

# Quadrantic deficit reveals anatomical constraints on selection

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Our conscious experience is of a seamless visual world, but many of the cortical areas that underlie our capacity for vision have a fragmented or asymmetrical representation of visual space. In fact, the representation of the visual field is fragmented into quadrants at the level of V2, V3, and possibly V4. In theory, this division could have no functional consequences and therefore no impact on behavior. Contrary to this expectation, we find robust quadrant-level interference effects when attentively tracking two moving targets. Performance improves when target objects appear in separate quadrants (straddling either the horizontal or vertical meridian) compared with when they appear the same distance apart but within a single quadrant. These quadrant-level interference effects would not be predicted by cognitive theories of attention and tracking that do not take anatomical constraints into account. Quadrant-level interference strongly suggests that cortical areas containing a noncontiguous representation of the four quadrants of the visual field (i.e., V2, V3, and V4) impose an important constraint on attentional selection and attentive tracking.

attentional interference | extrastriate cortex | multifocal attention | visual attention

Our visual experience consists of a relatively faithful depiction of the world, with little evidence that the underlying cortical representation of visual space is warped or noncontiguous. The lower visual field is overrepresented relative to the upper visual field. Studies in primates found the difference between the upper and lower visual fields to be quite small in V1 (1, 2). However, in higher visual areas like medial temporal cortex (3) and parietal cortex (4), the asymmetry was much more pronounced. More recently, the asymmetrical representation of visual space has been observed in humans (5). In primary visual cortex (V1), the cortical representation is also split along the vertical meridian as a consequence of the separation between the two hemispheres (Fig. 1). Outside of the fovea, V2 and V3 are separated into quadrants with a noncontiguous representation of the upper and lower visual fields. Initially observed in primates (6), this quadrantic representation of the visual field is also a prominent feature of human anatomy (7–9). An active debate remains concerning whether V4 maintains a quadrant or hemifield representation (10, 11).

Perhaps it is unsurprising that we perceive the world as integrated and seamless even though the underlying representation is noncontiguous in the cortex. Although it would be less economical, it is theoretically possible for cells to be scattered randomly throughout the brain and still perform the same functions, as long as they maintain their connectivity. If one assumes that there is no functional consequence of the topographic organization of cells in the cortex, then it naturally follows that the fragmented representation of space in the brain should have no consequences for behavior. However, counter to our subjective experience, visual field asymmetries and the division between the left and right hemifields appear to influence behavior in selective attention tasks. The overrepresentation of the lower visual field may underlie the greater resolution of attention in the lower visual field than in the upper visual field

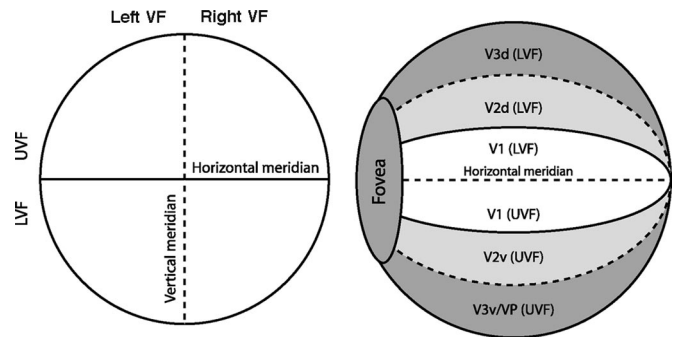


Fig. 1. Topography of visual areas. (Left) Layout of the visual field. (Right) Representation of the visual field in the right cerebral hemisphere. The representation of visual space in primary visual cortex (V1) is noncontiguous along the vertical meridian as a consequence of the separation between the two hemispheres. Areas V2 and V3 are further divided along the horizontal meridian, resulting in a quadratic representation of the visual space. LVF, UVF, Left VF, and Right VF indicate the lower, upper, left, and right visual fields, respectively.

(12, 13), and the separation between the left and right hemifields may underlie the greater capacity to attend to multiple items divided between the hemifields (14, 15). However, there has been little evidence to suggest there are quadrant-level effects on attentional selection. If quadrant-level effects were found, they could be directly linked to extrastriate areas V2 and V3 (16).

