

Current Biology

Transient perceptual enhancements resulting from selective shifts of exogenous attention in the central fovea

Highlights

- Exogenous attention selectively modulates perception in the central fovea
- Transient enhancements of high-acuity vision are observed at the cued location
- On a longer timescale, high acuity is enhanced at the other uncued foveal locations

Authors

Yue Guzhang, Natalya Shelchkova,
Rania Ezzo, Martina Poletti

Correspondence

martina_poletti@urmc.rochester.edu

In brief

Exogenous attention efficiently selects salient information and facilitates its processing. Guzhang et al. show that this type of attention can lead to highly localized transient enhancements of high-acuity vision even across the central fovea. Over longer time intervals, instead, sensitivity increases at the initially unattended foveal locations.



Report

Transient perceptual enhancements resulting from selective shifts of exogenous attention in the central fovea

Yue Guzhang,¹ Natalya Shelchkova,² Rania Ezzo,³ and Martina Poletti^{1,4,5,6,7,*}

¹Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY, USA

²Program in Computational Neuroscience, University of Chicago, Chicago, IL, USA

³Department of Psychology, New York University, New York, NY, USA

⁴Department of Neuroscience, University of Rochester, Rochester, NY, USA

⁵Center for Visual Science, University of Rochester, Rochester, NY, USA

⁶Twitter: @aplabUR

⁷Lead contact

*Correspondence: martina_poletti@urmc.rochester.edu

<https://doi.org/10.1016/j.cub.2021.03.105>

SUMMARY

Exogenous attention, a powerful adaptive tool that quickly and involuntarily orients processing resources to salient stimuli, has traditionally been studied in the lower-resolution parafoveal and peripheral visual field.^{1–4} It is not known whether and how it operates across the 1° central fovea where visual resolution peaks.^{5,6} Here we investigated the dynamics of exogenous attention in the foveola. To circumvent the challenges posed by fixational eye movements at this scale, we used high-precision eye-tracking and gaze-contingent display control for retinal stabilization.⁷ High-acuity stimuli were briefly presented foveally at varying delays following an exogenous cue. Attended and unattended locations were just a few arcminutes away from the preferred locus of fixation. Our results show that for short temporal delays, observers' ability to discriminate fine detail is enhanced at the cued location. This enhancement is highly localized and does not extend to the nearby locations only 16' away. On a longer timescale, instead, we report an inverse effect: paradoxically, acuity is sharper at the unattended locations, resembling the phenomenon of inhibition of return at much larger eccentricities.^{8–10} Although exogenous attention represents a mechanism for low-cost monitoring of the environment in the extrafoveal space, these findings show that, in the foveola, it transiently modulates vision of detail with a high degree of resolution. Together with inhibition of return, it may aid visual exploration of complex foveal stimuli.¹¹

RESULTS AND DISCUSSION

Covert attention, attending to an object/location without directing the gaze toward it, has been studied extensively. In a world crowded with stimuli, covert attention plays a crucial role in efficiently selecting information and facilitating its processing in humans^{1–4,12} and other species.^{13,14} Generally, we distinguish between two types of covert attention, endogenous and exogenous. Endogenous attention is sustained over time and allows the observer to voluntarily monitor the information at a given location in a goal-driven manner. On the other hand, exogenous attention is triggered by salient/sudden stimulation, resulting in an involuntary allocation of processing resources to a selected location. Differently from endogenous attention, which takes around 300 ms to deploy, exogenous attention effects have a quick onset but are short lived. Facilitatory effects associated with exogenous attention occur as early as 70–150 ms from cue onset.^{1,3,4,15–17} A phenomenon typically associated with exogenous attention is that of inhibition of return (IOR), the suppression of a stimulus that has been recently attended to.⁸

Exogenous attention initially facilitates the perception of nearby stimuli at the attended peripheral location; however, if no change occurs and attention has time to disengage, a reduction in sensitivity and increase in processing time will be observed at the originally cued location.^{9,18,19}

Until now, exogenous attention and IOR have been studied in the parafovea and in the visual periphery. This is primarily the result of viewing covert attention as a mechanism enhancing perception away from the foveated location where acuity and other visual functions quickly deteriorate with increasing eccentricity.^{20,21} However, fine spatial vision is not homogeneous even across the 1° foveola.^{5,6} It has also been shown that covert and overt voluntary (endogenous) attention can be selectively allocated within the central fovea, enhancing vision of detail just a few arcminutes away from the preferred locus of fixation.^{20,22} However, this attentional modulation occurs over a relatively long timescale (>300 ms), raising the question of whether involuntary (exogenous) attention, which operates on a shorter timescale, can lead to quick and transient enhancements of fine spatial vision. Determining whether exogenous attention can



