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Object-based biased competition during covert spatial orienting

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Abstract

Biased competition models assert that spatial attention facilitates visual perception by biasing competitive interactions in favor of relevant input. In line with this view, past work has shown that the benefits of covert spatial attention are greatest when targets must compete with interfering stimuli. Here, we propose a boundary condition for the resolution of interference via exogenous attention: Attention resolves visual interference between targets and distractors, but only when they can be individuated into distinct representations. Thus, we propose that biased competition may be object-based. We replicated previous observations of larger attention effects when targets were flanked by irrelevant distractors (interference present displays) compared to targets presented alone (interference absent displays). Critically, we then show that this amplification of cueing effects in the presence of interference is eliminated when strong crowding hampers the individuation of targets and distractors. Likewise, when targets were embedded within a noise mask that did not evoke the percept of an individuated distractor, attention effects were equivalent across noise and lone target displays. Thus, we conclude that exogenous spatial attention resolves interference in an object-based fashion that depends on the perception of individuated targets and distractors.

Introduction

A natural scene typically contains more information than the visual system can simultaneously process. Selective attention biases perceptual processing towards behaviorally relevant input-- at the expense of irrelevant input-- on the basis of spatial location, object identity, and/or feature values. Studies of space-based attention, the most investigated selective mechanism, have shown that items within an attended region are processed more effectively than those in unattended regions (Posner, 1980); in fact, one may even be unaware of salient unattended items (Neisser & Becklen, 1975; Simons & Levin, 1998). This facilitation is often explained via the biased competition model of attention. According to this perspective, all items in a given scene compete for selection and further

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processing, but this competition is biased toward the attended items (Desimone & Duncan, 1995).

The biased competition model has been supported in both neurobiological (e.g., Beck & Kastner, 2005; Bles, Schwarzbach, De Weerd, Goebel, & Jansma, 2006; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Moran & Desimone, 1985) and behavioral studies of space-based attention (e.g., Awh, Matsukura, & Serences, 2003; Awh, Sgarlata, & Kliestik, 2005; Shiu & Pashler, 1994; reviewed in Beck & Kastner, 2009; Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004; Carrasco, 2011; Vecera, 2000). Moran and Desimone (1985) found that responses to unattended stimuli were attenuated within macaque V4 and IT cortex when both attended and unattended stimuli were simultaneously positioned in the same receptive field. This finding was extended in a human fMRI study (Kastner et al., 1998): In the absence of attention, simultaneously presented images competed in a mutually suppressive fashion in V4. When participants selectively attended to one of the images, the suppressive influences of the unattended items were attenuated.

The neural evidence in favor of biased competition indicates that space-based attention facilitates perceptual decision making in part by filtering out external interference so that relevant items can be selected for further processing. Mechanistically, this involves suppressing the response of sensory neural populations that are “tuned to” the distractors, below what would be observed from passive sensory stimulation (e.g., Moran & Desimone, 1985). This model predicts that spatial cueing effects should be relatively greater in the presence of interference compared to displays containing a lone target (where no external interference is present to compete with target processing). Across several studies that have confirmed this prediction, “interference” has been broadly defined. For example, Awh et al. (2005) used non-predictive peripheral cues to measure accuracy-based attention effects in the presence and absence of interference in the form of letter distractors. Critically, the benefits of spatial cueing were much larger when a target number was surrounded by irrelevant letters, indicating that target identification was facilitated by suppressing external distractors. Similarly, Shiu and Pashler (1994) observed greater attention effects in a number identification task in the presence of backward masks (number signs that onset immediately after target offset). Cheal and Gregory (1997) found larger cueing effects in a target identification task when targets were either surrounded by co-occurring distractors and/or followed by backward masks. Thus, a broad array of psychophysical data support the account that attention helps aid target selection by excluding external interference when present.

Not all results can be easily explained by interference resolution alone, however. For instance, reliable attention effects can be observed in displays that do not contain explicit distractors (henceforth broadly termed “interference absent” displays). These findings demonstrate that spatial attention also serves to enhance the signal from items presented in attended locations (Carrasco, 2011; Doshier & Lu, 2000; Lu & Doshier, 1998). This could be accomplished via increased fidelity of the neural representation and/or by a reduction of internally-generated noise. Thus, we acknowledge that both signal enhancement and interference resolution contribute to spatial attention effects. The central goal of the present work, however, is to refine our understanding of the boundary conditions for interference

resolution via spatial attention. Thus, we focused in particular on the conditions under which we observed the signature of biased competition: larger benefits of spatial attention in the presence of significant interference.

We reviewed cases above that have demonstrated this signature of biased competition, but there are other cases where this empirical pattern has not been observed. Lu and Doshier (1998) manipulated target discriminability using superimposed interference patterns that obscured a target grating (henceforth termed “embedded noise”). They found that exogenous space-based attention effects *declined* as the intensity of the embedded noise increased, contrary to a biased competition account, and thus concluded that the results solely implicated signal enhancement (without concurrent external noise exclusion). Likewise, Scolari et al. (2007) measured spatial cueing effects while manipulating the spacing between targets and flanking distractors. Notably, targets and distractors contained highly similar physical properties (rotated Ts and Is), which is likely to produce relatively strong interference effects (Duncan & Humphreys, 1989; Baylis & Driver, 1992). Nevertheless, the results produced no evidence that attention effects were larger when distractors closely flanked the target. These results seem to contradict the conclusion that spatial cueing effects are larger in the context of any forms of external interference.

Boundary conditions of biased competition

Here, we propose a refined hypothesis that may reconcile these apparently conflicting findings. Specifically, we argue that exogenous spatial attention may specifically resolve competition *between discrete object representations*, such that this effect is contingent on the successful *individuation* of targets and distractors. This account predicts that the behavioral signature of biased competition – augmented benefits of spatial cueing in the presence of distractor interference – may not be observed when target-distractor individuation is impeded. One such impediment is visual crowding. In cluttered peripheral displays, signals from physically discrete objects are often inappropriately pooled together to form the perception of an incoherently bundled object. While there is debate regarding the nature of this pooling process (e.g., Ester et al., 2013), a growing consensus concedes that crowding impairs the observer’s ability to individuate the feature values of tightly clustered items (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Greenwood, Bex, & Dakin, 2009, 2010; Chen, Bao & Tjan, 2018). Barring eye movements, this jumbled percept is unlikely to be fully resolved by unlimited time or attention (Pelli et al., 2004; Scolari et al., 2007). Thus, we hypothesized that strong crowding would preclude effective individuation of targets and distractors, thereby eliminating the enhanced cueing effects that are often seen in the presence of strong distractor interference. We suspect that such perceptual integration may be occurring in Scolari et al. (2007), given high inter-stimulus similarity and close proximity of targets and distractors. Likewise, because Lu and Doshier (1998) employed embedded noise masks that were not perceived as individuated objects, interference resolution via spatial attention may have been precluded.

To test our hypothesis, we measured exogenously-driven spatial cueing effects while manipulating crowding strength by altering the intensity and nature of the interference in the display. We predicted that cueing effects would be equivalent between interference present

and interference absent displays when visual crowding was sufficiently strong. In addition, we examined the consequences of embedding targets within a noise mask (i.e., a speckled surface that obscured the target without eliciting the percept of a discrete distractor element). Here, we predicted that spatial cueing effects would be equivalent as with a completely clean target display in contrast to a condition with individuated distractors, which was nonetheless matched for perceptual difficulty.

Experiment 1

Awh, et al. (2005) demonstrated relatively larger attention effects when irrelevant distractors were present compared to lone target displays. The interaction between display type (with and without interference) and the size of the attention effect is the critical empirical pattern, as it provides evidence for biased competition. Our first goal was to replicate this empirical pattern using a similar procedure. In Experiment 1, subjects reported the identity of a target digit that was presented in parafoveal space either alone (distractor absent condition) or flanked by letter distractors (distractor present condition), and we compared the size of the attention effects between these two conditions, as measured by performance accuracy. Any attention effects in the distractor absent condition indicate signal enhancement, wherein target identification is facilitated by suppressing internally-generated noise and/or increasing the fidelity of the internal representation (Lu & Doshier, 1998; Doshier & Lu, 2000). Comparatively larger effects observed in the distractor present condition indicate that target identification is further improved via external noise reduction, such that the signals generated from distracting elements are suppressed.

Methods

Subjects—A total of 24 subjects participated in Experiment 1, matching the largest sample size reported in Awh, et al. (2005; across five experiments, sample sizes ranged from 8–24 subjects, with a mean of 16.4). All subjects were students from the University of Oregon with normal or corrected-to-normal vision and gave written informed consent before participating. All experimental sessions were 90 minutes in length, and each student received partial course credit for their participation.

Stimuli—Stimuli were generated using Microsoft Visual Basic 6.0 and presented on an 18-inch CRT monitor with a refresh rate of 120 Hz. Each stimulus display consisted of one target and six distractors. The target was a single digit selected randomly from a set of integers 1–9. The distractors were randomly drawn without replacement from a set of 24 English alphabet characters (excluding I and O). All stimuli were presented in a dark gray calculator font on a white background and measured 0.70 width \times 0.80° height of visual angle. On each trial, the target was presented along the horizontal meridian either to the left or right of a fixation point at a distance of approximately 3.5° . Six distractors were simultaneously presented, 3 centered above the target and 3 centered below (the center distractor of each trigram was approximately 1.4° away from the target and spaced 0.6° from neighboring distractors). Each stimulus in the target display was masked with a “window-pane” stimulus (i.e., an open square divided into four equal quadrants; see Figure 1).

Experimental Procedure—See Figure 1 for an illustration of the sequence of events. Subjects were seated comfortably at a desk in a completely dark room at a distance of approximately 60 cm from the computer monitor. Each trial began with a fixation point in the center of the screen measuring 0.35° of visual angle. Following 103 ms of fixation, a peripheral cue (a black dot measuring 0.27° in diameter) appeared in one of the two possible target locations for 33 ms, followed by a 50 ms blank period. The target display then appeared for a duration that was predetermined in a previous staircased timing procedure (see Timing Procedure below). The target was equally likely to appear in the cued (valid condition) and uncued (invalid condition) locations, rendering the peripheral cue wholly uninformative. On half of all trials, the target appeared alone (distractor absent condition) or surrounded by six distractors (distractor present condition). All four conditions (valid-distractor absent, valid-distractor present, invalid-distractor absent, and invalid-distractor present) were intermixed. The target display was followed by window-pane masks for 325 ms, after which a “?” probe appeared in the correct target location and remained onscreen until the end of the trial. Subjects reported the identity of the number target that had appeared in the probed location with an unspeeded button press using the number pad on a standard QWERTY keyboard. To avoid incorrect responses due to errant presses, subjects could change their responses by selecting a different key and pressed “Enter” once they were ready to submit their answer. After each response, subjects were given written feedback on their single trial performance. Subjects completed 8 blocks of this procedure, for a total of 320 trials.

