly higher than those of neutral and invalid cues for both exogenous and endogenous attention. Similar to Experiment 1, the valid peripheral cue had a greater and earlier effect on crowding than the central cue, but the effects of peripheral cue were smaller than those in Experiment

1. When the predictive validity was decreased to 50% in Experiment 3, that is, when the cue was uninformative of target's location, crowding was still affected by the peripheral cue but was nearly not influenced by the central cue.

Earlier studies have demonstrated that crowding can be effectively reduced when attention is directed to the target's location by a peripheral cue (Grubb et al., 2013; Kewan-Khalayly et al., 2022; Scolari et al., 2007; Yeshurun & Rashal, 2010). This finding was confirmed by the current investigation. In contrast to prior research that solely used one SOA of roughly 120 ms (Scolari et al., 2007; Yeshurun & Rashal, 2010), we varied the SOA, ranging from 100 ms to 700 ms, to characterize the temporal dynamics of how peripheral cue alleviates crowding. Exogenous attention was shown to diminish crowding at the shortest SOA, and this effect persisted and even increased as the SOA lengthened. However, it is worth noting that participants may voluntarily control their attention at long SOAs even if the cues are exogenous, because endogenous attention takes around 300 ms to be deployed, whereas exogenous attention is much more transient (e.g., Anton-Erxleben & Carrasco, 2013). In other words, peripheral cues may start to develop into endogenous cues at \sim 300 ms from cue onset. As a result, at long SOAs, participants may shift their attention to the peripherally cued location if the peripheral cues are predictive and away from it if they are nonpredictive.

Rather than focusing exclusively on the influence of exogenous attention on crowding like earlier studies have done (e.g., Yeshurun & Rashal, 2010), the present study additionally investigated the effect of endogenous attention on crowding. Earlier studies have investigated the impact of endogenous attention on target recognition in the presence of nearby distractors (Awh, Matsukura, & Serences, 2003; Awh, Sgarlata, & Kliestik, 2005; Carrasco & McElree, 2001; Desimone & Duncan, 1995; Giordano et al., 2009; Lankheet & Verstraten, 1995; Yeshurun, Montagna, & Carrasco,

2008), in which crowding is present in the stimulus displays. Despite this, it is important to note that the effects of crowding on targets in these studies cannot be isolated. In these studies, some distractors were presented close to the target (adjacent flankers, which were the sole distractors in traditional crowding tasks), whereas simultaneously other distractors were presented farther away (extra distractors, which were not included in traditional crowding tasks) (Awh et al., 2003; Awh et al., 2005; Desimone & Duncan, 1995; Giordano et al., 2009; Lankheet & Verstraten, 1995; Yeshurun et al., 2008). The presence of extra distractors may result in perceptual grouping of distractors (Herzog & Manassi, 2015), which can significantly affect crowding (Manassi, Hermens, Francis, & Herzog, 2015; Manassi, Sayim, & Herzog, 2012; Manassi, Sayim, & Herzog, 2013; for a review, see Herzog, Sayim, Chicherov, & Manassi, 2015), and even lead to uncrowding of the target (Manassi, Sayim, & Herzog, 2013). By contrast, the traditional crowding task used in our study differs from prior research and allows us to isolate the phenomenon of crowding.

This design also allows for a direct comparison of the effects between the two types of attention on crowding. It was shown that crowding could also be effectively reduced by endogenous attention. Therefore, the present research indicates that directing attention to the target's location, either through peripheral or central cues, can alleviate crowding. Nevertheless, the degree and time course of the two types of attention in alleviating crowding differ. First, peripheral cues had a larger effect on crowding than central cues, replicating previous research (e.g., Müller & Rabbitt, 1989). Second, central cues took longer than peripheral cues to relieve crowding. Central cues did not alleviate crowding at short SOAs (100 ms and 275 ms in Experiment 1, and 200 ms in Experiment 2), which is consistent with prior findings that shorter SOAs (less than 300 ms) are ineffective for endogenous attention (e.g., Cheal & Lyon, 1991), because the central cue takes a longer time to be deployed (for a review, see Carrasco, 2011). Peripheral cues, on the other hand, began to alleviate crowding at the shortest SOA of 100 ms. This result was in line with previous findings that exogenous and endogenous attention exhibit distinct temporal dynamics (e.g., Dugué et al., 2020).