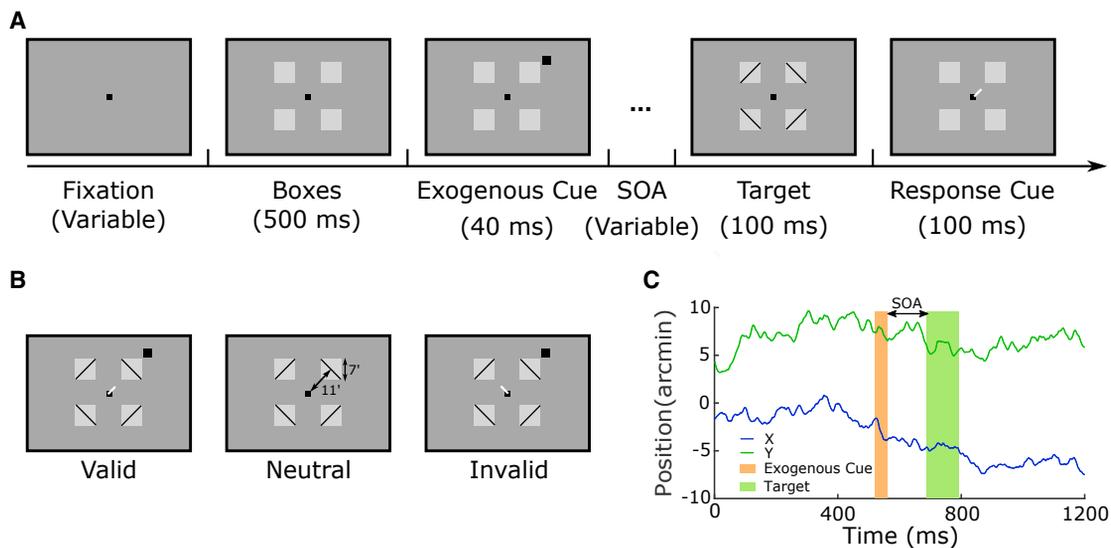


Figure 1. Experimental protocol

(A) Trials started with a brief period of fixation, and then an exogenous cue was flashed for 40 ms next to one of the four squares surrounding the fixation marker. After a variable stimulus-onset asynchrony (SOA), four tilted ($\pm 45^\circ$) lines were displayed, one in each square, for 100 ms. A response cue followed stimulus offset and observers were instructed to report the orientation of the stimulus previously presented at the location indicated by this cue.

(B) In valid trials, the exogenous (flash) and response cue indicated the same spatial location. In invalid trials, they pointed to different locations. In neutral trials, no exogenous cue was presented. All types of trials had the same probability of occurrence.

(C) An example of eye movements during the course of a trial.

be selectively shifted within the foveola, and examining its temporal dynamics, is important for a better understanding of the factors contributing to fine spatial vision, and of how foveal sensitivity is modulated in time during the course of fixation.

To address these questions, here we used a variant of the classical Posner cueing task¹ in the central fovea. Subjects performed a two-alternative forced-choice fine spatial discrimination ($\pm 45^\circ$ orientation discrimination) task. Tiny stimuli were presented simultaneously at four locations a few arcminutes away from the center of gaze. The onset of these stimuli was preceded by an exogenous cue, a briefly flashed black square appearing nearby one of the four locations tested (Figures 1A and 1C). To examine the time course of exogenous attention, we used a variable stimulus-onset asynchrony (SOA) between the exogenous cue onset and stimulus appearance. After stimulus offset, a response cue pointed to one of the four locations, and participants ($n = 9$) were instructed to report the orientation of the stimulus that was previously presented at that location. The exogenous cue and the response cue could either indicate the same (valid trials) or different (invalid trials) locations. In neutral trials, instead, the exogenous cue was not presented (Figure 1B). All three trial types had the same probability of occurring in the task, and observers were told that the exogenous cue was not informative.

Studying attentional control in the foveola is challenging. Incessant microscopic eye movements during fixation result in a continuous displacement of the retinal image. These fixational eye movements pose a problem when studying covert attention in the central foveola, because maintaining the attended stimulus at the same retinal location becomes nearly unfeasible, particularly in trials with longer SOAs. To overcome these difficulties, we relied on high-precision eye-tracking and gaze-contingent display control, i.e., each stimulus was maintained

approximately at the same retinal location throughout the trial. In addition, to eliminate the influence of microsaccades on attentional effects,^{22,23} we selected only trials without microsaccades for data analysis. Observers' performance was examined at different time intervals between the exogenous cue onset and target onset (SOAs, ranging from 70 to 790 ms).

The effects of exogenous attention in the central fovea

Our results show that exogenous attention exerts its effects in the foveola with SOAs as short as 100 ms. The ability to perceive fine spatial detail, measured as d' , was enhanced in valid trials compared to invalid and neutral trials at this SOA (1.91 ± 0.59 , 1.55 ± 0.47 , and 1.37 ± 0.43 for valid, neutral, and invalid trials, respectively; $F(2, 16) = 10.87$, $p = 0.0010$; Tukey's HSD post hoc tests: valid versus neutral, $p = 0.0207$; valid versus invalid, $p = 0.0008$; neutral versus invalid, $p = 0.2916$; Figure 2A). These results also suggest that the cost of switching attention exogenously is not as large as the enhancement at the attended location, i.e., performance in neutral trials was not statistically different from performance in invalid trials. Importantly, this perceptual enhancement at the attended location was not the result of a speed-accuracy trade-off: better performance in valid trials was not associated with longer reaction times (i.e., subjects were not more accurate because they were slower). We found no difference in reaction times across all trial types (804 ± 147 ms, 858 ± 160 ms, and 870 ± 177 ms for valid, neutral, and invalid trials, respectively; $F(2, 16) = 3.66$, $p = 0.0490$; Tukey's HSD post hoc tests: valid versus neutral, $p = 0.1223$; valid versus invalid, $p = 0.0549$; neutral versus invalid, $p = 0.9013$; Figure 2B).