In the current study, we investigated whether there are quadrant-level effects on attentional selection by using a multiple-object tracking task. Multiple-object tracking studies indicate that observers can attentively track multiple, independently moving objects (17). In these tasks, all of the items are identical in physical appearance, and thus, successful tracking requires sustained attentional selection of multiple targets over extended periods of time. If these attentional foci have a negative impact on one another, as studies in target identification suggest (18, 19), then bringing attentively tracked targets in closer proximity would increase the amount of interference between them. Furthermore, if target tracking is mediated by cortical areas with a fractured representation of the world, the amount of interference might depend on the relative position of the targets in the visual field.

To preview our results, the current experiments demonstrate spatial limitations in attentive tracking that suggest strong links to the warped and fragmented cortical representations. We observed

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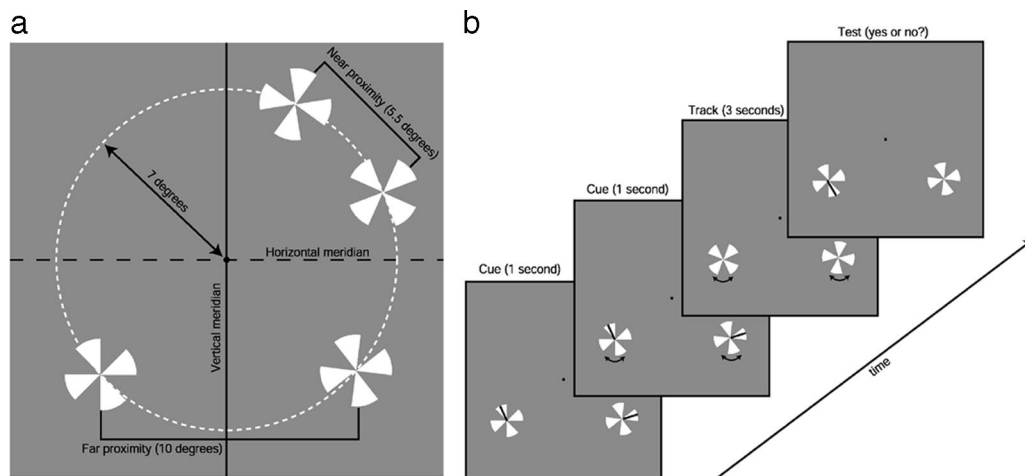
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**Fig. 2.** Stimulus and procedure. (a) Graphical depiction of the near- and far-proximity conditions. Stimuli were shown symmetrically about the tangent of imaginary radial lines extending from fixation on an imaginary circle with a diameter of  $14^\circ$  of visual angle. Two example conditions are shown in the figure: a far-proximity condition in which the two pinwheels are displayed in the lower visual field separated by the vertical meridian and a near-proximity condition in which the two pinwheels are located in the upper right quadrant. (b) Tracking procedure. At the beginning of each trial, one of the spokes on each of the two pinwheels was cued. Subjects would track the targets for a period of 3 s. One of the spokes on the two pinwheels was then cued, and subjects would report whether the cue was located on one of the spokes they were tracking.

a lower field advantage for tracking (see also ref. 12) that can be attributed to the asymmetrical representation of the upper and lower visual fields. More interestingly, we observed a quadrant-level effect on attentional selection, in which there was stronger interference between targets within the same quadrant than between those in separate quadrants. This result suggests that the interference between attended targets is mediated by areas that maintain a quadratic topographical representation of the visual field (i.e., V2, V3, and possibly V4).

## Results

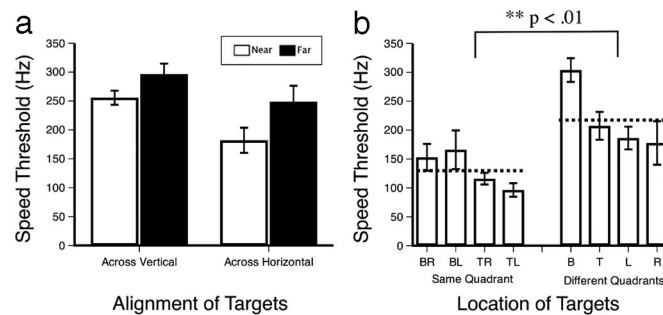
### Experiment 1: Attentional Interference Measured by Speed Thresholds.

