Invalid Trials Are Not Required to Observe Neural Correlates of Object-based Attention in Retinotopic Visual Cortex

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Abstract

■ A central debated question in the study of object-based attention (OBA) is whether attention to the object-mediated deployment of attention is obligatory and automatic [Chen, Z., & Cave, K. R. Reinstating object-based attention under positional certainty: The importance of subjective parsing. *Perception & Psychophysics*, *68*, 992–1003, 2006] or whether the pattern of results is driven by other non-obligatory factors, such as prioritization of invalid target locations [Shomstein, S., & Yantis, S. Object-based attention: Sensory modulation or priority setting? *Perception & Psychophysics*, *64*, 41–51, 2002]. However, virtually all behavioral measures attributed to OBA are based on examining performance on invalid-cue trials, the inclusion of which confounds the assessment of the automaticity hypothesis. Our approach to resolve this issue is to determine whether effects of OBA can be observed in a 100% valid cueing paradigm. In this article, we investigate the obligatory nature of OBA by leveraging the spatial specificity of fMRI and the retinotopic organization of early visual cortex. We aimed to identify potential neural correlates of OBA in the complete absence of invalid trials. Participants perform a version of the classic two-rectangle OBA paradigm while we simultaneously measure changes in BOLD signals arising from retinotopically organized cortical areas V1, V2, and V3. In the first half of the experiment, we used the classic two-rectangle OBA paradigm except that the cue was 100% valid. In the second half, we reduced cue validity to more closely match standard OBA paradigms (runs containing invalid trials). We analyzed BOLD signals arising from our ROIs in V1, V2, and V3 according to their topographic correspondences with the ends of the rectangles in the visual field and compared these. We then compared responses in each ROI according to where the cue had occurred (cued, uncued-same-object, uncued-other-object location). We replicated this procedure in Experiment 2, but changed the layout of the two rectangles from a vertical to a horizontal configuration. Critical result: We observed statistically significant effects of OBA in V3 (Experiment 1) and V1–2 (Experiment 2) in both the 100% valid runs and in runs containing invalid trials. Moreover, the effects of OBA were no smaller in the 100% runs compared with runs containing invalid trials. Conclusion: We see BOLD modulation at the uncued locations consistent with neural correlates of OBA. ■

INTRODUCTION

To experience the world around us in a meaningful way, our visual system allows us to selectively prioritize the selection and processing of relevant sensory information in our stimulus-rich environment. Over the years, researchers have classified the behavioral and neural mechanisms of selective attention into three broad categories: attention to a specific location in space (Reynolds & Chelazzi, 2004; Corbetta, 1998; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Moran & Desimone, 1985; Posner, Cohen, & Rafal, 1982; Posner, 1980), to features of a visual scene (Gaspelin & Luck, 2018; Carrasco, 2011; Maunsell & Treue, 2006; Saenz, Buracas, & Boynton, 2002; Luck, 1995; Baylis & Driver, 1992; Driver & Baylis, 1989), and to objects (Ekman, Roelfsema, & de Lange, 2020; Erlikhman, Lytchenko, Heller, Maechler, & Caplovitz, 2020; Chen, 2012; Serences, 2004; Müller & Kleinschmidt, 2003; Scholl, 2001; Moore, Yantis, & Vaughan, 1998; Valdes-Sosa, Bobes, Rodriguez, & Pinilla, 1998; Duncan, 1984). The central hypothesis concerning object-based attention (OBA) concerns whether attention to the full extent of an object is obligatory, implying an automatic spread of attention away from the cued location (Cavanagh et al., 2023; Pooresmaeili & Roelfsema, 2014; Zhao, Kong, & Wang, 2013; Chen & Cave, 2006, 2008; Richard, Lee, & Vecera, 2008; Roelfsema, Lamme, & Spekreijse, 1998). Alternatively, attentional allocation to the entire object may be non-obligatory, as may occur in cases of prioritization (Drummond & Shomstein, 2010, 2013; Shomstein, 2012; Shomstein & Behrmann, 2008; Shomstein & Yantis, 2002, 2004), attentional shifting (Lamy & Egeth, 2002), and attentional focusing (Goldsmith & Yeari, 2003). Because the majority of OBA paradigms use a variation of a Posner cueing task (Posner, 1980), which inherently contains trials with probes in

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noncued locations, it is not yet known whether OBA findings are an underlying mechanism of attention or a by-product of the cueing paradigm. In this article, we apply fMRI to investigate the neural mechanisms of OBA, specifically testing whether the mechanism of OBA selects the entire object, by addressing potential confounds associated with common paradigms used to probe OBA.