Timing Procedure—The amount of time needed to sufficiently encode a stimulus can vary widely between individuals. To account for these individual differences and to ensure task difficulty could not explain any of the observed results, each subject participated in 8 blocks of a staircase timing procedure to estimate exposure durations for valid trials in the main experiment (e.g., Awh, Matsukura & Serences, 2003; Awh, Sgarlata & Kliestik, 2005; Williamson, et al., 2009; Stevens, et al., 2012). Here, subjects were presented with a similar procedure as described above, with the following important exceptions. The peripheral cue was 100% valid, meaning no invalid trials were presented. Targets were equally likely to appear with or without distractors. On the first instance of each display type, the stimuli were onscreen for 167 ms (20 frames). In the event of a correct response, exposure duration was reduced by 8.33 ms (1 monitor refresh cycle) on the next trial of the same display type; an incorrect response resulted in an increased exposure duration by 16.66 ms (2 refresh cycles). These trial-by-trial adjustments were made separately for valid-distractor absent and valid-distractor present displays, resulting in independent exposure duration estimates for each display type that should conform to a common performance criterion of approximately 68%. The last two blocks of this procedure were checked by eye to ensure that each subject reached asymptotic performance; if this was not the case, the subject was asked to complete two more blocks. Exposure durations of the final two blocks were averaged together, and these averages were used to set the timing in the subsequent main experiment for both valid conditions, as well as their (previously unseen) invalid counterparts. In the event that estimates exceeded 200 ms, exposure durations were set to this cap to reduce the likelihood that subjects could make volitional attentional shifts or eye movements following stimulus display onset (e.g., Itti & Koch, 2001).

The staircase procedure described above has been used in many previous studies (e.g., Awh, et al., 2003; Awh, et al., 2005; Williamson, et al., 2009; Stevens, et al., 2012). Given the potential for large individual differences in encoding time between distractor present and absent displays, even when fully attended, using one duration across subjects or even across display types is likely to result in floor or ceiling effects in one or the other condition. Such floor and ceiling effects can obscure the behavioral measures of attention effects. By ensuring that both valid conditions are at an acceptable accuracy level (approximately 68%), we allow for both small and large attention effects for each display type (and even reversals, should they occur). Furthermore, our goal here is to evaluate the presence or absence of biased competition effects, defined as the difference in attention effect sizes between distractor present and absent displays (see *Analysis* below). Thus, pinning the two valid conditions to a (near) matched accuracy level makes comparing attention effects across the two display types much more straightforward, where we can confidently rely on a simple subtraction. Finally, we used the exposure duration estimates determined in the timing procedure for the valid-distractor absent and valid-distractor present displays as an operational measure of the strength of interference, described in full detail below.

Analysis

Interference Effects.: We employed a staircase procedure that estimated for each subject the exposure durations needed to obtain criterion performance in distractor present and absent displays, respectively, when attention was voluntarily and consistently directed to their locations (see *Timing Procedure* above). In addition to compensating for individual differences in perceptual ability, the results of this task serve as an objective measure of distractor interference, or crowding. As stated in the Introduction, the absence of time pressure does not fully ameliorate spatial crowding. However, exposure duration has been shown to mediate the extent of spatial crowding, such that the area of feature integration increases with decreased exposure durations (Tripathy & Cavanagh, 2002). We therefore surmised that stimulus displays with relatively stronger interference would require longer presentation times to reach a common performance criterion (this expectation holds for all forms of visual interference effects, and not only ones classified as spatial crowding). We used the difference between each subject's valid-distractor absent and valid-distractor present exposure durations to calculate the degree to which the distractors interfered with target identification, where comparatively greater interference would result in greater duration differences. Note that while the exposure durations used for the main experimental task were by necessity expressed in monitor refresh rate frames and thus rounded to the nearest integer, the analyses reported below utilized the millisecond estimate value prior to rounding.

Attention & Biased Competition Effects.: Given that we were interested in attention effects on perceptual sensitivity rather than decision time, our subjects were explicitly instructed to emphasize accuracy over speed and were even given an opportunity to change their responses before submitting. Thus, we chose to forego measuring reaction time (RTs; often used in classic attention studies; e.g., Posner, 1980; Posner, Snyder & Davidson, 1980) in favor of accuracy as an objective measure of attention effects. Performance accuracy for each condition (valid-distractor absent, valid-distractor present, invalid-distractor absent, and

invalid-distractor present) was calculated on a subject-by-subject basis. Attention effects are defined as the difference between valid and invalid performance scores.

The central question posed in this study is whether the presence of external interference elicits larger attention effects compared to interference-free displays. We term this the biased competition effect, as this pattern of results is implicitly predicted by the neurally-supported theoretical account of the same name. Biased competition effects are thus defined as the difference between attention effects for distractor present and distractor absent displays, or written as:

$$\text{Biased Competition} = \text{Distractor present}_{(\text{Valid} - \text{Invalid})} - \text{Distractor absent}_{(\text{Valid} - \text{Invalid})}$$

Because our primary focus in this manuscript is to compare attention effect sizes between interference present and absent displays, we elected to include a scaled-information Bayes factor analysis for each comparison pertaining to the biased competition effect, which allows for a direct comparison between the alternative and null hypotheses (Rouder et al., 2009). Thus, this offers additional evidence, in conjunction with the traditional p-value, as to whether the biased competition effect is present.

Results and Discussion

Interference Effects.—Across all subjects, the staircase procedure revealed that the valid-distractor present condition required a longer exposure duration ($M = 49.68$ ms) to reach the same level of performance as the valid-distractor absent condition ($M = 32.99$ ms), $t(23) = 4.56$, $p = .00014$, $d = 0.93$ (see Figure 2A). Thus, the letter distractors effectively interfered with digit target processing, even when the target location was pre-cued with solely valid cues.

Attention & Biased Competition Effects.—Figure 2B depicts mean target identification accuracy in the main experiment as a function of display type (distractor absent vs. distractor present) and the validity of the pre-cue (valid vs. invalid). A two-way analysis of variance (ANOVA) revealed a significant interaction between these two factors (valid-distractor absent: $M = 72\%$; valid-distractor present: $M = 71\%$; invalid-distractor absent: $M = 66\%$; invalid-distractor present: $M = 56\%$), $F(1,23) = 8.74$, $p = .007$, $d = 0.6$. Strong evidence in favor of a significant biased competition effect is further given by the Bayes factor analysis: $BF_{10} = 8.02$. For both display types, subjects performed better when the exogenous pre-cue drew their attention to the upcoming target location (attention effects: distractor absent: $M = 6\%$; distractor present: $M = 15\%$). Planned comparisons between the valid and invalid trials revealed that these effects were significant for each display type, distractor absent: $t(23) = 2.63$, $p = .015$, $d = 0.54$; distractor present: $t(23) = 10.02$, $p < .0001$, $d = 2.04$. Importantly, however, the attention effects were greater in the presence of interference, resulting in a significant biased competition effect, as revealed by the interaction described above between display type and validity ($M = 9\%$).

Using number and letter stimuli presented in parafoveal space with a fully exogenous pre-cue, we observed significant attention effects as measured by accuracy in both the presence

and absence of external interference. Because the target was presented alone on distractor absent displays, attention effects in this condition serve as evidence that covert attention enhanced the target signal. Furthermore, we interpret the increased size of attention effects in interference displays as evidence of distractor suppression that reduced the undue influence from irrelevant stimuli. Thus, the interaction between cueing effects and display type serves as a signature of biased competition.

While we used Awh, et al. (2005) as a template for the design of Experiment 1, there are several noteworthy differences. The previous study presented an interference display on a filled 6×6 grid, where the target could appear in one of four quadrants at a Euclidean distance of 2.6° from fixation and with a 1° spacing between neighboring stimuli. Here we presented six distractors surrounding the target only, which could appear in one of two locations along the horizontal meridian 3.5° away from fixation (and a 1.4° distance from distractors; see Experiment 1 Methods: Stimuli). Despite these differences, we observed the same biased competition pattern previously reported. A similar pattern is also reported in the Supplemental Material of this paper (see Supplementary Experiment 1), where interference was reduced to just one letter above and below the target number. Together, these results suggest that the behavioral biased competition effect generalizes across a range of displays.

Nonetheless, as described in the Introduction, behavioral biased competition effects are not consistently observed in the literature. In a previous study using oriented Ts as targets (Scolari, et al., 2007), we did not find evidence that interference from perceptually similar distractors increased the size of the attention effect. This suggested to us that despite the growing evidence that the biased competition effect is robust against small changes in number-letter displays, it may be susceptible to manipulations in target-distractor similarity. Admittedly, however, observing this effect was not the primary goal of the previous study. Thus, we set out to replicate the observation that biased competition effects can be eliminated when unfamiliar targets are surrounded by perceptually similar distractors.

Experiment 2

In Experiment 2, we employed a design where high target-distractor similarity should lead to substantially stronger crowding effects (e.g., Duncan & Humphreys, 1989; Baylis & Driver, 1992; Pelli et al., 2004; Kimchi & Pirkner, 2015; Kooi et al., 1994; Scolari et al., 2007; Treisman, 1991). Subjects reported the orientation of a target T that appeared either alone or flanked by a set of oriented Is. We predicted that the stronger crowding induced by high inter-stimulus similarity would hinder the individuation of targets and distractors, thereby yielding equivalent attention effects between distractor present and distractor absent displays.

Methods

The methods used in Experiment 2 were similar to those of Experiment 1, with the following changes.

Subjects—A new group of 12 subjects participated in Experiment 2; all were naïve to the purpose of the study. This sample size is within the range of those reported from the relevant

studies in Scolari, et al (2007; across Experiments 1–4, sample sizes ranged from 8–27 with a mean of 15.25). In all cases, significant differences in accuracy between valid and invalid trials were observed. Furthermore, a pilot study conducted prior to this one also produced large attention effects regardless of whether distractors were present with a sample size of 9 subjects (see Supplementary Experiment 2).

All subjects were students from the University of Oregon with normal or corrected-to-normal vision, and each gave written informed consent before participating. All experimental sessions were 90 minutes in length, and students received partial course credit for their participation.

Stimuli—The target was a letter “T” (subtending $.70 \times .70^\circ$ of visual angle) which was rotated either 0, 90, 180, or 270° , allowing for four possible targets. Each of the six distractors was a randomly selected letter “I” (also subtending $.70 \times .70^\circ$ of visual angle) rotated either 0 or 180° . The stimuli were presented in Arial font, with the target centered at approximately 3.5° away from fixation (see Figure 3A).

Experimental Procedure—As in Experiment 1, the peripheral cue was wholly uninformative, and the target was equally likely to appear alone (distractor absent condition) or surrounded by six distractors (distractor present condition). The most notable changes between this and Experiment 1 are the target and distractor stimuli (see above) and response mapping. Subjects reported the identity of the target oriented T with an unspeeded button press using the number pad on a standard QWERTY keyboard. Following the spatial configuration of the keys themselves, subjects pressed “5” to report an upright (0°) target, “1” to report a target oriented leftward (90°), “2” to report an upside-down (180°) target, and “3” to report a target oriented rightward (270°). Once made, the target stimulus associated with the subject’s button press was displayed in place of the probe. As in Experiment 1, subjects were given the opportunity to change their responses, and pressed “Enter” to confirm their answer. After each response, subjects were given written feedback on their single trial performance. Subjects completed 8 blocks of this procedure, for a total of 320 trials.