A subgroup of participants ($n = 6$) was tested on SOAs of 70 ms. However, we did not find a statistically significant

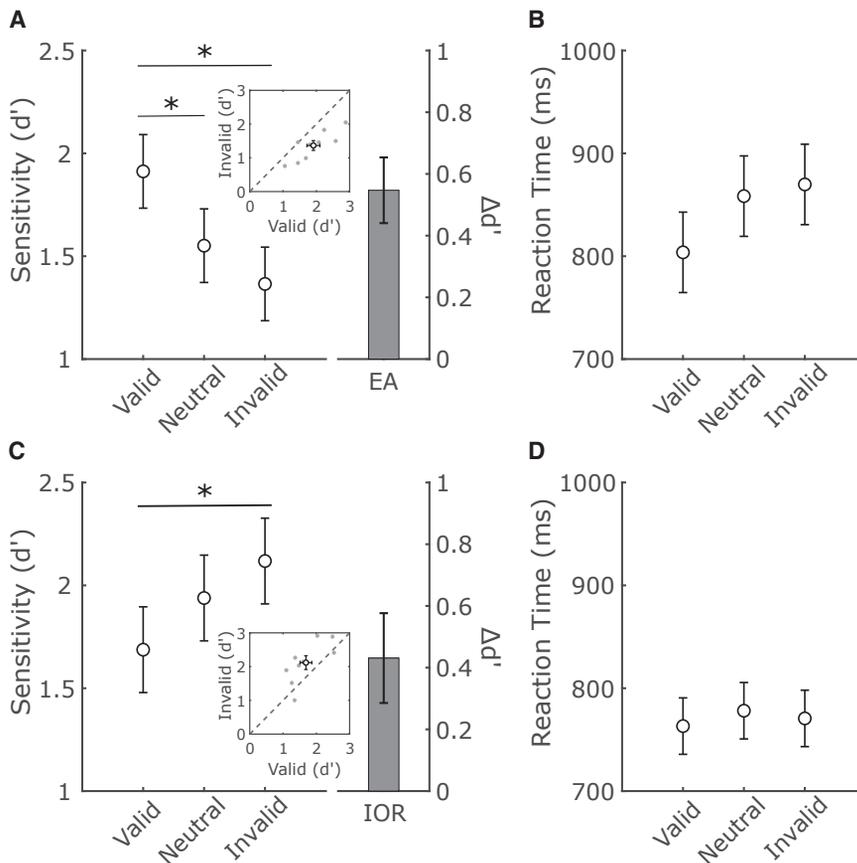


Figure 2. Exogenous attention and inhibition of return

(A) Average sensitivity (d') at the SOA of 100 ms. Error bars represent group means and within-subject confidence intervals.²⁴ Asterisks mark a statistically significant difference ($p < 0.05$, Tukey's post hoc test). Right: average difference in sensitivity ($\Delta d'$) between valid and invalid trials across observers. Error bars represent SEM.

(B) Average reaction times at a SOA of 100 ms. Right: average difference in sensitivity ($\Delta d'$) between valid and invalid trials across observers.

(C) Average sensitivity (d') at the SOA associated with the largest IOR effect in each observer ($n = 9$). Right: average difference in sensitivity ($\Delta d'$) between valid and invalid trials across observers.

(D) Average reaction times at the SOA showing the largest IOR effect in each observer. Insets in (A) and (C) show single-subject performance (gray dots). Empty circles represent the group mean with SEM.

See also Figure S1.

enhancement of performance in valid trials (Figure S1; $\Delta d' = 0.11 \pm 0.48$ [valid-invalid], $t(5) = 0.55$, $p = 0.6072$), suggesting that exogenous attention in the foveola needs at least ≈ 100 ms to be allocated.

IOR in the central fovea

It is known that the effect of exogenous attention in the extrafoveal space vanishes, and eventually reverses (i.e., performance is lowest at the attended location), when longer time intervals separate the cue from the target presentation. This phenomenon is known as IOR.^{1,9} To determine whether IOR occurs at the foveal scale, we examined how performance changed with longer SOAs after the exogenous attention effect reached its peak. Because the exact time IOR occurred differed across observers, we measured the average strength of the effect at the time when $\Delta d'$, the difference in sensitivity between valid and invalid trials, was lowest in each individual.

The exogenous attention effect disappeared at longer SOAs, indicating that this type of attention is, indeed, short lived. Seven out of nine observers showed a reversal in performance, which is typical of IOR (Figures 2C and 2D; 1.69 ± 0.53 , 1.94 ± 0.60 , and 2.12 ± 0.61 for valid, neutral, and invalid trials, respectively; $F(2, 16) = 4.85$, $p = 0.0225$; Tukey's HSD post hoc tests: valid versus neutral, $p = 0.1988$; valid versus invalid, $p = 0.0178$; neutral versus invalid, $p = 0.4190$).