The degree of interference between attentively tracked targets was measured as a function of two primary variables: (i) the distance between targets (near vs. far), and (ii) target location in the visual field (same quadrant vs. separate quadrants at a fixed distance). The stimuli were two four-spoke pinwheels rotating at a constant speed within a trial but varying speed across trials (see Fig. 2). Each pinwheel underwent random, independent changes in direction to prevent grouping between targets and to eliminate any systematic relationship in the positions of the targets. Observers were instructed to maintain fixation on a central dot and attentively track two targets (one spoke on each pinwheel). At the beginning of each trial, one spoke on each pinwheel was cued with a red line to designate it as a target. After a tracking period of 3 s, a randomly selected spoke from one of the two pinwheels was cued. The observer then made a yes/no response to indicate whether the cued spoke was one of the two they were tracking. The proximity between targets was manipulated by changing the distance between the two pinwheels ( $5.5^\circ$  and  $10^\circ$  in the near and far conditions, respectively). Location was varied by positioning the pinwheels symmetrically about points on an imaginary circle with a fixed diameter of  $14^\circ$  of visual angle. For each condition, the threshold speed limit for tracking targets with 85% accuracy was measured, and lower speed limits were taken as evidence for greater attentional interference between the targets.

**Proximity effects: Effect of distance across the horizontal and vertical meridians.** We observed a significant relationship between proximity and speed threshold, with slower speed limits for near targets than far targets [ $t(4) = 3.10$ ;  $P = 0.003$ ]. As shown in Fig. 3a, this distance effect was observed regardless of whether the targets were separated by the horizontal meridian [ $t(4) = 2.87$ ;

$P = 0.006$ ] or the vertical meridian [ $t(4) = 6.00$ ;  $P < 0.001$ ]. This result is striking in that attentive tracking is often considered to be a high-level process limited by factors such as the object status of the targets (20), perceptual grouping (21), and memory processes (22). These findings are, however, consistent with studies on target identification that have shown that attentional foci in close proximity can have a negative impact on one another (18, 19, 23). The current results show that there is interference between targets in an attention task that does not require target identification. This observation suggests interference between attended targets occurs before recognition. These results suggest the following conclusions: (i) that attentional interference between targets limits our ability to attentively track multiple targets, and (ii) attentional interference crosses both the vertical and horizontal meridians.

**Effect of target location: A quadrant-level interference effect.** The effect of target location with respect to the quadrants was tested with data from the near condition. In this condition, the two targets could either be located in different quadrants or within the same quadrant. As shown in Fig. 3b, subjects could track two targets at higher speeds when they appeared in different quadrants



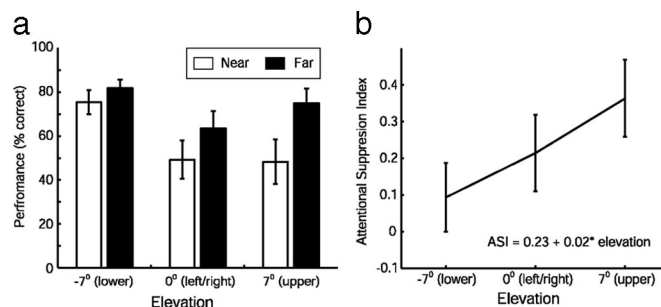
**Fig. 3.** Performance thresholds. (a) Threshold tracking speed for near targets (open bars) and far targets (filled bars) separated by the vertical meridian and horizontal meridian. Thresholds were slower for near targets across both the vertical and horizontal meridians. (b) Threshold tracking speed as a function of target location in the visual field. Threshold speeds were slower when the targets appeared within the same quadrant (BR, bottom right; BL, bottom left; TR, top right; TL, top left) than when the targets were the same distance apart but appeared in separate quadrants (B, bottom; T, top; L, left; R, right).