Timing Procedure—The timing procedure matched that reported in Experiment 1.

Analysis—The same analyses were performed as in Experiment 1. Notably, we predicted that the biased competition effect should be equivalent between display types in this experiment, and hence we anticipate accepting the null hypothesis for this comparison. To more rigorously evaluate the evidence for a null result in these instances, as in Experiment 1 we again included a scaled-information Bayes factor analysis that allows for a direct comparison between the alternative and null hypotheses (Rouder et al., 2009).

Results and Discussion

Interference Effects.—Across all subjects, the valid-distractor present condition required a longer exposure duration ($M = 50.43$ ms) to reach the same performance criterion as the valid-distractor absent condition ($M = 23.5$ ms), $t(11) = 9.16$, $p < .0001$, $d = 2.64$ (see Figure 3B).

Attention & Biased Competition Effects.—Figure 3C depicts mean target identification accuracy in the main experiment as a function of display type and pre-cue validity. Subjects exhibited strong attention effects in both the distractor absent ($M = 27\%$; $t(11) = 10.91$, $p < .0001$; $d = 3.15$) and distractor present ($M = 27\%$; $t(11) = 13.06$, $p < .0001$; $d = 3.77$) conditions. However, there was no difference in the size of the effects across display conditions, $F(1,11) = .034$, $p = 0.86$, $d = 0.05$, $BF_{01} = 3.54$, and hence no biased competition effect.

As in Experiment 1, we used an uninformative peripheral cue to manipulate the locus of exogenous spatial attention. While we observed the behavioral signature of biased competition in the first experiment, spatial cueing effects between distractor present and distractor absent displays were equivalent in Experiment 2. A similar result – equivalent attention effects across display types -- was observed in Supplementary Experiment 2 (see Supplemental Material). Reliable attention effects in the distractor absent display point to a signal enhancement effect of spatial cueing, similar to (albeit larger than) that observed in Experiment 1. However, equivalent attention effects between distractor present and absent displays suggests that attention did not reduce influences from external interference in Experiment 2.

The absence of distractor suppression coupled with the considerably large attention effects (a 12% increase from Experiment 1 for distractor present displays) may lead one to surmise that the distractors had no deleterious impact on performance. Despite the equally large attention effects across displays, however, it is clear that the highly similar distractors impeded target processing. Subjects needed significantly more time to encode flanked targets compared to those presented alone. Indeed, interference was stronger here relative to Experiment 1 (judging by the increased difference in exposure durations between display types¹), in line with past work showing that crowding is amplified as the similarity between targets and flankers increases (e.g., Duncan & Humphreys, 1989; Baylis & Driver, 1992; Kimchi & Pirkner, 2015; Kooi et al., 1994).

While the stimuli were arguably the most pertinent difference between Experiments 1 and 2, there were other noteworthy differences. The number of target and distractor alternatives were reduced in Experiment 2, and the discrimination required of the subjects was different. To enable a more direct comparison between experiments, Experiment 3 employed the same number-letter displays used in Experiment 1. Here, we increased the influence of the letter distractors by moving the whole display into peripheral space, a manipulation known to increase the strength of visual crowding (Bouma, 1970). We predicted that this would eliminate the biased competition pattern observed in Experiment 1, while holding constant the stimuli employed as targets and distractors.

¹While a between subjects t-test comparing crowding strength for Experiments 1 and 2 did not reach significance ($t(34) = 1.823$, $p = .077$), a scaled-information Bayes factor analysis weakly favored the alternative hypothesis: $BF_{10} = 1.41$.

Experiment 3

In Experiment 2, the behavioral signature of biased competition was absent; attention effects were equivalent in the presence and absence of distractors, unlike in Experiment 1. Although we suggested that stronger crowding may have disrupted effective suppression of the distractors, this factor was confounded with a change in the type of stimuli and the kind of discrimination required of subjects. Thus, in Experiment 3 we sought to increase crowding using the same stimuli and discrimination task as in Experiment 1. The display was presented in peripheral (5.6° eccentricity) rather than parafoveal (3.5° eccentricity) space to increase the strength of visual crowding (Bouma, 1970; Bouma, 1973; Pelli et al., 2004; Kimchi & Pirkner, 2015). We hypothesized that stronger crowding would impair distractor suppression by preventing target-distractor individuation, thereby yielding equivalent attention effects across displays.

Methods

The methods used in Experiment 3 were similar to those of Experiment 1, with the following changes.

Subjects—A total of 23 new subjects participated in Experiment 3. All subjects were students from the University of Oregon with normal or corrected-to-normal vision and gave written informed consent before participating. All experimental sessions were 90 minutes in length, and each student received partial course credit for their participation.

Stimuli—The stimuli matched exactly those used in Experiment 1, except that the target display was now centered at 5.6° from fixation.

Experimental Procedure—The procedure matched Experiment 1.

Timing Procedure—The timing procedure matched Experiment 1.

Analysis—The same analyses were employed here as in Experiment 1.

Results and Discussion

Interference Effects.—Consistent with both Experiments 1 and 2, exposure durations were estimated to be significantly longer for the valid-distractor present condition ($M = 99.72$ ms) relative to the valid-distractor absent condition ($M = 47.92$ ms), $t(22) = 5.73$, $p < .0001$, $d = 1.19$ (see Figure 4A). Given that interference should be amplified for far-- relative to close-- displays, we next compared the size of the crowding effects observed here to those observed in Experiment 1. This post-hoc analysis revealed that by virtue of positioning the display further into the periphery, we succeeded in increasing the size of the crowding effect (heteroscedastic between-subjects t-test²: $t(29.046) = 3.6$, $p = .001$, $d = 1.34$, where $a = .017$ following a conservative Bonferroni correction to account for multiple statistical tests since a similar comparison is made in Experiment 5 below).

²The variances between groups were not homogeneous via Levene's Test for Equality of Variances, $p = .019$.

Attention & Biased Competition Effects.—Figure 4B depicts mean target identification accuracy in the main experiment as a function of display type and pre-cue validity. Again, subjects exhibited strong attention effects in both the distractor absent ($M = 9\%$), $t(22) = 5.03$, $p < .0001$, $d = 1.049$, and distractor present ($M = 13\%$), $t(22) = 5.90$, $p < .0001$, $d = 1.23$, conditions. However, despite using the same stimuli as in Experiment 1--albeit presented at a greater eccentricity-- there was no difference in the size of the effects across display conditions (biased competition effect: $M = 3.4\%$), $F(1,22) = 2.51$, $p = 0.13$, $d = 0.33$. Evidence in favor of the null hypothesis was further provided, albeit weakly, via the Bayes factor analysis: $BF_{01} = 1.49$. While these results indicate that biased competition was effectively absent, a post-hoc between-subjects comparison of the size of the effects across Experiments 1 and 3 did not reach significance, $t(45) = 1.407$, $p = .17$, $d = 0.42$, $BF_{01} = 1.44$.

This experiment used a near identical design and procedure to Experiment 1, with the exception of the peripheral position of the stimulus display. Just by moving the stimuli further from fixation, we eliminated the behavioral signature of biased competition. The larger eccentricity increased crowding strength, in line with the known link between eccentricity and crowding (Bouma, 1970). This explanation is further supported by the significantly larger interference effects observed here compared to Experiment 1. We conclude that, similar to Experiment 2, increased crowding prevented target-distractor individuation and thereby prevented the resolution of distractor interference by spatial attention. Unlike Experiment 2, though, the attention effects were comparable in size to those reported in Experiment 1. This provides evidence against the possibility that biased competition is absent only when signal enhancement alone produces large attention effects (as was the case in Experiment 2).

While we report no differences in the attention effect sizes between display conditions in Experiment 3, this pattern was not significantly different from the biased competition pattern observed in Experiment 1. This null result is not too surprising because we were relying on a between-subjects comparison of a relatively small effect. Thus, in Experiment 4, we presented both parafoveal and peripheral stimulus displays to a single set of subjects to provide a more sensitive test of whether the biased competition effect varies as a function of display eccentricity.

Experiment 4

In Experiment 4, subjects viewed single digit or number-letter displays (intermixed) presented either at a close (3.5° as in Experiment 1) or far (5.6° as in Experiment 3) eccentricity. The order of the eccentricity conditions was blocked (and counterbalanced between subjects), allowing subjects to maintain stable attention sets with respect to expected target locations over the course of the experiment. We predicted that the biased competition effect would only be observed when the display was presented at a relatively close eccentricity.

Methods

The methods used in Experiment 4 were similar to those of Experiment 1 and 3, with the following changes.

Subjects—Twenty-three subjects participated in Experiment 4. All subjects were students from the University of Oregon with normal or corrected-to-normal vision and gave written informed consent before participating. All experimental sessions were 90 minutes in length, and each student received partial course credit for their participation. Two subjects were removed from the analyses: One due to experimental error, and a second one because she reported after the session that she had not been wearing her prescription glasses which made the task difficult. All analyses include the remaining 21 subjects.

Stimuli—Targets and distractors matched exactly those used in Experiment 1 and Experiment 3. The stimulus display was centered 3.5° from fixation (close condition) or 5.6° from fixation (far condition).

Experimental Procedure—Each subject completed two experimental tasks: 4 blocks of 32 trials each of the close eccentricity condition and 4 blocks of the far eccentricity condition; the order of conditions was counterbalanced across subjects. See Experiment 1 *Procedures* for all other design and procedural details relating to this experiment.

Timing Procedure—Subjects completed between 5–11 blocks of the timing procedure for each of the eccentricity conditions. For most of the subjects, the timing procedures and main experimental tasks were interleaved, with the relevant timing procedure preceding the corresponding experimental task (for two subjects, both timing procedures were completed first before starting the main experiment). See Experiment 1 *Timing Procedures* for all other details relating to this task.

Analysis—The same analyses were employed here as in Experiment 1.

Results and Discussion

Interference Effects.—Just as we saw in Experiment 1, exposure durations were significantly longer for valid-distractor present displays ($M = 50.86$ ms) than for valid-distractor absent displays ($M = 34.54$ ms) at the close eccentricity, $t(20) = 4.42$, $p = .00026$, $d = 0.96$. This was true for the far eccentricity condition as well (valid-distractor present: $M = 145.31$ ms; valid-distractor absent: $M = 63.58$ ms), $t(20) = 8.92$, $p < .0001$, $d = 1.95$. The crowding effect was significantly greater for the far displays compared to the close displays, $F(1,20) = 58.52$, $p < .0001$, $d = 1.67$ (see Figure 5A), consistent with our comparison between Experiments 1 and 3 (See Experiment 3 *Results*), and in line with the known properties of visual crowding.