The present study also demonstrates that the effects of exogenous and endogenous attention on crowding are differentially influenced by the predictive validity. Experiments 1 and 2 both provided an informative attentional cue (with 100% and 70% predictive validity, respectively), whereas Experiment 3 provided an uninformative cue (with 50% predictive validity). Valid peripheral cues reduced crowding, regardless of predictive validity, whereas valid central cues reduced crowding only when the cue was informative. This result was in line with previous studies (Barbot et al., 2012; Doallo et al., 2004; Giordano et al., 2009). Cues that appear abruptly in the visual periphery draw attention automatically (i.e., in a bottom-up way), it is hard for participants to ignore them, even when they do not predict the location of target (Giordano et al., 2009; Pestilli & Carrasco, 2005; Yeshurun & Rashal, 2010). As for the endogenous attention, a valid cue is more effective than an invalid cue in reducing crowding at longer SOAs when the cue was informative (Experiments 1 and 2), but there was no difference when the cue is uninformative (Experiment 3). These results indicate that participants followed the cues when they were predictive of the target's location but did not follow them when they are nonpredictive. This finding is in line with previous research demonstrating that participants are capable of flexibly allocating attentional resources based on the validity of central cues (Carrasco & Barbot, 2015; Giordano et al., 2009; Jonides, 1981; Jonides & Yantis, 1988; Kinchla, 1980; Sperling & Melchner, 1978), because endogenous attention is under top-down voluntary control (e.g., Müller & Rabbitt, 1989). Collectively, the current research suggests that exogenous and endogenous attention differ in the degree of flexibility in relieving crowding, with endogenous attention being more flexible than exogenous attention because it can adapt its operation based on predictive validity (Giordano et al., 2009).

The disparate influences of peripheral and central cues on crowding indicate that separate mechanisms are involved in exogenous and endogenous attention. Exogenous attention is triggered by salient stimuli, which occurs involuntarily and very rapidly (e.g., Nakayama & Mackeben, 1989). Therefore exogenous attention is also known as reflective attention (Müller & Rabbitt, 1989). Endogenous attention, on the other hand, is goal-driven, which is under voluntary control and occurs slowly (e.g., Barbot et al., 2012; Carrasco, 2011; Carrasco & Barbot, 2015). Thus endogenous attention also means sustained attention (Barbot et al., 2012; Carrasco, 2011; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). In line with behavioral findings, disassociable neural mechanisms between the two types of attention have also been reported (Beck & Kastner, 2009; Chica, Bartolomeo, & Lupianez, 2013). They differ in the activation of occipital areas (Dugué et al., 2020) and the visual subregions of temporoparietal junction (Dugué, Merriam, Heeger, & Carrasco, 2018). Also, exogenous attention is related to the activation of superior parietal gyrus, while endogenous attention is associated with the activation of the inferior frontal gyrus (Santangelo, Olivetti Belardinelli, Spence, & Macaluso, 2009). Electrophysiological research has also shown that exogenous attention dominate early stages of visual processing (such as the P1 component), whereas endogenous attention dominates later stages (such as the P300 component) (Hopfinger & West, 2006).

According to the attentional resolution model (He et al., 1996; Intriligator & Cavanagh, 2001), crowding reflects a limited spatial resolution of attention, and it can be greatly alleviated when attentional resolution is enhanced. Since both exogenous and endogenous attentional cues enhance the attention resolution of cued locations (Anton-Erxleben & Carrasco, 2013; Carrasco & Barbot, 2015; Carrasco, 2011), the current findings are in accordance with the attentional resolution model. Noteworthy, this does not imply that our study directly supports this model. Indeed, increased attentional resolution can also reduce the pooling of features of target and flankers or the mistaken reporting of flankers instead of the target. In other words, our findings cannot rule out the pooling model (Dakin, Cass, Greenwood, & Bex, 2010; Greenwood, Bex, & Dakin, 2009; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001) or the substitution model (Ester, Klee, & Awh, 2014).