(separated by the vertical or the horizontal midline) than when they appeared within the same quadrant [collapsed across locations, same quadrant,  $133 \pm 15$  Hz; different quadrants,  $219 \pm 10$  Hz (data are given as mean  $\pm$  SEM);  $t(4) = 6.88$ ,  $P < 0.01$ ]. This effect is not driven entirely by the relatively high thresholds in the lower visual field (bottom condition), because the effect held whether the targets were separated by the vertical meridian [ $t(4) = 6.00$ ;  $P < 0.001$ ] or the horizontal meridian [ $t(4) = 2.87$ ;  $P = 0.006$ ]. We refer to the greater interference between targets in the same quadrant, indexed by slower speed limits, as a “quadrantic deficit.” A cognitive model might explain attentional interference as the result of suppression around a focus of attention (24). However, for targets at a fixed distance apart, a purely cognitive model would have no reason to predict that surround suppression would vary as a function of location in the visual field and thus would offer no obvious explanation for the quadrantic deficit observed here.

By taking known anatomy into account, we can find some important clues as to the cause of the quadrantic deficit. Allman and Kaas (6) were the first to make the distinction between hemifield and quadrantic representations, which were termed first and second order, respectively. Later, in their critical analysis of cortical lesions in humans, Horton and Hoyt (16) argued that visual deficits that respect both the horizontal and vertical meridian can be directly linked to extrastriate areas V2 and V3, which maintain a noncontiguous representation of the four quadrants of the visual field (see Fig. 1), a proposal that recently gained support from a neuroimaging study examining a patient with quadrantanopia (25). Taking the same logic, the quadrantic deficit observed here can be linked to areas V2 and V3, suggesting the possibility that cortical distance plays an important factor in determining the degree of attentional interference between targets. Increasing the distance between the cortical representations of each target appears to decrease the amount of attentional interference between them. There are a number of possible reasons cortical distance might be an important factor. One possibility is that cortical distance is a proxy for another important factor, such as the receptive fields of neurons. In this view, the amount of attentional interference is a function of the overlap between the receptive fields of neurons at two attended locations. In terms of the observed quadrantic deficit, the release from interference over the meridians suggests that receptive fields of neurons located on these intraareal borders may be elongated perpendicularly to the meridian. This account is purely speculative, but for our purpose the important point is that there are quadrant-level attentional interference effects, and anatomical constraints offer some potential explanations.

**Visual field asymmetries: Effect of upper vs. lower visual field.** The resolution limit of visual attention, the minimal spacing at which it is possible to individuate targets with attentive processes, is coarser in the upper visual field (12, 13). This asymmetry also was evident in our data in that subjects had marginally higher speed thresholds in the lower visual field [ $t(4) = 2.7$ ;  $P = 0.054$ ] (see Fig. 3b). With the size and eccentricity of the pinwheels fixed across locations, one explanation for the observed decrease in threshold is the observer’s limited ability to individuate targets from local distracters in the upper visual field. A second contributing factor may be that attentional interference between targets increases in the upper visual field (18). We explored this possibility further in experiment 2.

The aforementioned differences between the upper and lower visual fields motivated a further subdivision of the data. In a separate test, we examined the effect of attentional interference over the vertical meridian for the upper and lower visual fields. This subdivision revealed that the effect of proximity was significant in the upper visual field [ $t(4) = 4.06$ ;  $P = 0.008$ ], but not the lower visual field [ $t(4) = 0.86$ ;  $P = 0.219$ ]. One expla-



**Fig. 4.** Attentional interference. (a) Performance for near and far conditions as a function of elevation (chance = 25%). (b) Attentional suppression index [(Perf<sub>far</sub> - Perf<sub>near</sub>)/Perf<sub>far</sub>] as a function of elevation. Shown is the fit of a linear model [ $F_{(1,18)} = 6.05$ ;  $P = 0.024$ ].

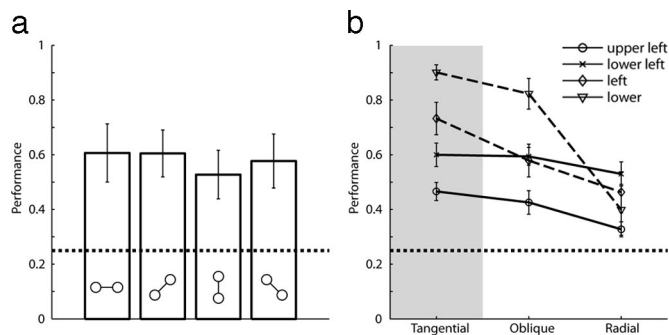
nation for this asymmetry is that spatial extent of attentional interference is dictated by the size of the attentional field (18). When attentive fields are large, as has been shown to be the case in the upper visual field (13), the suppressive region surrounding the attended target might also be larger. Consequently, we can observe attentional interference in the upper visual field in which the attentive fields and negative surrounds are large. In the lower visual field, attentive fields are small, and thus there is no observable interference between targets.