Attention & Biased Competition Effects.—Figure 5B depicts mean target identification accuracy in the main experiment as a function of display eccentricity (close vs far), display type (distractor present vs distractor absent) and pre-cue validity (valid vs invalid). A repeated measures ANOVA produced a significant 3-way interaction between

these variables of interest: $F(1,20) = 7.461$, $p = .013$, $d = 0.6$. Attention effects for the two nearly-identical distractor absent conditions were equivalent (close eccentricity: $M = 3.3\%$; far eccentricity: $M = -2.1\%$; $t(20) = 1.6$; $p = 0.13$, $d = 0.35$), while attention effects for the two distractor present conditions differed significantly (attention effects: close eccentricity: $M = 13\%$; far eccentricity: $M = -3.6\%$; $t(20) = 6.81$; $p < .0001$, $d = 1.49$). Planned comparisons also revealed significant attention effects for distractor present displays at a close eccentricity, $t(20) = 5.079$, $p < .0001$, $d = 1.11$, but not for their distractor absent counterparts, $t(20) = 1.115$, $p = .278$, $d = 0.24$, resulting in a significant biased competition effect ($M = 10\%$), $F(1,20) = 4.797$, $p = .041$, $d = 0.48$, $BF_{10} = 1.82$. Conversely, attention effects were equivalently absent for both distractor present, $t(20) = 1.632$, $p = .118$, $d = 0.36$, and distractor absent, $t(20) = 0.677$, $p = .51$, $d = 0.15$, displays presented at a far eccentricity (biased competition effect: $M = -1.5\%$; no interaction: $F(1,20) = 0.138$, $p = .71$, $d = 0.081$, $BF_{01} = 4.65$).

Experiment 4 was designed as a within-subjects test of Experiments 1 and 3, and we replicated the pattern of biased competition effects reported across both experiments. Namely, biased competition was only observed when the targets were presented relatively close to fixation, and crowding was reduced. In the far eccentricity condition, in which stronger crowding impeded target-distractor individuation, cueing effects were equivalent in the presence or absence of distractors. That said, a curious finding was that cueing effects were not observed in both distractor absent displays and in far eccentricity distractor present displays, in contrast to other studies reported here and in the literature. We do not have a firm explanation for why cueing effects did not emerge in these conditions, except to note that such effects for lone target displays are often quite modest, particularly when perceptual task demands are low (e.g., Grindley & Townsend, 1968; Shiu and Pashler, 1994; Doshier & Lu, 2000), as is the case with our high contrast single digit stimuli.

The absence of a cueing effect in distractor present displays is less common, and raises the possibility that long exposure durations inadvertently eliminated the effect. By setting exposure durations based on individual estimates, we ensure that stimulus encoding time differences do not influence attention effects. However, we also run the risk of reducing or eliminating attention effects if the durations are unduly long, especially if subjects are given sufficient time to disengage from an invalidly cued location and shift attention to the target location before the display offsets. Fortunately, there are wide individual differences in encoding time: Estimates ranged from 56.66 ms to 320.6 ms for the validly cued peripheral distractor present displays in Experiment 4 (note that durations used in the main experiment were restricted to 200 ms or less; see Experiment 1 *Methods: Timing Procedure*). This variability lends itself well to a post-hoc split-half analysis on the data, allowing us to determine whether subjects with relatively short and long exposure duration estimates show attention effect size differences. The 11 subjects with the shortest exposure durations required on average 104.56 ms to identify a validly cued crowded target at the performance criterion, which is comparable to the estimate for the full group of subjects from Experiment 3 ($t(32) = 0.29$, $p = 0.77$, $d = 0.10$). Despite the shorter exposure durations used for these subjects, the attention effect remained absent ($M = -4.3\%$), and did not differ from the other half of subjects with exposure duration estimates averaging 190.25 ms ($M = -2.8\%$; $t(19) = 0.32$, $p = 0.75$, $d = 0.15$). This analysis rules out longer exposure duration estimates, in and

of themselves, as being responsible for the absent cueing effect. We thus conclude that these findings still fall in line with our hypothesis that the interaction between cueing effects and interference is eliminated when target-distractor individuation is impeded.

Experiment 5

Experiments 1–4 produced results consistent with our prediction that the amplification of cueing effects in the presence of distractors can be eliminated when visual crowding impedes target-distractor individuation. This was demonstrated by manipulating crowding strength in two ways. Increased target-distractor similarity and increased eccentricity of targets yielded amplified crowding effects, as shown by the threshold durations from the staircased timing procedure. In turn, increased crowding effects eliminated the interaction between spatial cueing effects and the level of interference in the display. While there is ongoing debate regarding the specific consequences of visual crowding (e.g., Agaoglu & Chung, 2016; Greenwood, et al., 2009; 2010; Harrison & Bex, 2015; Parkes, et al., 2001; Ester, et al., 2014; Ester, et al., 2015; Gheri & Baldassi, 2008; Strasburger, 2005; Wolford, 1975), researchers generally agree that visual properties across crowded stimuli are erroneously integrated in some fashion (Pelli et al., 2004). This motivates our hypothesis that the behavioral signature of biased competition, amplified attention effects in the presence of distractors, is contingent on the individuation of targets and distractors.

If our object-based account of biased competition is correct, any kind of visual interference that is not perceived as a distinct object from the target should fail to yield increased attention effects compared to a clean display. Thus, to generalize the earlier findings, we created displays in which number targets were embedded within a speckled noise pattern that was not perceived as a distinct distractor object. Even though this noise mask produced similar interference to that evoked by the distractors in the earlier studies, we predicted that subjects would perceive target and noise as a single integrated signal, and that attention effects in this study should be equivalent between clean and noise displays.

Methods

Subjects—Twenty subjects participated in Experiment 5.

Stimuli—The single digit targets used in Experiments 1, 3 and 4 were included here at the original (parafoveal) eccentricity; however, targets were embedded in a noise mask (i.e., random speckled patterns that were not intended to elicit a percept of a discrete distractor element) on interference trials. One of four possible speckled patterns was randomly selected and presented simultaneously with the target on noise present trials (see Figure 6A). The target was presented alone on noise absent trials.

Experimental Procedure—See Experiment 1 for a description of the procedure.

Timing Procedure—See Experiment 1 for a description of the timing procedure.

Analysis—See Experiment 1 for a description of the analyses.

Results and Discussion

Interference Effects.—Exposure durations were estimated to be significantly longer for valid-noise present trials ($M = 74.15$ ms) relative to valid-noise absent trials ($M = 36.03$ ms), $t(19) = 6.44$, $p < .0001$, $d = 1.44$ (see Figure 6B). We next compared the size of the interference effects observed here to those observed in Experiment 1. This analysis revealed that interference in these noise present displays was stronger than that observed in the distractor present displays of Experiment 1 (between-subjects t-test: $t(42) = 3.19$, $p = .003$, $d = 0.98$; where $a = .017$, following a conservative Bonferroni correction to account for multiple statistical tests since a similar comparison was made in Experiment 3 above).

Attention & Biased Competition Effects.—Figure 6C depicts mean target identification accuracy in the main experiment as a function of display type and pre-cue validity. Subjects exhibited strong attention effects in both the noise absent ($M = 6\%$), $t(19) = 2.20$, $p = .04$, $d = 0.49$, and noise present ($M = 9\%$), $t(19) = 3.92$, $p = .001$, $d = 0.88$, conditions. Furthermore, there was no difference in the size of the effects across display conditions (biased competition effect: $M = 3\%$), $F(1,19) = 1.14$, $p = 0.3$, $d = 0.24$, $BF_{01} = 2.63$.

Here, we compared attention effects across conditions in which a target was presented alone or embedded within a speckled noise pattern. As we saw when we increased the strength of visual crowding, attention effects were equivalent across display conditions. In another study (see Supplemental Material: Supplementary Experiment 3), we replicated this pattern using a different stimulus set (a rotated target T, as in Experiment 2). We take the results of this experiment as further evidence that attention failed to resolve external interference that could not be individuated into discrete distractor elements. That said, a post-hoc between-subjects comparison of biased competition effects in Experiments 1 and 5 did not reach significance, $t(42) = 1.36$, $p = .18$, $d = 0.42$, $BF_{01} = 1.48$. Thus, Experiment 6 was conducted to test this prediction with a more sensitive within-subjects design.

Experiment 6

In Experiment 6, subjects were presented with digit targets either flanked by letter distractors or embedded in speckled noise, allowing us to make a within-subjects comparison of biased competition effects with the two display types. We predicted significantly larger attention effects in the presence of letter distractors compared to a target presented alone, but that interference from a speckled noise mask would yield cueing effects similar to that with the lone target displays.

Methods

Subjects—Fifteen naïve subjects participated in Experiment 6. All subjects were students from the University of Oregon with normal or corrected-to-normal vision and gave written informed consent before participating. Experimental sessions were 90 minutes in length, and each student received partial course credit for their participation.

Stimuli—The target was a single digit. Distracting elements were either letters, identical to those used in Experiment 1, or speckled noise patterns, identical to those used in Experiment 5.

Experimental Procedure—Subjects viewed digit targets either alone or in the presence of interference (intermixed), where interference was defined as either flanking letter distractors (as in Experiment 1) or embedded noise patterns (as in Experiment 5). Subjects completed one timing task followed by one experimental task for each of the two interference conditions, for a total of four unique tasks. The order of the interference conditions was counterbalanced across subjects.

Timing Procedure—See Experiment 4 *Methods* for a description of the timing procedure.

Analysis—See Experiment 1 *Methods* for a description of the analyses.

Results and Discussion

Interference Effects.—Exposure durations on valid trials were significantly longer in the presence of flanking letter distractors ($M = 48.95$ ms) compared to no distractors ($M = 31.14$ ms), $t(14) = 3.44$, $p = .004$, $d = 0.89$. This was true for the embedded noise task as well (noise present: $M = 53.02$ ms; noise absent: $M = 29.29$ ms), $t(14) = 6.03$, $p < .0001$, $d = 1.56$. The strength of interference did not differ between the two types of interference, $F(1,14) = 1.40$, $p = .256$, $d = 0.31$ (see Figure 7A).