There are some limitations to our study. First, eye movements are likely to occur for longer SOAs in this study, which could potentially invalidate visual crowding. Our study showed that the benefits of peripheral cues on crowding relief increased with the length of SOA. However, the effect at lengthy SOAs could have been caused by eye movements to the cued location. Although we made an effort to minimize eve movements by emphasizing to each participant the importance of keeping their eyes on the central fixation both through the instruction and verbally, we could not be certain that all participants would adhere to our instruction. However, this does not mean that the cues did not contribute to relieving crowding. Eye movements to an unexpected location take 150 to 200 ms to initiate (Carpenter, 1988; Findlay, 1997). Given that the stimuli in our study were presented in a more peripheral location than earlier studies (e.g., Findlay, 1997), it should take even longer to make a saccade to the target even if eye movements did occur. Thus for exogenous attention, eye movements could not have occurred at short SOAs of 100 ms and 175 ms, yet it had significant effects even at that times. Endogenous attention takes about 300 ms to be deployed (e.g., Carrasco, 2011), but the present study showed that endogenous attention had significant effects even at the shorter SOAs (e.g., 275 ms) even though eye movements are unlikely to have occurred at that short time. Furthermore, eye movements caused by following endogenous cues may have been minimal in Experiment 3, even at lengthy SOAs. This is because participants tend to ignore endogenous cues that are not predictive of the target's location (Giordano et al., 2009; Kinchla, 1980; Sperling & Melchner, 1978).

Therefore, although we cannot rule out the possibility of eye movements, the pattern of results could not, at least not entirely, be explained by them. If eye movements were well controlled, we would anticipate that the cueing effects would be the same at shorter SOAs but smaller at longer SOAs than what our results revealed. That is, the results would follow a similar pattern but with a lower curve plateau. Future research may use eye-trackers to monitor eye movements to examine if the pattern of results shown in our study could be replicated. Second, because of the drop of the uncrowded condition in Experiments 2 and 3, we cannot determine how the two types of attention alleviate crowding effect differently. In Experiments 2 and 3, a new independent variable—cue validity—was included, so the number of total trials would tremendously increase if other designs were the same as Experiment 1. To prevent potential fatigue effect, we had to simplify the experimental design. Considering that the main purpose of the current study was to compare how exogenous and endogenous attention differ in relieving the discrimination of crowded targets, we removed the uncrowded condition. However, without the uncrowded condition as a baseline, we cannot know how the two types of attention differentially alleviate crowding effect (the difference between the performance on the crowded and uncrowded displays).

In conclusion, the present study demonstrates that both peripheral and central cues reduce visual crowding, but peripheral cues have a larger influence than central cues. Moreover, the peripheral cues start to reduce crowding at the shortest SOA, whereas the central cue works at a much longer SOA. The effects of both attentional cues are modulated by the probability of valid trials, but the central cue is more critically affected. Indeed, the central cue almost no longer affects crowding when it is uninformative (i.e., 50% predictive validity).

Keywords: visual crowding, endogenous attention, exogenous attention, cue validity, predictive validity

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References

- Albonico, A., Martelli, M., Bricolo, E., Frasson, E., & Daini, R. (2018). Focusing and orienting spatial attention differently modulate crowding in central and peripheral vision. *Journal of Vision*, 18(3), 4–4, https://doi.org/10.1167/18.3.4.
- Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: Linking behavioural and neurophysiological evidence. *Nature Reviews Neuroscience*, 14(3), 188–200, https://doi.org/10.1038/nrn3443.
- Awh, E., Matsukura, M., & Serences, J. T. (2003). Top-down control over biased competition during covert spatial orienting. *Journal of Experimental Psychology: Human Perception and Performance*, 29(1), 52–63, https://doi.org/10.1037/0096-1523.29. 1.52.
- Awh, E., Sgarlata, A. M., & Kliestik, J. (2005). Resolving visual interference during covert spatial orienting: Online attentional control through static records of prior visual experience. *Journal of Experimental Psychology: General*, *134*(2), 192–206, https://doi.org/10.1037/0096-3445.134.2.192.
- Barbot, A., Landy, M. S., & Carrasco, M. (2012). Differential effects of exogenous and endogenous attention on second-order texture contrast sensitivity. *Journal of Vision*, 12(8), 6, https://doi.org/10.1167/12.8.6.
- Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, 49(10), 1154– 1165, https://doi.org/10.1016/j.visres.2008.07.012.
- Bertoni, S., Franceschini, S., Ronconi, L., Gori, S., & Facoetti, A. (2019). Is excessive visual crowding causally linked to developmental dyslexia? *Neuropsychologia*, 130, 107–117, https: //doi.org/10.1016/j.neuropsychologia.2019.04.018.
- Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature*, 226, 177–178, https://doi.org/10.1038/226177a0.
- Busse, Laura, Katzner, Steffen, & Treue, Stefan. (2008). Temporal dynamics of neuronal modulation during exogenous and endogenous shifts of visual attention in macaque area MT. *Proceedings of the National Academy of Sciences*, 105(42), 16380–16385.
- Callens, M., Whitney, C., Tops, W., & Brysbaert, M. (2013). No deficiency in left-to-right processing of words in dyslexia but evidence for enhanced visual crowding. *Quarterly Journal*

of Experimental Psychology, *66*(9), 1803–1817, https://doi.org/10.1080/17470218.2013.766898.