Remarkably, even when there were three unattended locations versus only one attended location, the ability to resolve

fine detail increased at these locations by almost 0.75 unit of d' , compared to performance in invalid trials at shorter SOAs (Figures 2A and 2C; $t(8) = 5.43$, $p = 0.0006$, $n = 9$). On the other hand, performance at the previously attended location decreased by about 0.23 ± 0.37 unit of d' compared to that at shorter SOAs, a change that was not statistically significant (Figures 2A and 2C; $t(8) = 1.84$, $p = 0.1033$). Note that also the overall performance in neutral trials increased over longer time intervals (1.55 ± 0.47 versus 1.94 ± 0.60 for short and long SOAs, respectively; $t(8) = 2.47$, $p = 0.0385$), suggesting an effect of time on sensitivity at the foveal scale. Therefore, the effect of IOR mostly enhances fine spatial vision at the uncued location and only leads to a minor suppression of sensitivity at the cued location compared to shorter time intervals. Figures 2A and 2C also show that the magnitudes of the exogenous attention effect and that of IOR were comparable ($\Delta d' 0.55 \pm 0.32$ versus 0.43 ± 0.44 for facilitation and IOR, respectively; $t(8) = 0.62$, $p = 0.5513$).

The effect of IOR requires at least 300 ms to occur in peripheral vision.^{10,25} We observed a similar pattern in the foveola. As the SOA increased, $\Delta d'$ decreased and fell below zero after 280 ms (Figures 3A, 3D, and 3E). The exogenous attention effect was strongest on average at 103 ± 23 ms. Although there were large variations across observers, on average, the IOR exerted its strongest effect at 537 ± 214 ms (Figures 3A–3C).

Our findings reveal that involuntary covert attention can be fine-tuned at the foveal scale, leading to an enhancement of fine spatial vision. The temporal onset of exogenous attention in the central fovea is comparable to what has been reported at much larger eccentricities. The facilitatory effect at the cued location takes about 100 ms to build up, approximately the same time range reported in the visual periphery and parafovea.^{4,26–28} This finding is surprising if one considers that foveal processing is generally slower than peripheral processing:

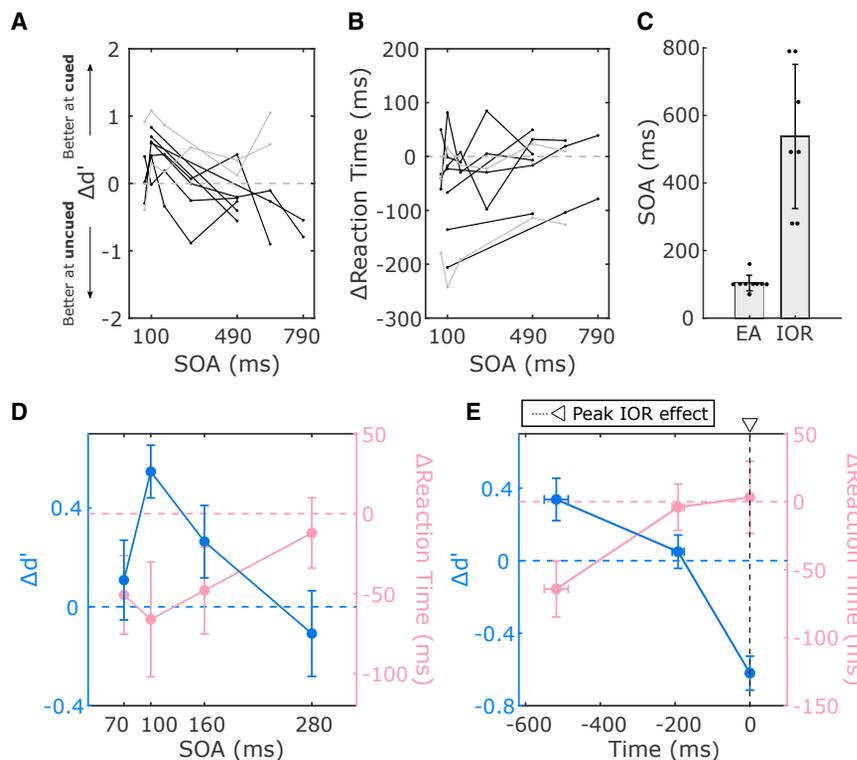


Figure 3. Time course of attention and IOR effects in the foveola

(A and B) Difference in (A) sensitivity and (B) reaction time between valid and invalid trials for individual observers as a function of SOA. Each line represents one observer. Black lines indicate observers who showed the effect of inhibition of return (IOR). Gray lines mark the two observers who did not show the IOR effect. The dashed line marks zero difference between the two trial types. (C) Average SOA associated with the strongest exogenous attention effect (EA) and IOR effect. Error bars are standard deviations; black dots are single subjects.

(D) Average difference in sensitivity (blue) and reaction times (red) between valid and invalid trials across observers at different SOAs.