#### Experiment 2: Attentional Interference Measured by Performance at a Fixed Speed.

Experiment 2 replicates and extends the findings of experiment 1 by using performance measures with a fixed rotation speed. The experiment was similar to experiment 1, except stimuli were tested at a fixed speed of 180°/s and used four-alternative forced choice. Experiment 2a examines the effects of attentional interference over the vertical and horizontal meridians, along with upper–lower visual field asymmetries in attentional interference. Experiment 2b examines the quadrantic deficit with control conditions to rule out the possibility that the deficit can be attributed to tracking stimuli displayed in oblique orientations. Finally, experiment 2c examines the possibility that the observed quadratic deficit might be attributed to a nonanatomical reference frame.

**Experiment 2a: Attentional interference across the visual field.** The results of experiment 2a are displayed in Fig. 4. In large part, the results are similar to experiment 1. Performance was less in the upper visual field [ $t(9) = 3.10$ ;  $P = 0.013$ ]. There was an effect of proximity [ $t(19) = 4.72$ ;  $P < 0.001$ ] that was significant over both the horizontal [ $t(9) = 3.68$ ;  $P = 0.014$ ] and vertical meridian [ $t(9) = 3.04$ ;  $P = 0.005$ ]. As in experiment 1, there was an effect of proximity in the upper visual field [ $t(4) = 4.36$ ;  $P = 0.012$ ] but not in the lower visual field [ $t(4) = 0.96$ ;  $P = 0.392$ ].

One important difference in using the superthreshold measure was that there was no significant difference in performance between the upper and lower visual fields in the far proximity condition [ $t(4) = 1.04$ ;  $P = 0.357$ ]. Thus, at the superthreshold speed tested here, individuating the targets from the local distracters does not appear to be an issue. This allows us to examine the effects of attentional interference as a function of elevation in the visual field without this confounding factor. To this end, we constructed a plot showing attentional interference as a function of elevation (Fig. 4). The relationship between attentional interference and elevation suggests that attentive fields gradually become larger as the targets appear higher in the visual field, as opposed to showing an abrupt distinction between the upper and lower visual fields. This result, taken with the earlier observations that attentional interference crosses the vertical midline only in the upper visual field, further supports



**Fig. 5.** Quadrantic deficits and target orientation. The dotted line indicates chance level performance. (a) Performance as a function of global orientation. (b) Performance as a function of orientation relative to radial lines extending from fixation. The shaded region highlights the points at which the two pinwheels were oriented tangentially, as in experiment 1. Dashed lines indicate the two conditions in which the targets were oriented about the horizontal and vertical meridians.

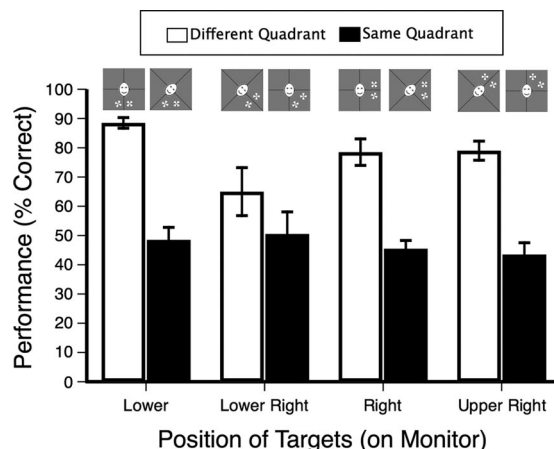
the hypothesis that attentional inference scales with the size of attentional fields (18).