In the early 1980s, the field of attention began to shift from a perspective that attention may only operate over locations in space (the spotlight of attention; Posner, 1980; Eriksen & Eriksen, 1974), the zoom lens (Cave & Bichot, 1999; Eriksen & St James, 1986), or gradients (Downing, 1988), to a more integrated model that attention can also select object-based representations (Kahneman & Henik, 2017; Egeth & Yantis, 1997; Rock & Gutman, 1981). Among the most compelling studies in support of attention to object representations was Duncan's (1984) overlapping-objects paradigm. In his experiment, participants discriminated features of the same object (such as the size of the box, big or small, and which side the gap was on, left or right) and features of a different, but overlapped object (such as the orientation of the line passing through the box, tilted either to the left or right, and whether it was dotted or dashed) see adapted stimuli in Figure 1A. His results showed that participants more accurately identified multiple features of the same object than a single feature of two different objects, highlighting a cost in accuracy when participants had to attend to two objects simultaneously. Because the objects were overlapping, a line drawn over a box, his findings suggested that a space-based selection mechanism alone could not account for the results, and therefore, there must also involve a component of object-based selection.

Since the initial findings in Duncan (1984), attention to objects has been probed using a wide variety of stimuli and paradigms (Figure 1). The most commonly used model to study this form of attention is Egly, Driver, and Rafal's (1994) so-called two-rectangle paradigm (Figure 1B). In this paradigm, participants are presented with two rectangles on a screen, in both vertical and horizontal configurations across the duration of the experiment. In a typical trial, participants are first shown a cue at one end of one rectangle and then a target at any one of four ends of the two rectangles. The target could appear either at the same location as the cue, defined as the valid location, or at one of two invalid locations; the other end of the same rectangle was defined as the invalid-same-object location, or at the end of the uncued object, equidistant from the location of the cue, defined as invalid-other-object location. Typical behavioral results using this paradigm consistently show that participants are fastest and most accurate to respond at the valid location. More importantly, they are faster and more accurate at the