Attention & Biased Competition Effects.—Figure 7B depicts mean target identification accuracy in the main experiment as a function of interference type (letter distractors vs embedded noise), display type (interference present vs absent) and pre-cue validity (valid vs invalid). A repeated measures ANOVA produced a marginally significant 3-way interaction between these variables of interest, $F(1,14) = 4.41$, $p = .054$, $d = 0.54$. Because the interaction was marginal, we conducted an additional scaled-information Bayes factor analysis (Rouder et al., 2009); the results favored the alternative hypothesis: $BF_{10} = 1.68$. Attention effects for the two identical lone target conditions were equivalent (intermixed with trials where interference was defined as flanking letters: $M = 3\%$; where interference was defined as embedded noise patterns: $M = 2\%$; $t(14) = 0.57$; $p = 0.58$, $d = 0.15$). Conversely, attention effects for the two interference conditions differed significantly (flanking letters: $M = 16\%$; embedded noise: $M = 7\%$; $t(14) = 3.42$; $p = 0.0041$, $d = 0.88$). Planned comparisons revealed significant attention effects for flanking letter distractor displays, $t(14) = 7.97$, $p < .0001$, $d = 2.058$, but not for their distractor absent counterparts, $t(14) = 1.20$, $p = .25$, $d = 0.31$, and these patterns were significantly different from each other (biased competition effect: $M = 12.4\%$), $F(1,14) = 25.68$, $p < .0001$, $d = 1.31$, $BF_{10} = 274.2$. While within-subjects t-tests revealed attention effects were similarly absent in lone target displays ($t(14) = 0.75$, $p = 0.47$, $d = 0.19$) and significant in interference displays ($t(14) = 3.44$, $p = 0.004$, $d = 0.89$) for the embedded noise task, there was no significant interaction between display types (biased competition effect: $M = 5.4\%$, $F(1,14) = 3.611$, $p = .078$, $d = 0.49$). A scaled-information Bayes factor analysis similarly, albeit weakly, indicated the absence of an interaction: $BF_{10} = 0.807$.

Overall, the results of Experiment 6 confirm the qualitative pattern observed between Experiments 1 and 5. We found a significant biased competition effect using a parafoveal number-letter display, but no such effect when flanking letter distractors were replaced with embedded speckled noise patterns. The degree to which the target and external interference are treated as a uniform object is likely increased in the case of embedded noise, given their spatial overlap. We argue when stimuli are integrated into a single percept, external interference cannot be appropriately marked as irrelevant, leading to a failure to suppress distracting information. In this case, the attentional system may instead enhance the pooled representation of all elements in a manner similar to interference absent displays.

While we suspected the integration of relevant and irrelevant elements should be strongest with embedded noise displays compared to our previous crowding manipulations, the interaction between attention effects in the presence and absence of interference was only marginally significant. Similarly, the biased competition effect for the embedded noise display, while not statistically reliable, was trending towards a positive effect. Thus, to more rigorously evaluate the evidence for a null result, we conducted a Bayes factor analysis that allowed a direct comparison of the alternative and null hypotheses (Rouder et al., 2009). Though each of these comparisons resulted in values that provided relatively weak evidence in favor of one alternative over the other, they nonetheless conformed to our interpretations of the traditional p-values. It is also worth noting that the size of the embedded noise attention effect was consistent across Experiments 5 and 6, as measured by Cohen's d (0.88 and 0.89, respectfully). It seems, then, that the potentially marginal interaction between attention effects in the noise present and absent conditions are driven mainly by the noise absent trials. Notably, the noise absent condition was entirely equivalent in design and procedure across the two experimental tasks completed by each subject, and statistically, the attention effects between both were equivalent. We therefore ran a repeated measures ANOVA again comparing attention effects between display conditions, this time substituting noise absent values with the equivalent condition intermixed with flanking distractor trials. We observed no reliable interaction: $F(1,14) = 2.196$, $p = 0.16$, $d = 0.38$, and this conclusion was echoed by the Bayes factor ($BF_{01} = 1.45$).

Meta-analysis: Individual differences in crowding susceptibility

To further test our claim that exogenous attention fails to suppress irrelevant external signals when they are effectively integrated with the target, we conducted a meta-analysis correlating each subject's interference effect and biased competition effect. We predicted an inverse relationship between these factors across all display types, where large interference effects reflect substantial target-distractor integration and small biased competition effects reflect inadequate interference suppression.

The relationship between interference strength and biased competition was assessed via a simple linear regression, including data from 121 subjects across seven independent experiments: Experiments 1–3 and 5, and three supplementary experiments that followed a very similar methodological design to those included here (see Supplementary Materials for a description of the methods and the results for each of the three supplementary experiments). Experiments 4 and 6 were excluded from this meta-analysis as each subject

participated in two tasks manipulating different aspects of the stimulus display (i.e., the eccentricity of the target in Experiment 4, and the type of interference presented in Experiment 6), and there is no obvious choice to include the data from one task over the other (while including data from both would violate the assumption of independent samples). Note, however, that all the conditions included in Experiments 4 and 6 are nonetheless represented in the meta-analysis. Because we are concatenating data across experiments utilizing flanking distractor and embedded noise displays, we have opted to relabel conditions with the all-encompassing terms “interference present” and “interference absent” in the *Results and Discussion* below.

Results and Discussion

A linear regression revealed a moderate and robust negative relationship between the strength of interference and the size of biased competition effects: $R = -0.22$, $t(119) = 2.44$, $p = .016$ (see Figure 8). Thus, subjects who could more easily disambiguate the target from irrelevant elements also showed greater evidence that attention resolved the competitive interactions between stimuli.

Because we objectively measured interference effects with individual exposure duration estimates that were utilized during the main experiment, it is possible that exposure duration, and not strength of interference, predicts the presence or absence of biased competition effects. By this argument, longer exposure durations directly lead to reduced attention effects (and thereby reduced biased competition effects) because subjects were given sufficient time to disengage from any interference and process the target. The most obvious evidence we have that points against this explanation is the biased competition effect itself. That is, if exposure duration could explain attention effect sizes, then we should see larger effects when interference is absent compared to when it is present, given the significantly shorter exposure durations. With the exception of Supplementary Experiment 3, we never observed larger attention effects when the target was presented alone even when the biased competition effect was absent, nor was this pattern reported in Awh, et al. (2005). Furthermore, when we analyze together all five experiments that failed to produce a measurable biased competition effect (Experiments 2, 3, 5, and Supplementary Experiments 2 and 3), attention effects between the interference present and absent conditions are equivalent (interference present: $M = 14.9\%$; interference absent: $M = 14.9\%$), $t(76) = -.014$, $p = .99$, $d = .0016$. The fact that the attention effects for lone target displays rarely exceeded those for interference displays, despite a wide range of exposure duration differences, suggests to us that the effects we are observing are most likely due to a common attention mechanism across display types rather than the durations themselves. Specifically, we argue when an interference display is not readily segregated into its relevant and irrelevant component parts, the observer must rely on signal enhancement in a manner that is consistent with lone target displays, whereby the signal of the entire display is amplified (we return to this point below).

Nonetheless, the concern remains valid that longer exposure durations specifically in the interference present conditions could reduce or eliminate attention effects. As described previously, this is particularly an issue given that we are targeting transient, exogenous

attention with an uninformative peripheral cue. If the duration is set for too long, on invalid trials, subjects may have enough time to disengage from the cued location and shift attention to the other (target) location. This would result in smaller attention effects due to improved performance on invalid trials. It is worth highlighting again that the timing procedure used to estimate exposure durations only included valid trials, meaning any shifts of attention that could happen after stimulus onset did not contribute in any way to these estimates. Furthermore, when we removed all subjects from the meta-analysis whose estimates exceeded 150 ms in the interference present conditions ($N = 3$)³, the inverse relationship qualitatively improved: $R = -0.31$, $t(116) = 3.46$, $p = 0.00076$, contrary to the predictions of this alternative account.

To further investigate whether our results are driven solely by longer exposure durations, we re-examined our meta-analysis. First, we sorted all included 121 subjects based on their exposure durations for the interference present conditions, and next correlated the interference effects with the biased competition effects for only the 61 subjects with the shortest durations. In this analysis, every experiment (1–3, 5, SE 1–3) is represented by at least 4 subjects and exposure duration estimates range from 23–54 ms. If exceedingly long exposure durations in the interference present condition account for the absent biased competition effects, then we would expect that the relationship observed in our meta-analysis is driven primarily by the excluded 60 subjects, and that such a relationship should be absent or considerably weaker here. Instead, we observe a very robust inverse relationship: $R = -0.31$, $t(59) = -2.51$, $p = .015$. Furthermore, when we consider only subjects with exposure duration estimates of 100 ms or greater ($N = 15$), we still observe significant attention effects in the presence of interference ($M = 9\%$; $t(14) = 6.07$, $p < .0001$, $d = 1.57$). Finally, and perhaps most convincingly, exposure durations from interference present conditions alone fail to significantly predict individual biased competition effects across all 121 subjects: $R = -0.15$, $t(119) = -1.64$, $p = 0.104$. Taken all together, we are confident that long exposure durations, in and of themselves, cannot account for the observed inverse relationship.

We argue that in the face of strong interference, relevant and irrelevant elements in a visual display become perceptually integrated and, due to this excessive integration, attention fails to inhibit the irrelevant signals. This is evident by the fact that when the strength of interference was increased, attention effects on interference present displays were not significantly different from lone target ones. Instead, attention may unduly enhance the irrelevant elements along with the target. To the extent that signal enhancement is deployed on both display types, one might surmise that we should observe poorer performance in the presence of interference when concurrent distractor suppression is absent, even despite the timing procedures that were designed to equate task difficulty. As noted above, when we failed to observe biased competition, attention effects (defined as valid - invalid performance) were decidedly not smaller for the interference present conditions. However, when we consider valid trials only, we do notice a consistent, albeit negligible, difference in

³With the removal of these subjects (all from Experiment 3), a significant inverse relationship also emerges when only including studies reported the main text: $R = -0.26$, $t(74) = -2.33$, $p = 0.023$. Thus, this result does not critically depend on the inclusion of the three supplementary experiments.

line with this prediction. While differences in accuracy between valid-interference absent and valid-interference present trials rarely reached significance within an individual experiment (Experiment 3 and the letter noise display in Experiment 6 being the exceptions; $t(22) = 2.091$, $p = 0.048$, $d = 0.44$ and $t(14) = 2.19$, $p = 0.046$, $d = 0.57$, respectively), most did conform to this qualitative pattern. We thus conducted a post-hoc analysis, in which we compared accuracies between valid-interference absent and valid-interference present conditions across all experiments included in the linear regression described above. Here, we observed significantly better performance on valid-interference absent trials (valid-interference absent: $M = 71\%$; valid-interference present: $M = 66\%$), $t(120) = 3.51$, $p = 0.00063$, $d = 0.32$ (this is similarly true for a comparison of the invalid trials: invalid-interference absent: $M = 60\%$; invalid-interference present: $M = 53\%$, $t(120) = 4.27$, $p < .0001$, $d = 0.39$). This indicates that even when attention was pre-allocated to the target location, irrelevant signals interfered with target identification. These results are consistent with a perceptual pooling of signals across targets and external interference.