**Experiment 2b: Orientation and quadrantic visual field deficits.** We next addressed the possibility that the observed quadrant deficit could be attributed to difficulty in tracking targets displayed in oblique orientations. We measured tracking performance in four locations (lower, lower left, left, and upper left) with four local orientations of the pairs of pinwheels ( $0^\circ$ ,  $45^\circ$ ,  $90^\circ$ , and  $135^\circ$ ). The results of the experiment are shown in Fig. 5. In terms of orientation with respect to the observer, there was no main effect of orientation across the four spatial locations (Fig. 5a), thus ruling out the contention that the observed quadrantic deficits could be attributed to tracking targets with an oblique arrangement.

The same data plotted with respect to radial lines extending from fixation are shown in Fig. 5b. In this format, the data become more meaningful. First, it is notable that the highest performance was in the tangential orientation in all four locations (shaded region), which was the orientation tested in experiment 1. Focusing exclusively on the tangential data, performance is highest in the conditions in which the pinwheels were separated by either the horizontal or vertical midline (dashed lines), again supporting the conclusion that there is greater competition between targets located within the same quadrant.

Tracking performance decreases monotonically as the pair of pinwheels is rotated away from the tangential orientation. If one accepts the notion that crowding results from a failure to distinguish local features (13), then this finding dovetails nicely with a report showing that crowding is strongest when distracters are aligned radially with the target (26). The most interesting aspect of the data is the change in performance from the tangential to radial orientations. In the two conditions in which both targets were located in the same quadrant, there was only modest decrease in performance (18%). The performance drop on the horizontal meridian (left) was 35% and on the vertical meridian (lower) was 55%. In these two locations (left and lower), the radial orientation places the two targets directly on the horizontal and vertical meridians, respectively, which effectively locates the two targets in the same quadrant. In this arrangement, absolute performance becomes comparable with performance when both targets are located entirely within a quadrant. This provides further support for the claim that areas with a quadrantic topographical representation of visual space mediate attentional interference.

**Experiment 2c: Quadrantic visual field deficits and reference frames.** In the final experiment, we further tested our anatomical interpretation of the observed quadrantic deficit by changing the observers'



**Fig. 6.** Quadrantic deficits and reference frames. Tracking performance for four locations on the monitor tested with two head orientations (upright, rotated clockwise  $45^\circ$ ). In all four locations, tracking performance was better when the targets were located in separate quadrants (open bars) than when targets were located in the same quadrant (filled bars).

reference frame (27). Specifically, we tested whether the quadrantic deficit follows a retinocentric reference frame that can be linked to anatomy or an allocentric reference frame, which could be linked to some other external factor (e.g., orientation of the monitor or gravity). The experiment measured observers' tracking performance in four locations for the near condition (lower, lower right, right, upper right) with the observers' head either held upright or tilted clockwise  $45^\circ$ . The predictions for the two reference frames are clear. If the quadrantic deficit has a retinocentric reference frame, then performance should rotate with the head. In contrast, an allocentric reference frame would predict that performance would be fixed by location.

The results of the experiment are shown in Fig. 6. At each location on the monitor, performance changed when the head rotated, indicating that quadrantic interference occurs within a retinocentric reference frame. Regardless of whether the head was upright or tilted, performance was higher when the two targets appeared in separate quadrants (open bars) than when they appeared in the same quadrant (filled bars). These results are inconsistent with an allocentric account for the quadrantic deficit and provide further support for our anatomical interpretation of the quadrantic deficit.

## Discussion

In their landmark paper on multiple-object tracking, Pylyshyn and Storm (17) proposed that a set of pointers could be used to index the spatial locations of objects. These pointers would then be used to access information in lower visual areas, thus forgoing the need to duplicate information in higher visual areas. The results of the present study are compatible with this idea but require a model with additional constraints that take the cortical anatomy into account. The model we propose is based on direct linkages between behavioral performance and the receptive field properties and the topography of visual areas. In the model, control signals from parietal areas continuously update and maintain the selection of attended targets. This conjecture is well founded in previous work establishing parietal areas as an important structure in attentional selection (28) and attentive tracking (29–31). We propose that parietal areas project an attentive field, shaped by the receptive fields of parietal areas, to early visual areas through a feedback process generating a suppressive surround around the target (24, 32).

Tracking multiple targets via attentive processes presents an interesting situation when viewed from within this framework.