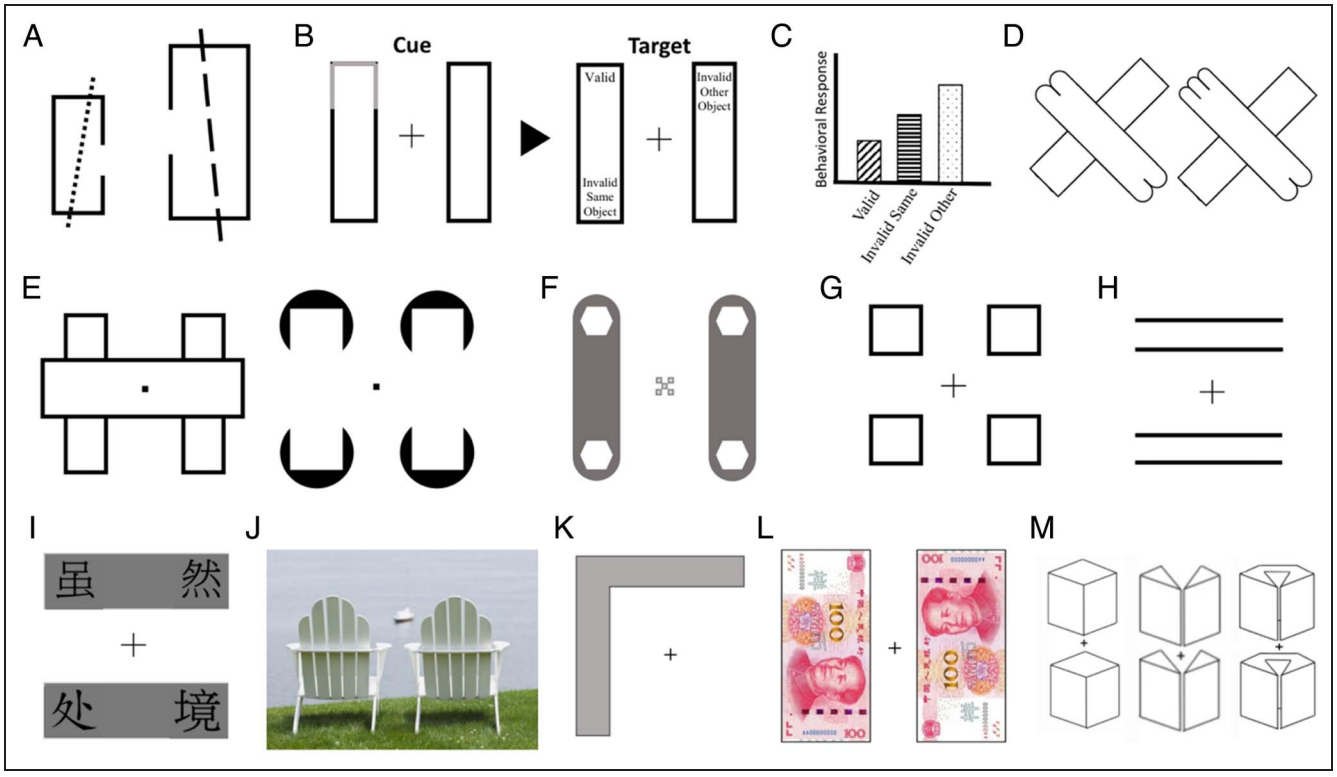

Figure 1. Stimuli used in various OBA paradigms. Adapted from: (A) Duncan (1984). (B) Egly et al. (1994). (C) Classic OBA findings such as in Egly et al. (1994). (D) Behrmann, Zemel, and Mozer (1998). (E) Moore et al. (1998). (F) Müller and Kleinschmidt (2003). (G) Shomstein and Yantis (2004). (H) Marino and Scholl (2005). (I) Li and Logan (2008). (J) Malcolm and Shomstein (2015). (K) Barnas and Greenberg (2016). (L) Zhao et al. (2020). (M) Erlikhman et al. (2020).

invalid-same-object location than to the invalid-other-object location (Figure 1C).

The classic theory of OBA proposes that this difference in attentional enhancement arises because attention automatically spreads over the cued object (Ho, 2011; Chen & Cave, 2006, 2008; Richard et al., 2008; Egly et al., 1994) to the boundaries of that object (Davis, 2001; Kramer, Weber, & Watson, 1997; Weber, Kramer, & Miller, 1997; Desimone & Duncan, 1995; Vecera & Farah, 1994). These findings are consistent across a wide range of stimuli and configurations (Figure 1D–M).

An alternative account for this automatic spread of attention to the same object was proposed by Shomstein and Yantis (2002), which attributed the attentional enhancement found in classic OBA paradigms (Egly et al., 1994) to the prioritization in object-based effects. The prioritization hypothesis posits that with a high degree of uncertainty in spatial position, when a participant is looking for the next likely location after the cued location, they are more likely to look within the object rather than between objects, prioritizing the same-object location rather than the other-object location. The authors speculated that the results in Duncan's (1984) study may have been due to prioritization established in the task; namely, when a participant was asked to report two feature attributes (line and texture), this was easily done for a single object because it was already selected. However, when asked to report a feature of two separate objects, accuracy diminished because multiple objects required processing. Moreover, because the mask interrupted this process, their sampling may also have been interrupted, resulting in decreased accuracy. In the Egly and colleagues (1994) two-rectangle paradigm, Shomstein and Yantis (2002) argued that the judgment participants had to make was in relation to a location on the rectangle, not the rectangle itself, and that attentional shifts from the cued location would be more efficient to the location within an already attended object than to location on the nonattended object. In addition, the time it would take to shift attention in the same object had minimal cost in RT compared with the other object. Their experiment showed that OBA effects became evident when the target could appear in multiple locations, so that attention had to be divided and a strategy applied to cover all the possible locations. Since this seminal study, further evidence for prioritization demonstrated that a variety of factors, including the percentage of invalid trials (Drummond & Shomstein, 2010; Shomstein & Behrmann, 2008; Shomstein & Yantis, 2004), removal of spatial cue (Donovan, Pratt, & Shomstein, 2017), and spatial bias to specific locations (Nah & Shomstein, 2020), can lead to differences relative to the classic findings of OBA.

There are therefore two types of theories accounting for the underlying mechanisms of OBA, one involving a prioritization strategy and the other an automatic spread of attention over objects away from a cued location. This led us to the realization that the classic results of OBA may arise as an artifact of the Posner-like cueing paradigm used to probe attention. The paradigms used in classic OBA literature have one common factor, they all use cue validity to drive attention to the target objects (Posner, 1980). To address this potential confound, we set out to test whether OBA is dependent on cue validity in a 100% valid-cue condition. Although there is an extensive behavioral literature that examine the effects of cue validity on OBA (see, e.g., Lou, Lorist, & Pilz, 2022; Chou & Yeh, 2018; Greenberg, 2009; He, Fan, Zhou, & Chen, 2004; Shomstein & Yantis, 2002), to our knowledge there is only a single behavioral study, which relies on a different paradigm, that has employed 100% valid cuing (Chen & Cave, 2008). When the target is presented 100% of the time in the cued location, there should be no need for participants to strategically monitor other locations. To probe attention in the absence of invalid trials, we could not use conventional behavioral methods, such as accuracy and RT, which would inherently show typical OBA results (see Figure 1C). Instead, we took advantage of the retinotopic organization of human early visual cortex (Golomb, Chun, & Mazer, 2008; Tootell et al., 1998) to measure the level of activation at critical locations on the cued and noncued objects in the absence of invalid trials.