(E) Average difference in sensitivity (blue) and reaction times (red) between valid and invalid trials time locked to the SOA associated with the peak IOR effect in each individual observer (marked by the vertical dashed line). Each dot is located at its average time with respect to the peak IOR effect at zero. Error bars represent SEM.

detection and discrimination reaction times are usually longer closer to the foveola,^{20,29} temporal sensitivity is lower in foveal than peripheral vision,^{30,31} and foveal cone response is characterized by a slower profile compared to peripheral cones.³² Oculomotor planning is also slower in the fovea: generating a microsaccade takes ≈ 150 ms longer than executing a saccade toward a stimulus in the periphery.^{20,33,34} Additionally, optimal processing of fine details (i.e., high spatial frequencies) is known to take longer than for low-spatial-frequency stimuli presented at the center of gaze.³⁵ Nonetheless, exogenous attention is capable of bypassing these limitations by focusing resources at selected foveal locations as quickly as it does across the visual periphery. The similar time course of the attentional effects in the foveola and visual periphery indicates that the mechanisms guiding transient covert attention operate at relatively constant speed across the visual field. Crucially, because stimuli were presented under retinal stabilization and data selected for analysis contained only drifts, the effects reported here were neither the result of fixational eye movements relocating the cued stimuli onto the preferred retinal locus nor the effects of attentional shifts due to microsaccades.

The enhancement at the exogenously cued location vanished over longer time periods. As the interval between cue and target increased, approximately by a third of a second, the facilitation at the attended location was replaced by IOR. The ability to perceive the high-acuity stimulus was enhanced at uncued locations. This is comparable to what was reported at more peripheral locations when using a similar discrimination task.¹⁶ Interestingly, no correlation was found between the peak time of the exogenous attention effect and that of IOR ($r = 0.40$, $p = 0.3737$). That is, an earlier onset of the exogenous attention

effect does not imply an earlier onset of IOR, suggesting that the two processes are independent from each other. This is coherent with previous studies showing a dissociation between exogenous attention and IOR.^{36–40}

IOR can be beneficial in the central fovea at fixation, especially when the foveal input is rich and crowded in details. A recent study, indeed, reported that active spatial exploration of natural and complex stimuli is carried out also within the high-acuity foveola during the course of normal fixation periods, and it follows scanning strategies similar to those used to explore larger scenes.¹¹ Thus, jointly, the high-resolution enhancements from exogenous attention and IOR could aid the visuomotor system during fine-grain visual exploration of complex foveal stimuli. By quickly highlighting salient details, which may drive microsaccades, and later enhancing the previously unattended regions, they may constitute an efficient mechanism for visual exploration of detail.

It is possible that, especially at longer SOAs, a sequential sampling strategy is adopted, that is, each foveal location is sampled sequentially by attention. This would be expected based on recent evidence supporting the existence of rhythmic sampling mechanisms underlying both perception⁴¹ and attention.^{42–44} In this study, performance was not sampled at a high enough rate to be able to capture potential oscillations in performance. It is possible that the initial exogenous capture of attention is mandatory and that in the first ≈ 200 ms there are no oscillations in performance, which only kick in at longer SOAs. Alternatively, rather than suppressing these oscillations for a brief period of time, the exogenous cue may simply reset their phase. How these oscillatory rhythms may evolve at the foveal scale remains an open question that warrants further investigation.

In summary, our work shows that transient covert orientation of involuntary attention is useful not only to improve

lower-resolution vision in the peripheral visual fields but also to provide a fast and effective mechanism by means of which high-acuity vision is selectively enhanced across the foveal field.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- **KEY RESOURCES TABLE**
- **RESOURCE AVAILABILITY**
 - Lead contact
 - Materials availability
 - Data and code availability
- **EXPERIMENTAL MODEL AND SUBJECT DETAILS**
 - Human subjects
- **METHOD DETAILS**
 - Apparatus
 - Data collection
- **QUANTIFICATION AND STATISTICAL ANALYSIS**
 - Analysis of oculomotor data
 - Analysis of performance

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2021.03.105>.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation grant BCS-1534932 (to M.P.) and by National Institutes of Health grant R01EY029788-01 (to M.P.).

AUTHOR CONTRIBUTIONS

M.P., Y.G., and R.E. designed research; Y.G. and R.E. performed research; Y.G., R.E., N.S., and M.P. analyzed data; and M.P. and Y.G. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: November 10, 2020