Specifically, multiple independently moving objects, with their respective suppressive surrounds, are going to interact not only with distracters but also with one another. That is, at some point in time these attentional foci collide. The suppressive surrounds serve to minimize the effects of nearby distractors but are spatially limiting in that attentive fields interfere with one another. One particularly intriguing aspect of this model is that spatial attention is a self-limiting process. Attending multiple spatial locations is possible, but attended regions inhibit one another, effectively nullifying the benefits of selective attention. The results of our study suggest specific neural correlates for interference in attentive tracking. Weaker interference over both the horizontal and vertical meridians implicates areas V2, V3, and possibly V4, the only cortical areas currently claimed to maintain a quadrant representation of the visual field.

## Methods

Stimuli were generated in MATLAB using functions provided by the Psychophysics Toolbox (33, 34) and displayed on a GT775 monitor (ViewSonic, Walnut, CA) (100 Hz, 1,024 horizontal lines  $\times$  768 vertical lines) viewed at a fixed distance of 50 cm.

**Observers.** Five observers including two of the authors (T.A.C. and G.A.A.) participated in the experiments. The three nonauthor observers were naïve to the purposes of the experiment. All were trained psychophysical observers with normal or corrected-to-normal vision.

**Experiment 1. Stimuli.** Stimuli were high-contrast pairs of pinwheels ( $3^\circ$  of visual angle in diameter). For the proximity manipulation, the pinwheels were displayed either  $45^\circ$  or  $90^\circ$  angular degrees apart from one another on an imaginary circle  $14^\circ$  of visual angle in diameter, which corresponded to a center-to-center distance of  $5.5^\circ$  and  $10^\circ$  of visual angle, for the near- and far-proximity conditions, respectively. The location of the pinwheels was varied by positioning the pairs symmetrically about points on the circle. Subjects were tested at  $0^\circ$  (upper),  $90^\circ$  (left),  $180^\circ$  (lower), and  $270^\circ$  (right) for both the near and far conditions. In these locations, the two targets were separated by either the horizontal or vertical meridian. The  $45^\circ$  (upper left),  $135^\circ$  (lower left),  $225^\circ$  (lower right), and  $315^\circ$  (upper right) positions were also tested for the near-proximity condition. Here, both targets were located in the same quadrant.

**Procedure.** Subjects were instructed to fixate on a central point located at the center of the imaginary circle. On each trial, one spoke on each of the pinwheels was cued with a red line to indicate the targets. The pinwheels rotated independently, undergoing random changes in direction with a constant speed

within a trial (but varying speed across trials) for 4 s. In the first second of the movement, the cues remained affixed to the target. The subject would then have to track the targets for a period of 3 s. After the pinwheels stopped moving, a probe was shown on one of the spokes on one of the two pinwheels. The subject's task was to report whether the probe was located on a target.

Speed thresholds were measured for each of the conditions using QUEST (35), an adaptive procedure, to strategically sample data near the 85% correct point on the psychometric curve. Subjects participated in multiple runs (a minimum of two), with 40 trials of each condition randomly interleaved with one another. Data were pooled across runs for individual subjects. The psignifit toolbox for MATLAB (36, 37) was used to determine 85% correct performance threshold for the data.

**Experiment 2. Procedure.** The procedure was similar to experiment 1. The speed was fixed at  $180^\circ/\text{s}$ . The experiment used a four-alternative forced choice procedure instead of the two-alternative forced choice method used in experiment 1. The initial cueing of the targets was the same as experiment 1. Subjects tracked the targets for 3 s plus a variable amount of time ranging from 0 to 250 ms. The additional time added was to allow one of the two pinwheels (randomly selected on each trial) to rotate into a position that resembled a cross. This pinwheel was then cued, and the subject would report the orientation of the tracked target (chance performance = 25%). The subject completed 40 trials for each condition. **Stimuli: Experiment 2a.** Stimuli were the same as experiment 1, excluding the four conditions in which both targets were located in the same quadrant.

**Stimuli: Experiment 2b.** Stimuli were the same as experiment 1 but only tested the near-proximity condition in the lower, lower left, left, and upper left positions. The pinwheels were locally oriented at these positions with respect to imaginary radial lines extending from fixation in four orientations, a tangential orientation (identical to experiment 1), a radial orientation, and two oblique orientations ( $45^\circ$  and  $135^\circ$ ).