Next, we set out to determine whether the presence or absence of a biased competition effect on an individual level mediated the pattern above. First, we sorted all subjects based on the size of their biased competition effects, and next compared accuracy differences between the valid-interference absent and valid-interference present trials from the one-third of subjects with the smallest effect sizes to the one-third of subjects with the largest effect sizes ($N = 40$ for each group). Those who did not exhibit a biased competition effect ($M = -10.8\%$) showed significant differences in performance accuracy across the two valid conditions (valid-interference absent: $M = 74\%$; valid-interference present: $M = 67\%$, $t(39) = 4.46$, $p < .0001$, $d = 0.71$). Conversely, those who exhibited the largest biased competition effects ($M = 17.1\%$) did not show accuracy differences between the valid conditions (valid-interference absent: $M = 72\%$; valid-interference present: $M = 71\%$, $t(39) = 0.57$, $p = 0.57$, $d = 0.09$, and these patterns were marginally different from each other, $F(1,78) = 3.81$, $p = 0.055$, $d = 0.44$). Thus, subjects who failed to exhibit a biased competition effect also demonstrated a larger degree of undue distractor interference, even when attention was accurately cued to the target location. These results are consistent with our argument that target-distractor integration leads to failed or insufficient external interference suppression. Instead, attention is enhancing, at least partially, the neural representations of irrelevant elements.

General Discussion

The biased competition model proposes that space-based selection improves the fidelity of behaviorally relevant input by filtering out unwanted clutter, hence reducing its impact on target processing. Ergo, attention should show the greatest facilitatory effect in the presence of irrelevant elements. While this pattern of results has been produced in many behavioral studies (e.g., Awh, et al., 2005; Shiu & Pashler, 1994; reviewed in Beck & Kastner, 2009), we noted exceptions to the model's predictions (e.g., Lu & Doshier, 1998; Scolari et al., 2007). We therefore set out to determine the boundary conditions in which biased competition effects are elicited.

We predicted that exogenous spatial attention would resolve interference only under conditions in which the target and nontarget elements are effectively represented as distinct

objects. We tested this hypothesis by systematically manipulating the strength of visual crowding-- a phenomenon known to hinder target-distractor individuation-- or by generating interference with embedded noise patterns intended to preclude a percept of individuated distractor elements. In all cases in which we presented a number-letter stimulus display in parafoveal space (Experiments 1, 4 and 6; Supplementary Experiment 1), increased cueing effects in the presence of interference compared to lone target displays suggested that attention had helped to resolve visual interference. However, increased visual crowding (Experiments 2–4; Supplementary Experiment 2) and integrated noise masks (Experiments 5–6; Supplementary Experiment 3) eliminated this biased competition effect.

In light of these experimental results, we wish to highlight two important conclusions. First, our accuracy-based measure was sensitive enough in almost all cases (with exceptions in Experiments 4 and 6; we return to this point below) to detect relatively small exogenous attention effects driven by signal enhancement. This is the most compelling explanation of cueing effects in lone target trials. In the absence of external irrelevant elements, space-based attention largely enables identification of a target stimulus by improving its associative signal and/or reducing internal noise (e.g., Carrasco, 2011). We argue when targets and distractors are perceptually integrated into a single object—as is the case under crowded conditions (Pelli et al., 2004)-- signal enhancement operates on the full display in the absence of concurrent distractor suppression. Consistent with this assertion, in cases where crowding was sufficiently strong, we generally found that attention effects on interference present trials were equivalent to those on interference absent trials, in line with the hypothesis that common mechanisms drove cueing effects. Notably, the claim that irrelevant elements are erroneously enhanced in highly crowded displays is further supported by 1) consistently longer stimulus exposure durations required on interference present trials (derived from our staircasing procedure), and 2) a small but overall significant performance decrement on valid-interference present trials compared to their lone target counterparts. Thus, when signal enhancement is the primary mode of selection, it may be more effective with displays that lack strong interference.

Second, we wish to highlight the wide differences across experiments in stimulus encoding time, particularly for interference displays, as measured by exposure duration estimates. The amount of interference generated by distracting elements varied between subjects, even for a single display type. We suspect when external interference for a given subject is particularly high—regardless of how it is defined—its signal is not sufficiently suppressed (and as we described above, subsequently enhanced). We took advantage of this large variability in encoding time across subjects to examine the relationship between interference and biased competition. A significant negative relationship emerged between the two factors: Individuals who exhibited relatively weaker interference effects also showed larger attention effects on interference present trials compared to trials where interference was absent. These results suggest that exogenously-driven spatial attention resolves visual interference only under specific display conditions: The relevant and irrelevant input must be individuated for distracting influences to be muted. The degree to which individuation is successful appears to be governed in part by individual differences.

The studies described in this paper suggest a critical boundary condition for the resolution of visual interference via spatial attention. Across six experiments, we interpret the results to show that attention resolves interference from competing distractors only when they can be individuated into discrete elements. This hypothesis may unify seemingly disparate results in the literature (e.g., Awh, Sgarlata, & Kliestik, 2005; Lu & Doshier, 1998; Scolari et al., 2007; Shiu & Pashler, 1994). We argue here that when crowding is sufficiently strong, the target and distractors are effectively integrated into a single percept, or object (see Pelli et al, 2004), precluding biased processing towards only the relevant elements in the display. Consistent with our interpretation, Chen, et al. (2018) recently showed in a clever neuroimaging study that selective attention successfully suppressed signals from distracting flankers in weakly crowded displays, but not strongly crowded ones, in area V4. Furthermore, when a pooling model was applied, they found that relatively more weight was given to the unattended flankers within the strong crowding context.

Throughout this paper, we have used the term “individuation” to refer to the process by which the target is selected as a unique object apart from surrounding distractors, and target-distractor “integration” in cases when this process fails, resulting at times in an incoherent percept. A large body of crowding research is specifically dedicated to investigating what form integration takes. Two broad models have received support in the literature: Pooling models propose that the perceptual result of crowding is a weighted average of all visual features (Agaoglu & Chung, 2016; Greenwood, et al., 2009; 2010; Harrison & Bex, 2015; Parkes, Lund, Angelucci, Solomon & Morgan, 2001), while substitution models assert that individual feature values are accessible, but their specific locations and spatial relationships to each other are confusable (Ester, Klee & Awh, 2014; Ester, Zilber & Serences, 2015; Gheri & Baldassi, 2008; Strasburger, 2005; Wolford, 1975). We are remaining purposefully agnostic on this debate here, as these data cannot distinguish between the two; nor can either be easily tested with the stimulus sets. None of our irrelevant items were associated with alternative response choices, precluding a straightforward test of substitution, and similarly, it is unclear what a subject would report as the average of a target number and set of six distracting letters. It is worth noting, however, that the relationship we are asserting between space-based attention and interference strength is orthogonal to this interesting question.

In hindsight, the data presented here are consistent with an object-based modulation of space-based attention. A long line of research has demonstrated that the selection of space may be governed, at least in part, by the presence of object contours: When attention is directed to only a part of an object, it has been shown to extend to the object boundaries such that irrelevant space is also selected (e.g., Abrams & Law, 2000; Baylis & Driver, 1993; Duncan, 1984; Egly, Driver & Rafal, 1994; Moore, Yantis & Vaughan, 1998). While demonstrations of object-mediated space-based attention are numerous, rarely do they convincingly show that such selection is automatic by explicitly discouraging an attentional spread (Scolari, Ester & Serences, 2014; but see Kramer & Jacobson, 1991; Scholl, Pylyshyn & Feldman, 2001). To the extent that crowded target and distractor elements are pooled into a single object representation as described above, the current study meets this challenge: The full stimulus display includes task-irrelevant information, the selection of which impedes target identification. Although we cannot determine from these experiments how much of the stimulus display is encompassed by the focus of attention on any given

trial, it is clear from the estimated exposure durations and overall accuracy differences between corresponding interference present and interference absent trials that at least some distracting input is included in the selected region. Furthermore, disparate findings in Experiments 1 and 2 suggest this is not simply due to a limited attentional resolution per se, as both stimulus displays occupied the same spatial region. A more parsimonious explanation is that high inter-stimulus similarity in Experiment 2 elicited stronger target-distractor integration. Thus, the locus of space-based attention may be governed, at least in part, by appropriate object-based segregation. This is somewhat complementary to Vecera's (2000) biased competition account of object-based segregation and attention. Though while Vecera argued biased competition facilitates object-based segregation, we argue that proper segregation is a necessary precursor to biased competition.

Descriptions of the biased competition model generally focus on perceptual consequences of sufficient distractor suppression, whereby target identification is facilitated when external interference is excluded from processing. Similarly, spatial crowding—as was manipulated in this study—is a perceptual phenomenon that is not fully resolvable even in the absence of time pressure, given stable fixation (Bouma, 1970; Pelli, et al., 2004). Thus, in the current study, we deliberately used unspeeded accuracy as our dependent measure. In most cases, accuracy-dependent measures were sufficient to detect attention effects, even for interference absent conditions. However, in the few cases where no attention effects were observed (i.e., Experiments 4 and 6), it is possible that our measure was simply too coarse to detect them, and that speeded responses would have produced detectable effects in RT. It remains an open question whether attention to perceptually integrated target-distractor displays results in a larger reduction in decision time—as measured by RT differences on valid and invalid trials—compared to interference absent displays.

In each of the experiments reported here, we made use of an uninformative, peripheral precue. Thus, our results may be specific to transient, exogenous spatial attention, while notable key differences between this and sustained, endogenous attention preclude sweeping generalizations beyond involuntary mechanisms. For example, while Lu and Doshier (1998) found no evidence for distractor exclusion in embedded noise displays in an exogenous attention task, the same group (Doshier & Lu, 2000) observed larger attention effects in the presence of external interference using the same class of stimuli and an endogenous, central cue. Other evidence suggests that endogenous and exogenous attention are best conceived of as independent systems, given differences in temporal dynamics, perceptual consequences, and neural mechanisms (e.g., Carrasco, 2011; Corbetta & Shulman, 2002; Hein, Rolke & Ulrich, 2006). Nonetheless, the two systems do share commonalities, and both have been shown to exhibit perceptual facilitation consistent with the biased competition account. Thus, whether the results reported here would hold with manipulations of endogenous attention is an interesting question for future research.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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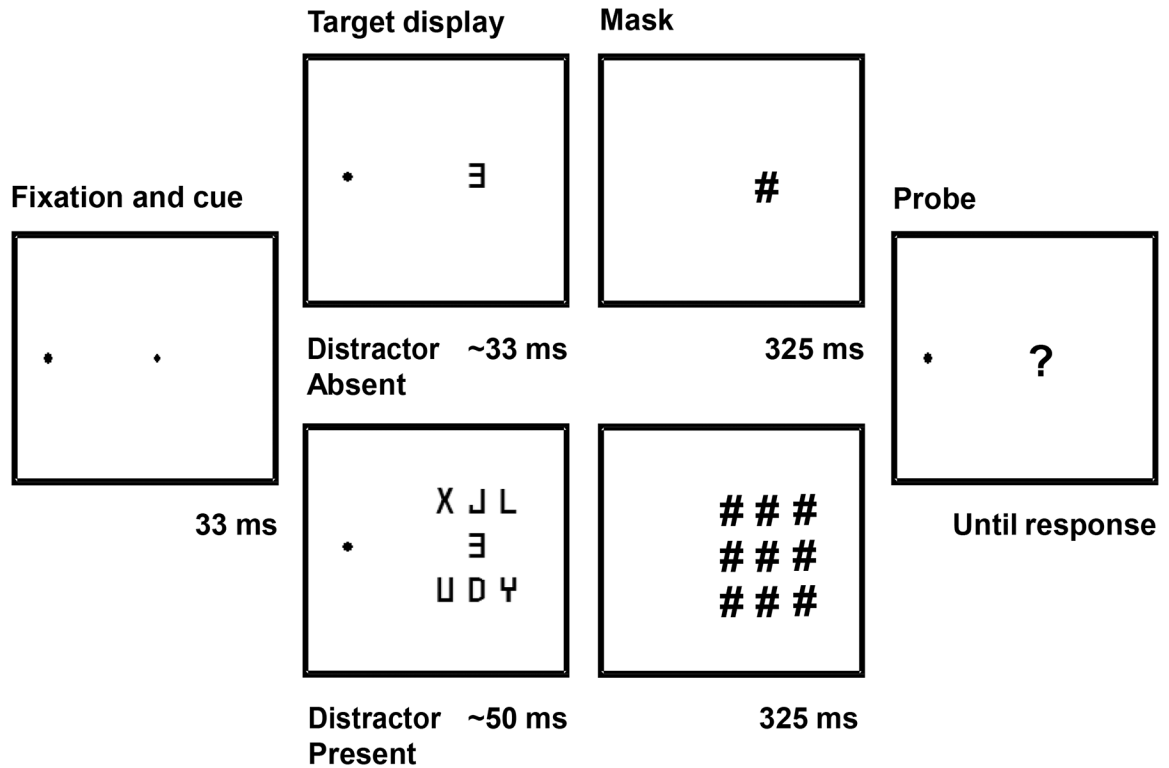


Figure 1.