Revised: March 1, 2021

Accepted: March 31, 2021

Published: April 29, 2021

REFERENCES

1. Posner, M.I., and Cohen, Y. (1984). Components of visual orienting. In *Attention and Performance X: Control of Language Processes*, H. Bouma, and D.G. Bouwhuis, eds. (Lawrence Erlbaum), pp. 531–556.
2. Carrasco, M. (2006). Covert attention increases contrast sensitivity: psychophysical, neurophysiological and neuroimaging studies. *Prog. Brain Res.* *154*, 33–70.
3. Carrasco, M. (2011). Visual attention: the past 25 years. *Vision Res.* *51*, 1484–1525.
4. Nakayama, K., and Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Res.* *29*, 1631–1647.
5. Poletti, M., Listorti, C., and Rucci, M. (2013). Microscopic eye movements compensate for nonhomogeneous vision within the fovea. *Curr. Biol.* *23*, 1691–1695.
6. Intoy, J., and Rucci, M. (2020). Finely tuned eye movements enhance visual acuity. *Nat. Commun.* *11*, 795.
7. Santini, F., Redner, G., Iovin, R., and Rucci, M. (2007). EyeRIS: a general-purpose system for eye-movement-contingent display control. *Behav. Res. Methods* *39*, 350–364.
8. Rafal, R.D., Calabresi, P.A., Brennan, C.W., and Sciolto, T.K. (1989). Saccade preparation inhibits reorienting to recently attended locations. *J. Exp. Psychol. Hum. Percept. Perform.* *15*, 673–685.
9. Klein, R.M. (2000). Inhibition of return. *Trends Cogn. Sci.* *4*, 138–147.
10. Samuel, A.G., and Kat, D. (2003). Inhibition of return: a graphical meta-analysis of its time course and an empirical test of its temporal and spatial properties. *Psychon. Bull. Rev.* *10*, 897–906.
11. Shelchkova, N., Tang, C., and Poletti, M. (2019). Task-driven visual exploration at the foveal scale. *Proc. Natl. Acad. Sci. USA* *116*, 5811–5818.
12. Hikosaka, O., Miyauchi, S., and Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. *Vision Res.* *33*, 1219–1240.
13. Gabay, S., Leibovich, T., Ben-Simon, A., Henik, A., and Segev, R. (2013). Inhibition of return in the archer fish. *Nat. Commun.* *4*, 1657.
14. Wang, L., and Krauzlis, R.J. (2018). Visual selective attention in mice. *Curr. Biol.* *28*, 676–685.e4.
15. Cheal, M., Lyon, D.R., and Hubbard, D.C. (1991). Does attention have different effects on line orientation and line arrangement discrimination? *Q. J. Exp. Psychol. A* *43*, 825–857.
16. Lupiáñez, J., Milán, E.G., Tornay, F.J., Madrid, E., and Tudela, P. (1997). Does IOR occur in discrimination tasks? Yes, it does, but later. *Percept. Psychophys.* *59*, 1241–1254.
17. Kurtz, P., Shapcott, K.A., Kaiser, J., Schmiedt, J.T., and Schmid, M.C. (2017). The influence of endogenous and exogenous spatial attention on decision confidence. *Sci. Rep.* *7*, 6431.
18. Sapir, A., Jackson, K., Butler, J., Paul, M.A., and Abrams, R.A. (2014). Inhibition of return affects contrast sensitivity. *Q. J. Exp. Psychol. (Hove)* *67*, 1305–1316.
19. Cheal, M., Chastain, G., and Lyon, D.R. (1998). Inhibition of return in visual identification tasks. *Vis. Cogn.* *5*, 365–388.
20. Poletti, M., Rucci, M., and Carrasco, M. (2017). Selective attention within the foveola. *Nat. Neurosci.* *20*, 1413–1417.
21. Anton-Erxleben, K., and Carrasco, M. (2013). Attentional enhancement of spatial resolution: linking behavioural and neurophysiological evidence. *Nat. Rev. Neurosci.* *14*, 188–200.
22. Shelchkova, N., and Poletti, M. (2020). Modulations of foveal vision associated with microsaccade preparation. *Proc. Natl. Acad. Sci. USA* *117*, 11178–11183.
23. Yuval-Greenberg, S., Merriam, E.P., and Heeger, D.J. (2014). Spontaneous microsaccades reflect shifts in covert attention. *J. Neurosci.* *34*, 13693–13700.
24. Loftus, G.R., and Masson, M.E. (1994). Using confidence intervals in within-subject designs. *Psychon. Bull. Rev.* *1*, 476–490.
25. Handy, T.C., Jha, A.P., and Mangun, G.R. (1999). Promoting novelty in vision: inhibition of return modulates perceptual-level processing. *Psychol. Sci.* *10*, 157–161.
26. Yeshurun, Y., and Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Res.* *39*, 293–306.
27. Hein, E., Rolke, B., and Ulrich, R. (2006). Visual attention and temporal discrimination: differential effects of automatic and voluntary cueing. *Vis. Cogn.* *13*, 29–50.
28. Ling, S., and Carrasco, M. (2007). Transient covert attention does alter appearance: a reply to Schneider (2006). *Percept. Psychophys.* *69*, 1051–1058.
29. Carrasco, M., McElree, B., Denisova, K., and Giordano, A.M. (2003). Speed of visual processing increases with eccentricity. *Nat. Neurosci.* *6*, 699–700.
30. Hecht, S., Schlaer, S., and Verrijp, C.D. (1933). Intermittent stimulation by light: II. The measurement of critical fusion frequency for the human eye. *J. Gen. Physiol.* *17*, 237–249.