**Stimuli: Experiment 2c.** Stimuli were the same as experiment 1 but tested only the near-proximity condition in the lower, lower right, right, and upper right positions. Observers were cued to orient their head at the beginning of each trial. The cue was either a horizontal line or a line tilted  $45^\circ$ . The cue indicating head orientation was removed from the display 1 s before the onset of the trial.

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- Tootell RB, Switkes E, Silverman MS, Hamilton SL (1988) *J Neurosci* 8:1531–1568.
- Van Essen DC, Newsome WT, Maunsell JH (1984) *Vision Res* 24:429–448.
- Maunsell JH, Van Essen DC (1987) *J Comp Neurol* 266:535–555.
- Galletti C, Fattori P, Kutz DF, Gamberini M (1999) *Eur J Neurosci* 11:575–582.
- Liu T, Heeger DJ, Carrasco M (2006) *J Vis* 6:1294–1306.
- Allman JM, Kaas JH (1974) *Brain Res* 76:247–265.
- DeYoe EA, Carman GJ, Bandettini P, Glickman S, Wieser J, Cox R, Miller D, Neitz J (1996) *Proc Natl Acad Sci USA* 93:2382–2386.
- Engel SA, Glover GH, Wandell BA (1997) *Cereb Cortex* 7:181–192.
- Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RB (1995) *Science* 268:889–893.
- Tootell RB, Hadjikhani N (2001) *Cereb Cortex* 11:298–311.
- Zeki S (2003) *Trends Neurosci* 26:23–26.
- He S, Cavanagh P, Intriligator J (1996) *Nature* 383:334–337.
- Intriligator J, Cavanagh P (2001) *Cognit Psychol* 43:171–216.
- Alvarez GA, Cavanagh P (2005) *Psychol Sci* 16:637–643.
- Sereno AB, Kosslyn SM (1991) *Neuropsychologia* 29:659–675.
- Horton JC, Hoyt WF (1991) *Brain* 114:1703–1718.
- Plyshyn ZW, Storm RW (1988) *Spat Vision* 3:179–197.
- Mounts JR, Gavett BE (2004) *Vision Res* 44:1575–1588.
- Bahcall DO, Kowler E (1999) *Vision Res* 39:71–86.
- Scholl BJ, Plyshyn ZW, Feldman J (2001) *Cognition* 80:159–177.
- Yantis S (1992) *Cognit Psychol* 24:295–340.
- Kahneman D, Treisman A, Gibbs BJ (1992) *Cognit Psychol* 24:175–219.
- Cutzu F, Tsotsos JK (2003) *Vision Res* 43:205–219.
- Tsotsos JK, Culhane SW, Wai YL, Davis N, Nuflo F (1995) *Artif Intell* 78:507–547.
- Slotnick SD, Moo LR (2003) *NeuroReport* 14:1209–1213.
- Toet A, Levi DM (1992) *Vision Res* 32:1349–1357.
- Howard IP (1982) *Human Visual Orientation* (Wiley, New York).
- Serences J, Liu T, Yantis S (2005) in *Neurobiology of Attention*, eds Itti L, Rees G, Tsotsos JK (Academic, New York), pp 35–41.
- Culham JC, Cavanagh P, Kanwisher NG (2001) *Neuron* 32:737–745.
- Culham JC, Brandt SA, Cavanagh P, Kanwisher NG, Dale AM, Tootell RB (1998) *J Neurophysiol* 80:2657–2670.
- Battelli L, Cavanagh P, Intriligator J, Tramo MJ, Henaff MA, Michel F, Barton JJ (2001) *Neuron* 32:985–995.
- Desimone R, Duncan J (1995) *Annu Rev Neurosci* 18:193–222.
- Brainard DH (1997) *Spat Vision* 10:433–436.
- Pelli DG (1997) *Spat Vision* 10:437–442.
- Watson AB, Pelli DG (1983) *Percept Psychophys* 33:113–120.
- Wichmann FA, Hill NJ (2001) *Percept Psychophys* 63:1293–1313.
- Wichmann FA, Hill NJ (2001) *Percept Psychophys* 63:1314–1329.