Our approach was similar to Müller and Kleinschmidt (2003), who conducted early research on neural correlates of OBA using fMRI and the Egly and colleagues' (1994) two rectangle paradigm. In their study, they presented participants with wrench-like objects, similar to the two rectangles used in Egly and colleagues (1994), and probed the three locations (valid, invalid-same-object, and invalid-other-object) at 75% cue validity. By analyzing the cue-to-target interval, they were able to show that in early visual cortex (V1–V4), the BOLD response was higher at the same-object location compared with the other-object location during the cue period. Our study seeks to determine whether this finding depends on the presence of the invalid trials.

We conducted two fMRI experiments to explore whether OBA is independent or dependent on the presence of invalid trials. Our critical test compared the BOLD signal response in two main conditions: differences in uncued locations where the cue was validly presented 100% of the time, compared with corresponding locations when the runs also contained invalid trials. This allowed us to assess whether cue validity is the sole driver of OBA attentional enhancement. On the basis of our predictions, if we were to observe a difference in the 100% valid runs between BOLD signals arising from the uncued same-object location compared with the uncued other-object location, we would conclude that OBA is at least in part independent of cue validity (Figure 2A). These results would be more indicative of classic OBA findings described above. However, if the BOLD signal arising from the same-object location would be no different from the other-object location, this would indicate that OBA is dependent on cue validity (Figure 2B). This would imply

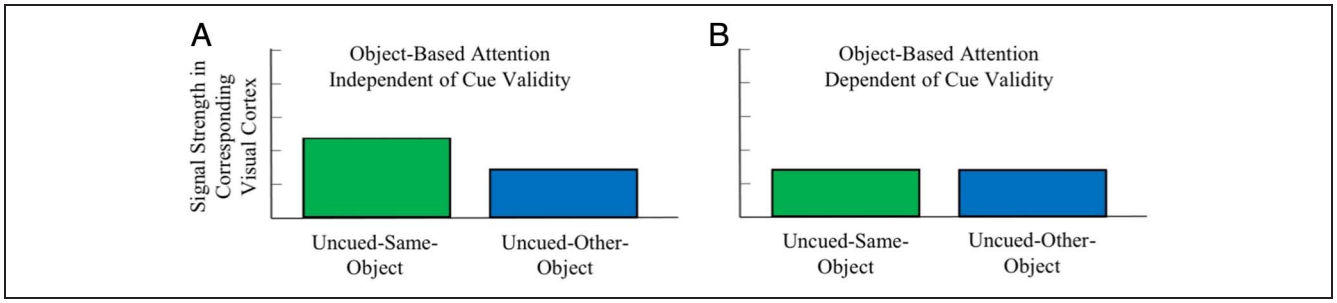

Figure 2. Hypothetical outcomes as predicted by competing hypotheses. (A) If OBA is independent of cue validity, we would predict greater signal strength in the corresponding visual cortex at the uncued-same-object location as compared with the uncued-other-object location. (B) No difference would be expected if OBA is dependent on the presence of invalid trials.

that classic OBA effects result in part from a confound introduced by invalid cuing. Our results in both Experiment 1 and Experiment 2 support the hypothesis that OBA is not solely dependent on validity-dependent mechanisms.

METHODS

Participants

We recruited participants from the Dartmouth College student community. All participants in Experiment 1 (n = 9, 5 female, mean age = 23.89 years, SD = 4.2 years) and Experiment 2 (n = 20, 12 female, mean age = 25.52 years, SD = 4.18 years) had normal or corrected-to-normal vision, reported no history of neurological disorders, completed a screening check using the Dartmouth Brain Imaging Center fMRI Subject Safety Screening Sheet, and provided written consent in accordance with the Committee for the Protection of Human Subjects at Dartmouth College. In Experiment 1, we scanned participants in two back-to-back 1-hr sessions, one for retinotopic mapping and one for the experiment. In Experiment 2, we scanned only 1-hr experiment session. The sample size for Experiment 1 was based on other experiments analyzing BOLD signals within retinotopically defined ROIs without explicit stimulation (Ekman et al., 2020; Erlikhman & Caplovitz, 2017; Erlikhman, Gurariy, Mruczek, & Caplovitz, 2016; Müller & Kleinschmidt, 2003). The sample size for Experiment 2 was doubled to account for the fact that we were relying on a structural atlas (Wang, Mruczek, Arcaro, & Kastner, 2015) for the definition of the ROIs. After the experiment, we compensated participants $20/hr for their time.