31. Tyler, C.W. (1985). Analysis of visual modulation sensitivity. II. Peripheral retina and the role of photoreceptor dimensions. *J. Opt. Soc. Am. A* 2, 393–398.
32. Sinha, R., Hoon, M., Baudin, J., Okawa, H., Wong, R.O.L., and Rieke, F. (2017). Cellular and circuit mechanisms shaping the perceptual properties of the primate fovea. *Cell* 168, 413–426.e12.
33. Wyman, D., and Steinman, R.M. (1973). Letter: latency characteristics of small saccades. *Vision Res.* 13, 2173–2175.
34. Kalesnykas, R.P., and Hallett, P.E. (1994). Retinal eccentricity and the latency of eye saccades. *Vision Res.* 34, 517–531.
35. Boi, M., Poletti, M., Victor, J.D., and Rucci, M. (2017). Consequences of the oculomotor cycle for the dynamics of perception. *Curr. Biol.* 27, 1268–1277.
36. Smith, D.T., Schenk, T., and Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *J. Exp. Psychol. Hum. Percept. Perform.* 38, 1438–1447.
37. Casteau, S., and Smith, D.T. (2020). Covert attention beyond the range of eye-movements: evidence for a dissociation between exogenous and endogenous orienting. *Cortex* 122, 170–186.
38. Sereno, A.B., Briand, K.A., Amador, S.C., and Szapiel, S.V. (2006). Disruption of reflexive attention and eye movements in an individual with a collicular lesion. *J. Clin. Exp. Neuropsychol.* 28, 145–166.
39. Smith, D.T., Rorden, C., and Jackson, S.R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Curr. Biol.* 14, 792–795.
40. Tipper, S.P., Rafal, R., Reuter-Lorenz, P.A., Starveltd, Y., Ro, T., Egly, R., Danzinger, S., and Weaver, B. (1997). Object-based facilitation and inhibition from visual orienting in the human split-brain. *J. Exp. Psychol. Hum. Percept. Perform.* 23, 1522–1532.
41. Dugué, L., and VanRullen, R. (2017). Transcranial magnetic stimulation reveals intrinsic perceptual and attentional rhythms. *Front. Neurosci.* 11, 154.
42. Busch, N.A., and VanRullen, R. (2010). Spontaneous EEG oscillations reveal periodic sampling of visual attention. *Proc. Natl. Acad. Sci. USA* 107, 16048–16053.
43. Fiebelkorn, I.C., Saalman, Y.B., and Kastner, S. (2013). Rhythmic sampling within and between objects despite sustained attention at a cued location. *Curr. Biol.* 23, 2553–2558.
44. Dugué, L., Marque, P., and VanRullen, R. (2015). Theta oscillations modulate attentional search performance periodically. *J. Cogn. Neurosci.* 27, 945–958.
45. Ko, H.K., Snodderly, D.M., and Poletti, M. (2016). Eye movements between saccades: measuring ocular drift and tremor. *Vision Res.* 122, 93–104.
46. Macmillan, N.A., and Creelman, C.D. (2005). *Detection Theory: A User's Guide*, Second Edition (Lawrence Erlbaum).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Original data	This paper	https://doi.org/10.17632/rk7jffdhz.1
Software and algorithms		
MATLAB code to process data	This paper & Mathworks	https://www.mathworks.com

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Martina Poletti martina_poletti@urmc.rochester.edu.

Materials availability

This study did not generate new unique reagents.

Data and code availability

The data-set gathered during this study has been deposited to Mendeley Data: <https://doi.org/10.17632/rk7jffdhz.1>. This study used standard, custom-built MATLAB programmed scripts that are available from the Lead Contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Human subjects

Nine human observers (2 males and 7 females; age range: 18-25 years) with normal, non-corrected vision participated in the experiments. The experiment was approved by the University of Rochester and Boston University Institutional Review Boards. The experimenter reviewed and explained the material in the consent form to the participant before conducting the experiment. The form was signed only after the participant fully understood the material and voluntarily agreed to take part in the study. Consent was obtained from all participants in the study.

METHOD DETAILS

Apparatus

Stimuli were displayed on an LCD monitor (Acer Predator XB272) at a refresh rate of 144 Hz and spatial resolution of 1920 × 1080 pixels. Observers performed the task monocularly with their right eye while the left eye was patched. A dental-imprint bite bar and a headrest were used to prevent head movements. The movements of the right eye were sampled at 1 kHz by a Generation 6 Dual Purkinje Image (DPI) eye tracker (Fourward Technologies), a system with an internal noise of 20 arcsec and a spatial resolution of 1 arcmin.⁴⁵

Stimuli were rendered by means of EyeRIS, a custom-developed system that allows flexible gaze contingent display control.⁷ This system acquires eye movement signals from the eye tracker, processes them in real time, and updates the stimulus on the display according to the desired combination of estimated oculomotor variables. Precise foveal stimulation was achieved by means of retinal stabilization. The stimulus moved in real time, under EyeRIS control, to compensate for the observer's eye movements, ensuring both the cue and target remained at fixed foveal eccentricities with respect to the estimated center of gaze. The delay of the system was 10 ms, which resulted in a stabilization error of approximately 1 arcmin, as measured a posteriori by comparing the recorded oculomotor traces to the coordinates of stabilized stimulus recorded by EyeRIS during the experiment.