Schematic of valid-distractor absent and valid-distractor present trials used in Experiment 1. Note that for half of all trials, the target appeared on the opposite side of fixation as the spatial cue (invalid trials). The timing listed below each target display type reflect the respective mean exposure durations across subjects. Note that the actual exposure durations used for each subject was determined via a staircased timing procedure. The probe item (“?”) always appeared in the target location, regardless of the validity of the cue, and stayed on screen until the subjects reported the identity of the target digit with an unspeeeded keypress. Similar displays were used in Experiments 3, 4 and 6.

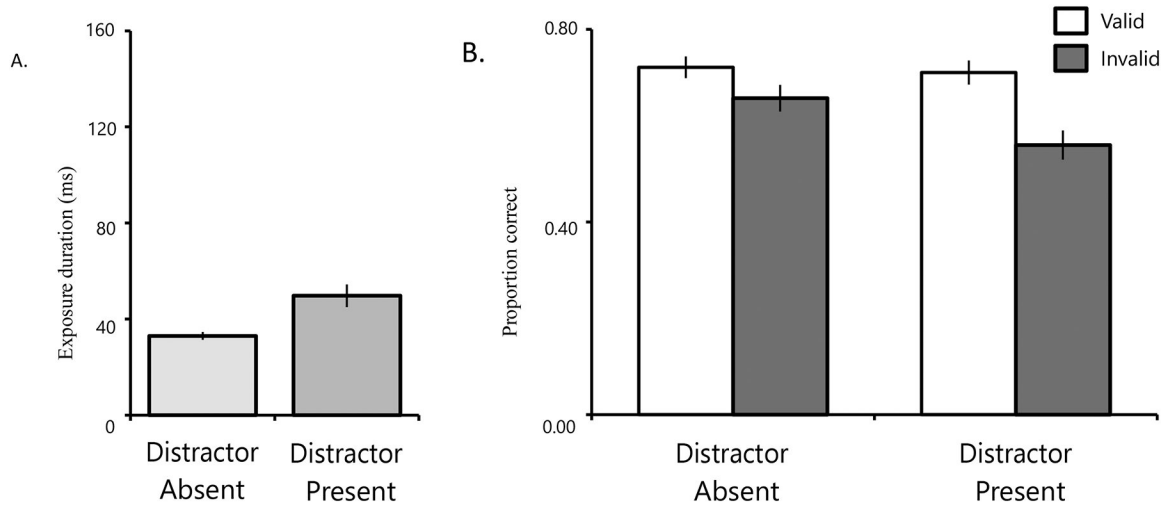


Figure 2.

Results from Experiment 1, where subjects reported the identity of a parafoveal target digit presented with or without flanking letter distractors. (A) Mean exposure durations for valid-distractor absent and valid-distractor present trials, as determined by a staircased timing procedure. (B) Proportion correct for each of the four conditions (valid-distractor absent, valid-distractor present, invalid-distractor absent, invalid-distractor present). Error bars represent ± 1 standard error of the mean. Note that because exposure durations for valid-distractor absent and valid-distractor present trials were independently staircased to a common performance criterion, accuracy is expected to be statistically equivalent between these two conditions. Replicating previous findings, the size of the attention effect was significantly greater for distractor present displays compared to distractor absent displays.

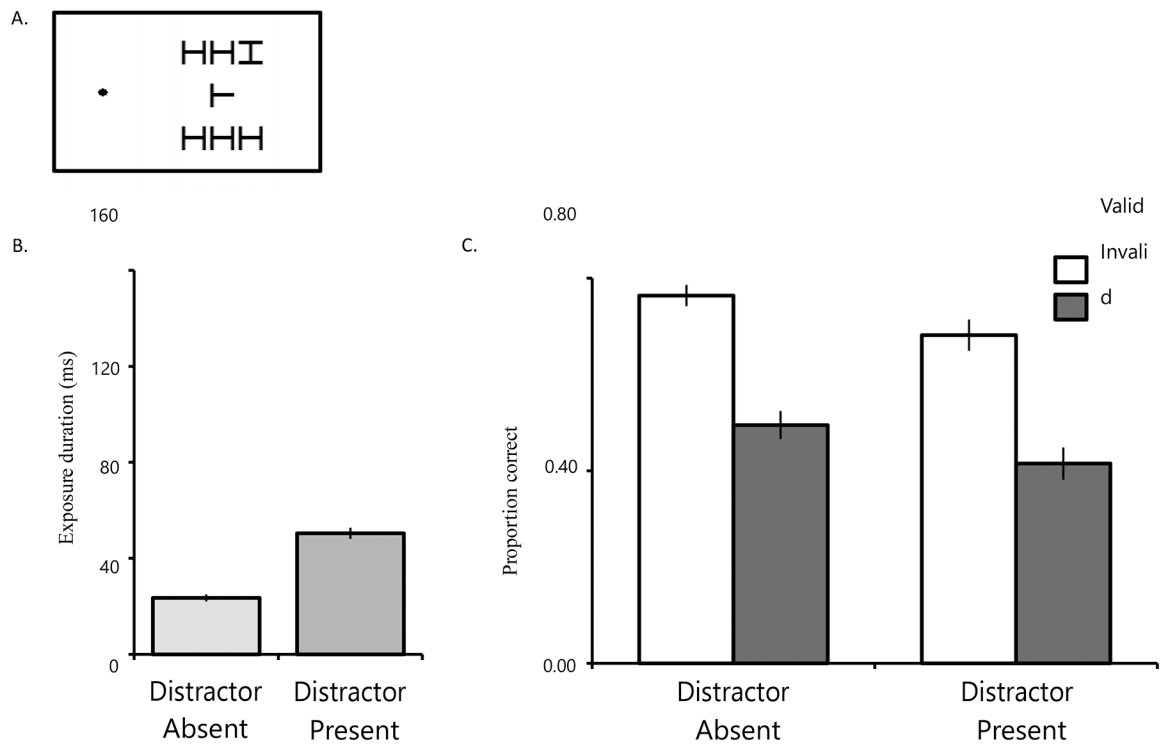


Figure 3.

Results from Experiment 2, where subjects reported the orientation of a rotated target “T” presented parafoveally with or without flanking distractors. (A) An illustration of the target display used in Experiment 2. (B) Mean exposure durations for valid-distractor absent and valid-distractor present trials. (C) Proportion correct for each of the four conditions (valid-distractor absent, valid-distractor present, invalid-distractor absent, invalid-distractor present). Error bars represent ± 1 standard error of the mean. In contrast to Experiment 1, the size of the attention effect did not differ between display conditions.

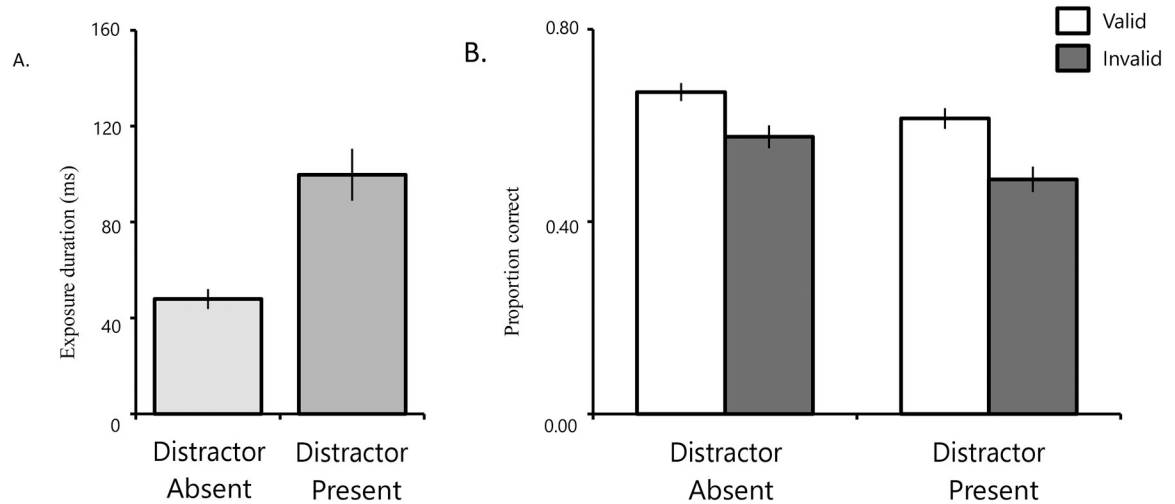


Figure 4. Results from Experiment 3, where subjects reported the identity of a peripheral target digit presented with or without flanking letter distractors. (A) Mean exposure durations for valid-distractor absent and valid-distractor present trials. (B) Proportion correct for each of the four conditions (valid-distractor absent, valid-distractor present, invalid-distractor absent, invalid-distractor present). Error bars represent ± 1 standard error of the mean. In contrast to Experiment 1, the size of the attention effect did not differ between display conditions.