Stimulus

Our OBA paradigm consisted of two objects, a cue and a target. Specifics of each are as follows:

Objects

As illustrated in Figure 3, we modeled the stimulus and basic task design of Experiment 1 (Figure 3A) and Experiment 2 (Figure 3C) after the classic Egly and colleagues' (1994) two rectangle paradigm (Figure 1B). For Experiment 1, we positioned two high-contrast white, vertically oriented rectangles (height of 4.25°, width of 1°) 1.125° away from a white fixation square (.05° × .05°) at the center of the screen, one to the left and one to the right of fixation (Figure 3A).

For Experiment 2, we switched the configuration to horizontally oriented rectangles (height of 2°, width of 8.5°) and positioned them 2.25° away from a white fixation square (.1° × .1°) at the center of the screen, one above and one below fixation. We adjusted the dimensions of the objects for Experiment 2 (Figure 3C) to closely match those previously used in literature (Müller & Kleinschmidt, 2003).

Thus, in both experiments, each of the four ends of the rectangles was located in one of the four quadrants of the visual field. It is this configuration that allowed us to leverage the retinotopic organization of visual cortex to test the cue-validity hypothesis. For the sake of simplicity and consistency with the way we analyzed fMRI data, we will at times subsequently use the term "quadrant" to generally describe these stimulus locations in the visual field and their corresponding representations in retinotopically organized visual cortex. We warn the reader that keeping track of specific visual quadrants and their mirror-symmetric representations in visual cortex can be a challenge and we give additional details in the sections below in the context of the analyses to provide the necessary specificity for replication.

Cue

On every trial, we cued attention by transiently decreasing the luminance (from white to gray) of the contour of one end of one of the rectangles. As illustrated in Figure 3: The cue subtended 1° in Experiment 1 (Figure 3A) and 2° in Experiment 2 (Figure 3C). As the cue was transiently flashed and predictive of the target location (100% predictive in the critical runs), it represents a combined exogenous and endogenous cue (Carrasco, 2011).