- Carpenter, R. H. S. (1988). *Movements of the Eyes*. London: Pion Limited.
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*, 1484–1525, https://doi.org/10.1016/j.visres.2011.04.012.
- Carrasco, M., & Barbot, A. M. (2015). How attention affects spatial resolution. *Cold Spring Harbor Symposia on Quantitative Biology*, 79, 149–160, https://doi.org/10.1101/sqb.2014.79.024687.
- Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Sciences*, 98(9), 5363–5367, https://doi.org/10.1073/pnas.081074098.
- Chakravarthi, R., Rubruck, J., Kipling, N., & Clarke, A. D. F. (2021). Characterizing the in-out asymmetry in visual crowding. *Journal of Vision*, *21*(11), 10, https://doi.org/10.1167/jov.21.11.10.
- Cheal, M. L., & Lyon, D. R. (1991). Central and peripheral precuing of forced-choice discrimination. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, 43(4), 859–880, https://doi.org/10.1080/14640749108400960.
- Chica, A. B., Bartolomeo, P., & Lupianez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research*, 237, 107–123, https://doi.org/10.1016/j.bbr.2012.09.027.
- Dakin, S. C., Cass, J., Greenwood, J. A., & Bex, P. J. (2010). Probabilistic, positional averaging predicts object-level crowding effects with letter-like stimuli. *Journal of Vision*, 10(10), 14, https://doi.org/10.1167/10.10.14.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193–222, https: //doi.org/10.1146/annurev.ne.18.030195.001205.
- Doallo, S., Lorenzo-López, L., Vizoso, C., Rodriguez Holguń, S., Amenedo, E., & Cadaveira, F. (2004). The time course of the effects of central and peripheral cues on visual processing: An event-related potentials study. *Clinical Neurophysiology*, *115*(1), 199–210, https://doi.org/10.1016/S1388-2457(03)00317-1.
- Dugué, L., Merriam, E. P., Heeger, D. J., & Carrasco, M. (2018). Specific visual subregions of TPJ mediate reorienting of spatial attention. *Cerebral Cortex*, 28(7), 2375–2390.
- Dugué, L., Merriam, E. P., Heeger, D. J., & Carrasco, M. (2020). Differential impact of endogenous and exogenous attention on activity in human

visual cortex. *Scientific Reports*, *10*(1), 21274, https://doi.org/10.1038/s41598-020-78172-x.

- Ester, E. F., Klee, D., & Awh, E. (2014). Visual crowding cannot be wholly explained by feature pooling. *Journal of Experimental Psychology: Human Perception and Performance, 40*(3), 1022–1033, https://doi.org/10.1037/a0035377.
- Farzin, F., Rivera, S. M., & Whitney, D. (2009). Holistic crowding of mooney faces. *Journal of Vision*, 9(6), 18, https://doi.org/10.1167/9.6.18.
- Fernández, A., Okun, S., & Carrasco, M. (2022). Differential Effects of endogenous and exogenous attention on sensory tuning. *Journal* of Neuroscience, 42 (7) 1316–1327, https: //doi.org/10.1523/JNEUROSCI.0892-21.2021.
- Findlay, J. H. (1997). Saccade target selection during visual search. *Vision Research*, *37*(5), 617–631, https://doi.org/10.1016/S0042-6989(96)00218-0.
- Freeman, J., & Pelli, D. G. (2007). An escape from crowding. *Journal of Vision*, 7(2), 22, https://doi.org/10.1167/7.2.22.
- Giordano, A. M., Mcelree, B., & Carrasco, M. (2009). On the automaticity and flexibility of covert attention: A speed-accuracy trade-off analysis. *Journal of Vision*, 9(3), 30, https://doi.org/10.1167/9.3.30.
- Gori, S., & Facoetti, A. (2015). How the visual aspects can be crucial in reading acquisition: The intriguing case of crowding and developmental dyslexia. *Journal of Vision*, *15*(1), 8, https://doi.org/10.1167/15.1.8.
- Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2009). Positional averaging explains crowding with letter-like stimuli. *Proceedings of the National Academy of Sciences of the United States of America*, 106(31), 13130–13135, https://doi.org/10.1073/pnas.0901352106.
- Grubb, M. A., Behrmann, M., Egan, R., Minshew, N. J., Heeger, D. J., & Carrasco, M. (2013). Exogenous spatial attention: Evidence for intact functioning in adults with autism spectrum disorder. *Journal of Vision*, 13(14), 9, https://doi.org/10.1167/13.14.9.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of awareness. *Nature, 383*, 334–338, https://doi.org/10.1038/383334a0.
- Herzog, M. H., & Manassi, M. (2015). Uncorking the bottleneck of crowding: A fresh look at object recognition. *Current Opinion in Behavioral Sciences*, *1*, 86–93, https: //doi.org/10.1016/j.cobeha.2014.10.006.
- Herzog, M. H., Sayim, B., Chicherov, V., & Manassi, M. (2015). Crowding, grouping, and object recognition: A matter of appearance. *Journal of Vision*, 15(6), 5, https://doi.org/10.1167/15.6.5.