Data collection

After re-calibration, a central fixation marker appeared with four 7' × 7' arcmin (10 × 10 pixel) squares located at four equidistant locations 11' (16 pixel) away from the fixation marker. Observers were instructed to maintain their fixation at the center of the display throughout the duration of the trial. An exogenous cue, a brief flash next to one of the four boxes, was presented for 40 ms. After the exogenous cue disappeared, and after a variable inter-stimulus interval, high-acuity stimuli were presented. Stimuli consisted of lines tilted 45 deg either leftward or rightward. Stimuli appeared in each of the four squares simultaneously for 100 ms. Once the stimuli disappeared, a response cue was presented. Observers were instructed to discriminate the orientation of the target line in the box prompted by the response cue by pressing a button on a joystick. The contrast of the stimuli

was adjusted to achieve 75% accuracy in neutral trials with a SOA of 100 ms. There were 16 possible combinations of orientations of the four lines. Subjects' ability to discriminate the orientation of single stimuli was not influenced by the global configuration of the stimuli in the array. There were three trial types, valid, invalid and neutral trials. In valid trials, the exogenous cue and the response cue indicated the same location. In invalid trials, they indicated different locations. No exogenous cue was present in neutral trials. All trial types had the same probability of occurring in each experimental block. Before a block of trials, preliminary set-up procedures, described in detail in previous publications, ensured optimal eye-tracking. These procedures included calibrating the eye-tracker and performing a gaze-contingent calibration procedure.⁵ The duration of each block of trials was under 10 minutes, and brief breaks between successive blocks allowed the observers to rest. The specific SOAs tested for each observer varied across but not within blocks, ranging from 70 ms to 790 ms. Data were collected on an average of 10 1-hour sessions.

QUANTIFICATION AND STATISTICAL ANALYSIS

Analysis of oculomotor data

Only trials with optimal, uninterrupted tracking in which the fourth Purkinje image was never eclipsed by the pupil margin, were selected for data analysis. Performance was evaluated only over trials with good retinal stabilization. Trials in which the gaze was > 30' away from the center position at trial onset, and trials with blinks, saccades or microsaccades occurring at any time during the period of interest (30 ms before the onset of the exogenous cue to 30 ms after the offset of the response cue), were discarded. Periods of blinks were automatically detected by the DPI eye tracker. Eye movements with minimal amplitude of 3' and a peak velocity higher than 3°/s were categorized as saccades. Saccades with an amplitude of less than 0.5° (30') were defined as microsaccades. Saccade amplitude was defined as the vector connecting the point where the speed of the gaze shift grew greater than 3°/s (saccade onset) and the point where it became less than 3°/s (saccade offset). Periods that were not classified as saccades or blinks were labeled as drifts.

Analysis of performance

Comparisons among three trial types across observers were tested using one-way within-subjects ANOVAs followed by Tukey post hoc tests. The group mean and standard deviation were calculated for each trial type across observers. Difference between any two conditions were examined by the means of paired t tests. On average, performance was evaluated over 100 trials per condition, per observer. Performance was expressed as a measure of the sensitivity index, d' , based on observers' performance in the visual discrimination task.⁴⁶ d' was calculated based on the following equation:

$$d' = z(HR) - z(FR) \quad (\text{Equation 1})$$

where $z(HR)$ and $Z(FR)$ are z transforms of hit rate (HR) and false alarm rate (FR), respectively. Because this study used a two-alternative forced choice task, hits (H) consisted of trials in which the target was right tilted and subject correctly reported a right tilt; false alarms (FA) consisted of trials in which the target was left tilted and subject reported a right tilt; misses (M) consisted of trials in which the target was right tilted and subject reported a left tilt; correct rejections (CR) consisted of trials in which the target was left tilted and subject reported a left tilt. Hit rate and false alarm rate were then calculated as following:

$$HR = H / (H + M)$$

$$FR = FA / (CR + FA)$$

All data will be made available upon reasonable request.

Current Biology, Volume 31

Supplemental Information

**Transient perceptual enhancements
resulting from selective shifts
of exogenous attention in the central fovea**

Yue Guzhang, Natalya Shelchkova, Rania Ezzo, and Martina Poletti

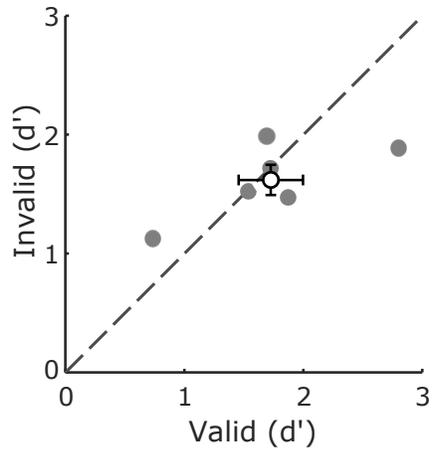


Figure S1. Performance with 70 ms SOA. Related to Figure 2. Accuracy expressed as index of sensitivity in valid against invalid trials at 70 ms SOA. Grey dots represent single subject performance. The open circle represents group mean with SEM ($n = 6$).