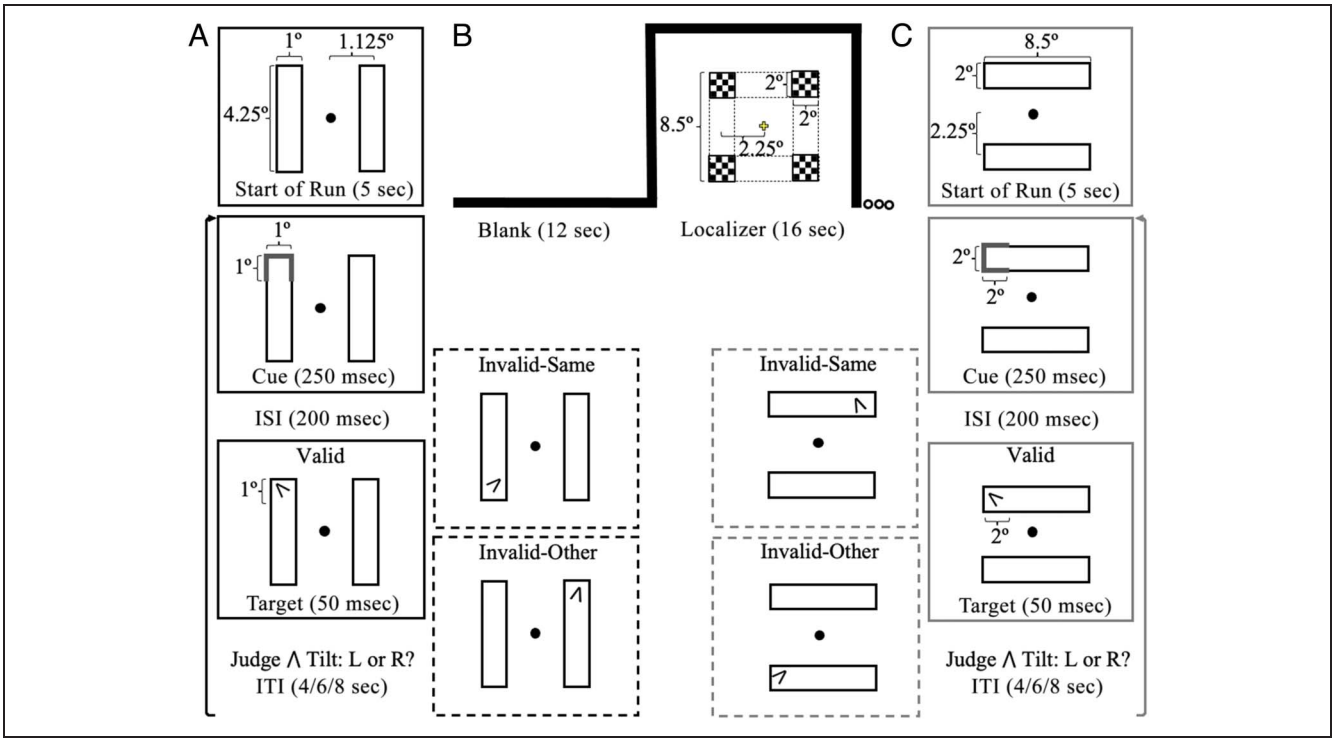

Figure 3. Illustration of run sequence and stimulus design for Experiments 1 and 2. In both experiments, each run began with a pair of rectangles on the screen for 5 sec before the first cue. (A) An example of a trial sequence in Experiment 1. In the first four functional runs (depicted in a column of solid black panels), the cue was 100% valid. The last four functional runs followed the same basic sequence, except on 16.7% of trials the cue was invalid with the target appearing at either uncued-same- or uncued-other-object locations (depicted in the right adjacent column, dashed black panels). The rectangles remained on the screen at all times, from the beginning to end of each functional run. (B) The stimulus for functionally localizing the ROIs used in Experiment 2. All four locations were stimulated at the same time. (C) An example of a trial sequence in Experiment 2, which followed a similar overall pattern as Experiment 1, with three exceptions: We increased the sizes of the objects, which were now horizontal (depicted in a column of solid gray panels), and included more invalid trials (28.6%) in the last four functional runs (depicted in the left adjacent column, dashed gray panels). Please note: In the experiment, the background was black, and the objects, cues, and targets were all white. Depicted labels and instructions were not shown during the experiment.

Target

As illustrated in Figure 3, on each trial, we presented a target centered in one of the four quadrants at one end of a rectangle. The target consisted of a white ^ subtending ~0.75° in Experiment 1 and ~1.5° in Experiment 2 and was tilted to either the left or right of vertical. On the basis of where the ^ appeared relative to the cue, a given trial could be classified as either valid or invalid: In a valid trial, the ^ appeared in the same quadrant as the cue (i.e., solid-outline panels of Figure 3A and C). In an invalid trial, the ^ appeared in either the uncued quadrant of the same object or in the opposite uncued quadrant of the other object (dashed-outline panels of Figure 3A and C). The ^ never appeared in the quadrant diagonally opposite from the cued quadrant.

Equating Task Difficulty across Participants

In Experiment 1, to equate task difficulty across participants, we varied the tilt of the target with a one-up-two-down interleaved staircase procedure, one for leftward tilts and one for rightward tilts. Participants were instructed to report via button press the target's tilt. The staircases were initiated at the beginning of the first run and again at the beginning of the fifth run.

In Experiment 2, for each participant, we set a single tilt angle used across all runs determined by a single one-up-two-down staircase procedure performed in the scanner immediately before the start of the experiment. In this procedure, the ^ could appear in one of the four quadrant locations (160 trials total, 40 trials × 4 quadrant locations), tilted either to the left or the right, but in the absence of the rectangles. On each trial of the experiment, the target orientation was jittered (±.05°) from the participant's obtained threshold.

Experiment Sequence

Instructions

At the start of the experiment, we verbally instructed the participants to keep their eyes fixated on the fixation square in the center of the screen at all times. Whenever they saw the target ^, they were instructed to indicate via the press of a button whether it was tilted to the left (Button 1) or to the right (Button 2) as quickly and

accurately as possible. To emphasize the importance of maintaining fixation, we informed the participants that it was more important to maintain fixation than get an accurate discrimination of the target. If they noticed that they happened to break fixation during the trial, we instructed them to press a third button, so the trial could be labeled as a "broken-fixation" trial and excluded from subsequent analysis.

Trial Sequence and Experimental Design

Each experimental run followed a rapid event-related design consisting of multiple trials probing OBA using the two-rectangle paradigm. As described above, each trial consisted of a cue, a target and a response. Recovery of condition-specific BOLD responses was enabled by varying the interval between the onset of consecutive cues.