- Hopfinger, J. B., & West, V. M. (2006). Interactions between endogenous and exogenous attention on cortical visual processing. *NeuroImage*, *31*(2), 774–789, https://doi.org/10.1016/j.neuroimage. 2005.12.049.
- Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology*, 43, 171–216, https://doi.org/10.1006/cogp.2001. 0755.
- Jigo, M., & Carrasco, M. (2020). Differential impact of exogenous and endogenous attention on the contrast sensitivity function across eccentricity. *Journal of Vision*, 20(6), 11, https://doi.org/10.1167/jov.20.6.11.
- Jonides, J. (1981). Voluntary vs. automatic control over the mind's eye's movement. In J. B. Long, & A. D. Baddeley (Eds.), *Attention and Performance IX* (pp. 187–203). Hillsdale, NJ: Erlbaum.
- Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics, 43*, 346–354, https://doi.org/10.3758/BF03208805.
- Joo, S. J., White, A. L., Strodtman, D. J., & Yeatman, J. D. (2018). Optimizing text for an individual's visual system: The contribution of visual crowding to reading difficulties. *Cortex*, 103, 291–301, https://doi.org/10.1016/j.cortex.2018.03.013.
- Keefe, J. M., & Störmer, V. S. (2021). Lateralized alpha activity and slow potential shifts over visual cortex track the time course of both endogenous and exogenous orienting of attention. *NeuroImage*, 225(5), 117495, https://doi.org/10.1016/j.neuroimage.2020. 117495.
- Kewan-Khalayly, B., Migó, M., & Yashar, A. (2022). Transient attention equally reduces visual crowding in radial and tangential axes. *Journal of Vision*, 22(9), 3. doi: 10.1167/jov.22.9.3.
- Kinchla, R. A. (1980). The measurement of attention. In R. S. Nikerson (Ed.), *Attention and Performance* IX. Hillsdale, NJ: Erlbaum.
- Lankheet, M. J. M., & Verstraten, F. A. J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research*, 35(10), 1401–1412, https: //doi.org/10.1016/0042-6989(95)98720-T.
- Levi, D. M. (2008). Crowding—An essential bottleneck for object recognition: A minireview. Vision Research, 48(5), 635–654, https://doi.org/10.1016/j.visres.2007.12.009.
- Levi, D., & Carney, T. (2009). Crowding in peripheral vision: Why bigger is not always better. *Journal of Vision*, 9(8), 982, https: //doi.org/10.1016/j.cub.2009.09.056.

- Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research*, 47(1), 108–113, https: //doi.org/10.1037/0096-3445.134.2.207.
- Manassi, M., Hermens, F., Francis, G., & Herzog, M. H. (2015). Release of crowding by pattern completion. *Journal of Vision*, 15(8), 16, https://doi.org/10.1167/15.8.16.
- Manassi, M., Sayim, B., & Herzog, M. H. (2012). Grouping, pooling, and when bigger is better in visual crowding. *Journal of Vision*, *12*(10), 13, https://doi.org/10.1167/12.10.13.
- Manassi, M., Sayim, B., & Herzog, M. H. (2013). When crowding of crowding leads to uncrowding. *Journal of Vision*, *13*(13), 10, https://doi.org/10.1167/13.13.10.
- Mareschal, I., Morgan, M. J., & Solomon, J. A. (2010). Attentional modulation of crowding. *Vision Research*, 50(8), 805–809, https://doi.org/10.1016/j.visres.2010.01.022.
- Montagna, B., Pestilli, F., & Carrasco, M. (2009). Attention trades off spatial acuity. *Vision Research*,49(7), 735–45, https://doi.org/10.1016/j. visres.2009.02.001.
- Montaser-Kouhsari, L., & Rajimehr, R. (2005). Subliminal attentional modulation in crowding condition. *Vision Research*, 45(7), 839–844, https://doi.org/10.1016/j.visres.2004.10.020.
- Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, 15(2), 315–330, https://doi.org/10.1037/0096-1523.15.2.315.
- Nakayama, K., & Mackaben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, 29, 1631–1647, https://doi.org/10.1016/0042-6989(89)90144-2.
- Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience*, 4(7), 739–744, https://doi.org/10.1038/8953.
- Pelli, D. G., Tillman, K. A., Freeman, J., Su, M., Berger, T. D., & Majaj, N. J. (2007). Crowding and eccentricity determine reading rate. *Journal of Vision*, 7(2), 20, https://doi.org/10.1167/7.2.20.
- Petrov, Y., & Meleshkevich, O. (2011a). Asymmetries and idiosyncratic hot spots in crowding. *Vision Research*, *51*(10), 1117–1123, https: //doi.org/10.1016/j.visres.2011.03.001.
- Petrov, Y., & Meleshkevich, O. (2011b). Locus of spatial attention determines inward-outward

anisotropy in crowding. *Journal of Vision*, 11(4), 1, https://doi.org/10.1167/11.4.1.

- Pestilli, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research*, 45(14), 1867–1875, https://doi.org/10.1016/j.visres.2005.01.019.
- Pinto, Y., Van der Leji, A. R., Sligte, I. G, Lamme, V., & Scholte, H. S. (2013). Bottom-up and top-down attention are independent. *Journal of Vision*, 13(3), 16, https://doi.org/10.1167/13.3.16.
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, 31(1), 3–25, https://doi.org/10.1080/ 00335558008248231.
- Santangelo, V., Olivetti Belardinelli, M., Spence, C., & Macaluso, E. (2009). Interactions between voluntary and stimulus-driven spatial attention mechanisms across sensory modalities. *Journal* of Cognitive Neuroscience, 21(12), 2384–2397, https://doi.org/10.1162/jocn.2008.21178.
- Scolari, M., & Awh, E. (2019). Object-based biased competition during covert spatial orienting. *Attention, Perception, & Psychophysics*, 81(5), 1366– 1385, https://doi.org/10.3758/s13414-018-01656-6.
- Scolari, M., Kohnen, A., Barton, B., & Awh, E. (2007). Spatial attention, preview, and popout: Which factors influence critical spacing in crowded displays? *Journal of Vision*, 7(2), 7, https://doi.org/10.1167/7.2.7.
- Sperling, G., & Melchner, M. J. (1978). The attention operating characteristic: Examples from visual search. *Science*, 202(4365), 315–318, https://doi.org/10.1126/science.694536.
- Tkacz-Domb, S., & Yeshurun, Y.(2017). Spatial attention alleviates temporal crowding, but neither temporal nor spatial uncertainty are necessary for the emergence of temporal crowding. *Journal of Vision*, 17(3), 9, https://doi.org/10.1167/17.3.9.
- Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research*, *32*, 1349–1357, https://doi.org/10.1016/0042-6989(92)90227-A.
- Turatto, M., Benso, F., Facoetti, A., Galfano, G., Mascetti, G. G., & Umiltà, C. (2000). Automatic and voluntary focusing of attention. *Attention*, *Perception, & Psychophysics*, 62(5), 935–952, https://doi.org/10.3758/BF03212079.
- Vossel, S., Thiel, C. M., & Fink, G. R. (2006). Cue validity modulates the neural correlates of covert endogenous orienting of attention in parietal and frontal cortex. *NeuroImage*, 32(3), 1257–1264, https://doi.org/10.1016/j.neuroimage.2006.05.019.
- Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious

perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160–168, https: //doi.org/10.1016/j.tics.2011.02.005.

Yeshurun, Y., Montagna, B., & Carrasco, M. (2008). On the flexibility of sustained attention and its effects on a texture segmentation task. *Vision Research*, 48(1), 80–95, https://doi.org/10.1016/j.visres.2007. 10.015.

Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision*, 10(10), 16, https://doi.org/10.1167/10.10.16.