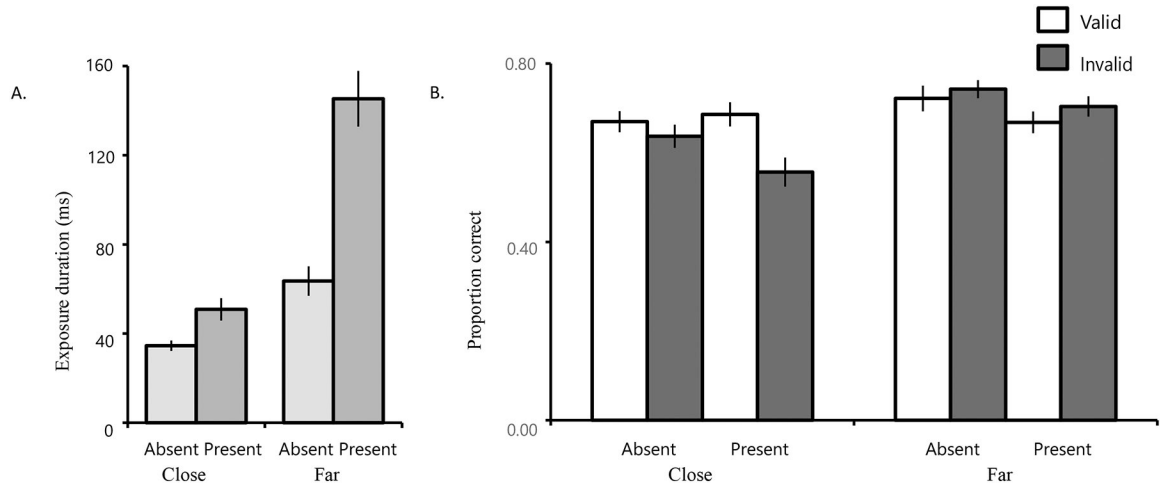


Figure 5.

Results from Experiment 4, where subjects reported the identity of a parafoveal (“close”) or peripheral (“far”) target digit presented with or without flanking letter distractors. (A) Mean exposure durations for valid-distractor absent and valid-distractor present trials for each of the two eccentricity conditions. (B) Proportion correct for each of the four conditions (valid-distractor absent, valid-distractor present, invalid-distractor absent, invalid-distractor present) for both eccentricity conditions. Error bars represent ± 1 standard error of the mean. There was a significant biased competition effect (i.e., greater attention effect for distractor present relative to distractor absent displays) for close displays but not for far displays, and this interaction was significant.

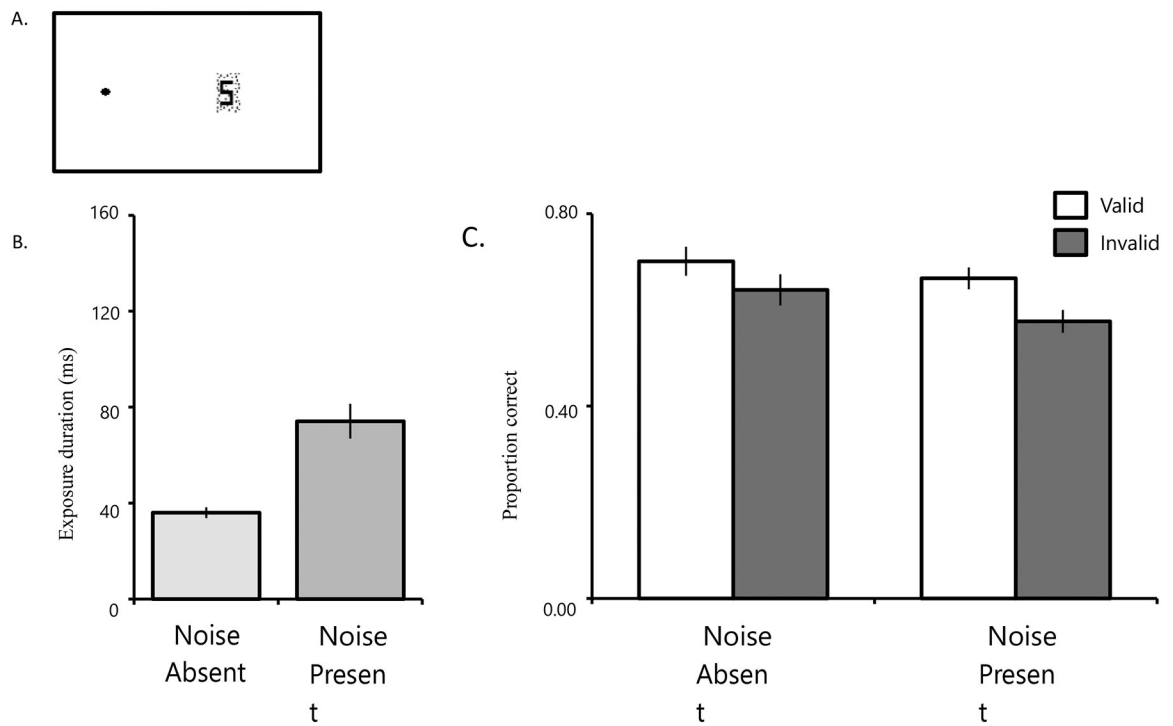


Figure 6.

Results from Experiment 5, where subjects reported the identity of a parafoveal target digit presented alone or embedded within a speckled noise pattern. (A) An illustration of the target display used in Experiment 5. (B) Mean exposure durations for valid-noise absent and valid-noise present trials. (C) Proportion correct for each of the four conditions (valid-noise absent, valid-noise present, invalid-noise absent, invalid-noise present). Error bars represent ± 1 standard error of the mean. In contrast to Experiment 1, the size of the attention effects did not differ between display conditions.

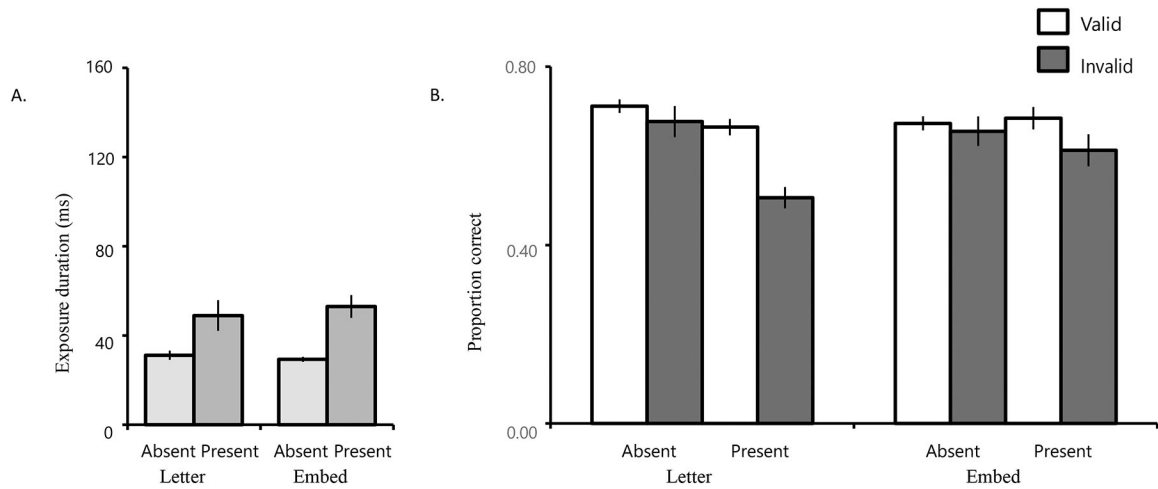


Figure 7.

Results from Experiment 6, where subjects reported the identity of a parafoveal target digit presented with or without interference, defined as flanking letter distractors (as in Experiment 1) or embedded noise (as in Experiment 5). (A) Mean exposure durations for valid-interference absent and valid-interference present trials for each of the two noise type conditions. (B) proportion correct for each of the four conditions (valid-interference absent, valid-interference present, invalid-interference absent, invalid-interference present) for both interference conditions. Error bars represent ± 1 standard error of the mean. There was a significant biased competition effect (i.e., greater attention effect for interference present relative to interference absent displays) for letter distractor displays but not for embedded noise displays, and this interaction was marginally significant.

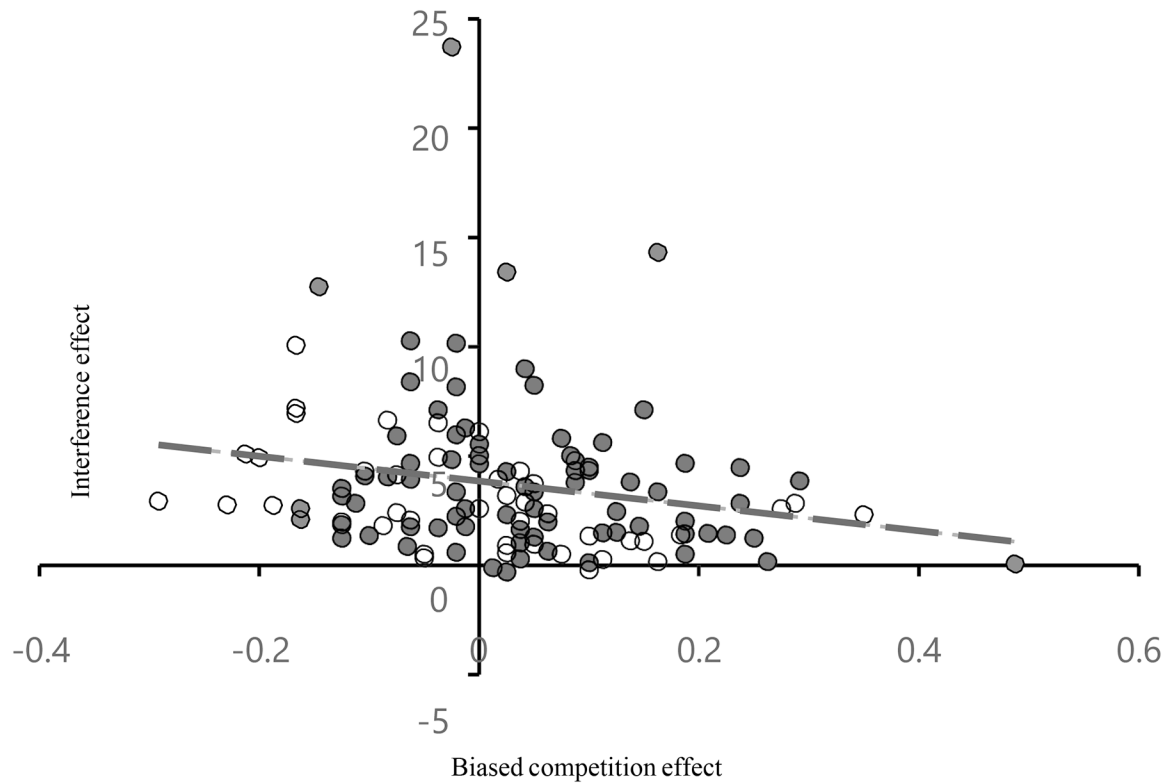


Figure 8.

Correlation between the size of the interference effect (defined as the difference between valid-interference present and valid-interference absent display exposure duration estimates) and the size of the biased competition effect (defined as the difference in attention effect sizes for interference present and interference absent displays) for 121 individuals across 4 experiments described in the main text (filled circles) and 3 supplementary experiments (open circles). A simple linear regression revealed a significant negative relationship, indicating that subjects who were better able to individuate target items from distractor elements exhibited larger biased competition effects.