Figure 3 shows an example of a trial sequence in Experiment 1 (Figure 3A) and Experiment 2 (Figure 3C). On each trial, the cue was presented for 250 msec, and the target for 50 msec followed by a response interval. The cue and target were separated by a 200-msec period during which time only the rectangles and fixation spot were present. In both experiments, we employed a rapid event-related design based on pseudorandomly assigned ISIs of 4.5, 6.5, or 8.5 sec between the onset of consecutive cues. This was accomplished by varying the duration of the response interval, which could be either 4, 6, or 8 sec, during which time the participants made a response whether they saw the target appear tilted to the left or the right. Each experimental run began and ended with a 5-sec interval during which only two rectangles were present, and the rectangles remained on the screen at all times from start to finish of the functional run.

Each experiment was divided into two 4-functional run conditions. The first four runs of each experiment contained only valid trials in which the target always appeared at the cued location (100% valid). Each of these runs consisted of 40 trials in which the target and cue appeared in each quadrant 10 times in pseudorandom order for a total run duration of 270 sec, during which we collected 135 volumes. Thus, across these four runs, we cued each quadrant 40 times. After completing these first four runs, we paused the scanner and instructed participants to passively view a sequence of 12 trials that included invalid cues (four valid trials, four invalid-same trials, four invalid-other trials). We presented each trial type one time in each quadrant, appearing in pseudorandom order with an intertrial interval of 4 sec. Although this pause in the experiment implicitly indicated that the task was changing by including invalid trials, we gave no additional explicit instructions. This lack of instruction was done to avoid introducing bias in participants' allocation of attention. To our knowledge, this was the first time any of our participants ever experienced this type of invalid cueing. We then had the participant proceed with the last four functional runs, which contained invalid trials. The 100% valid runs had to precede runs in which there were invalid trials, because if the latter preceded the former, participants may still have biased their attention away from the cued location.

In Experiment 1, in each of the last four functional runs, we included eight invalid trials, in which the target appeared at the other end of the cued object 4 times (invalid-same: 1 in each quadrant) or at the corresponding end of the uncued object 4 times (invalid-other: 1 in each quadrant). All other trials (40 trials, 10 per quadrant) were valid, with the target appearing at the same location as the cue. Each of these runs had 48 pseudorandomly presented trials corresponding to 83.3% cue validity, they lasted for 322 sec, during which we collected 161 volumes. Similar to Experiment 1, in Experiment 2, we presented 40 valid trials per run (10 per quadrant); however, we doubled the total number of invalid trials with the target appearing at the other end of the cued object 8 times (invalid-same: 2 in each quadrant) or at the corresponding end of the uncued object 8 times (invalid-other: 2 in each quadrant), thereby decreasing the cue-validity in these runs to 71.4%. Each run therefore consisted of 56 pseudorandomly presented trials. We collected 187 volumes for the duration of 374 sec for each run.

MRI Procedure

Apparatus and Display

We used Psychophysics Toolbox-3 (Kleiner et al., 2007; Brainard & Vision, 1997; Pelli, 1997) in MATLAB (2018) to generate our stimuli on a 3.1-GHz Quad-Core Intel Core i7 MacBook Pro. Using an LCD projector, we projected stimuli to a screen (60-Hz refresh, 1920 × 1080 pixel screen resolution, 42.5 cm width and 26.2 cm height) located at the back of the scanner at a viewing distance of 124.5 cm from the mirror mounted to the head coil. In both experiments, we time-locked the onset of the image acquisition trigger of the fMRI scanner to the stimulus presentation.

MRI Apparatus/Scanning Procedures

We collected data on a 3 T Siemens MAGNETOM Prisma MRI scanner (Siemens Medical Solutions), using a 32-channel head coil, at Dartmouth Brain Imaging Center. For each participant, we obtained BOLD signal intensity using the following EPI sequences for Experiments 1 and 2: T1 structural scans at high resolution (magnetization prepared rapid gradient echo, repetition time [TR] = 2.3 sec, echo time [TE] = 2.32 msec, flip angle [FA] = 8°, 256 × 256 matrix, res = 0.9 × 0.9 × 0.9 mm) and functional scans (TR = 2 sec, TE = 35.0 msec, 32 axial slices, voxel size = 3.0 × 3.0 × 3.0 mm, gap = .5 mm, matrix size = 80 × 80, interleaved slice acquisition, echo

spacing of 0.52 msec, FA = 75°). For Experiment 1, we asked each participant to complete an additional retinotopic mapping scan (TR = 2.5 sec, TE = 32.0 msec, 36 axial slices, voxel size = 2.0 × 2.0 × 3.0 mm, matrix size = 120 × 120, 3.0 mm thickness, interleaved slice acquisition, echo spacing of 0.53 msec, FA = 79°).

Preprocessing

Functional data preprocessing. We used FreeSurfer (https://surfer.nmr.mgh.harvard.edu/, Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999) for cortical reconstruction based on the T1 structural scans, as well as AFNI software (https://afni.nimh.nih.gov/, Cox & Hyde, 1997; Cox, 1996), SUMA (https://afni.nimh.nih.gov/, Saad & Reynolds, 2012; Saad et al., 2004), MATLAB (https://www.mathworks.com/products/matlab.html, 2018), and R (https://www.r-project.org/, Ihaka & Gentleman, 1996) for the fMRI analysis.

Functional data were slice-time corrected to the first slice of every volume and motion corrected both within and between runs. Functional data were smoothed using 6-mm FWHM Gaussian kernel and normalized to be percent signal change to be relative to the mean. We aligned a T1 structural scan to the slice-time and motion-corrected functional volumes and aligned the surface-based topographic ROIs (retinotopic for Experiment 1 / atlas for Experiment 2) with the resulting transformation matrix to the functional data.

Retinotopic Mapping: Experiment 1

Retinotopy. For Experiment 1, we collected retinotopic mapping scans using the same method our group has used previously and is reprinted here nearly verbatim to what we have published before (Erlikhman et al., 2016), updated only to include details specific to the current study.

A color and luminance-varying flickering checkerboard stimulus was used to perform standard retinotopic mapping (Arcaro, McMains, Singer, & Kastner, 2009; Swisher, Halko, Merabet, McMains, & Somers, 2007). Participants performed six runs of polar angle mapping and two runs of eccentricity mapping. For both polar angle and eccentricity mapping, participants were instructed to maintain fixation on a central spot while covertly attending to a rotating wedge (45° width, extending from the center of the screen to the edge of the display monitor, 40-sec cycle, alternating clockwise and counterclockwise rotation across runs) or expanding/contracting ring (1.7° width, traversing from the center of the screen to the edge of the display monitor, 40-sec cycle plus 10-sec blank between cycles, alternating expanding and contracting direction across runs) stimulus and to report via a button press the onset of a uniform gray patch in the stimulus that served as that target. Targets appeared, on average, every 4.5 sec.

Defining V1–V3. Polar angle and eccentricity representations were extracted from separate runs using standard phase encoding techniques (Engel et al., 1997; Sereno et al., 1995; Bandettini, Jesmanowicz, Wong, & Hyde, 1993). For each participant, we defined a series of topographic areas on each cortical hemisphere surface using AFNI/SUMA. Borders between adjacent topographic areas V1–V3 were defined by reversals in polar angle representations at the vertical or horizontal meridians as described in Wang and colleagues (2015) using standard definitions (Amano, Wandell, & Dumoulin, 2009; Arcaro et al., 2009; Konen & Kastner, 2008; Kastner et al., 2007; Larsson & Heeger, 2006; Brewer, Liu, Wade, & Wandell, 2005; Wade, Brewer, Rieger, & Wandell, 2002; Press, Brewer, Dougherty, Wade, & Wandell, 2001; Engel et al., 1997; DeYoe et al., 1996; Sereno et al., 1995; for a review, see Wandell & Winawer, 2011; Silver & Kastner, 2009). In total, we defined six topographic regions in each cortical hemisphere: V1v, V1d, V2v, V2d, V3v, V3d, each corresponding to a quadrant representation of the visual field. Retinotopy for a single sample participant is shown in Figure 4A. All regions were identified for all nine participants.

Localizer and Atlas: Experiment 2

Localizer. For Experiment 2, instead of collecting retinotopic mapping scans, we had each participant complete two localizer runs at the end of their scanning session. Using a block-design (Figure 3B), we presented participants with a 4 × 4 flashing checkerboard in each of the four quadrant locations. Each run had 8 blocks (16 sec on/12 sec off per block) with the checkerboard reversing every 500 msec. To ensure they maintained fixation and remained attentive, we instructed participants to detect a fixation change (1° × 1° fixation square changing from yellow to red for the duration of 250 msec, with five pseudorandom fixation changes per run) and press a button as soon as they detected it. At the end of the first localizer run, we presented the participants with their accuracy to ensure they remained attentive in the next run. We collected 118 volumes for the duration of 236 sec for each run.

ROIs. In Experiment 2, for each participant, we defined the six topographic regions in each cortical hemisphere using the Wang and colleagues (2015) probabilistic atlas. First, we converted the probabilistic ROIs into the participant's native space, by applying the max probability option (the most probable region for any given point), the Barycentric interpolation, and then the nearest neighbor interpolation. Once in the native space, in each cortical hemisphere, we defined six topographic regions: V1v, V1d, V2v, V2d, V3v, and V3d. All regions were defined for each of the 20 participants. Once we extracted voxel values from each ROI in the localizer, we intersected them with the voxels extracted for that participant's functional data set. We took only the overlapping voxels, localized to

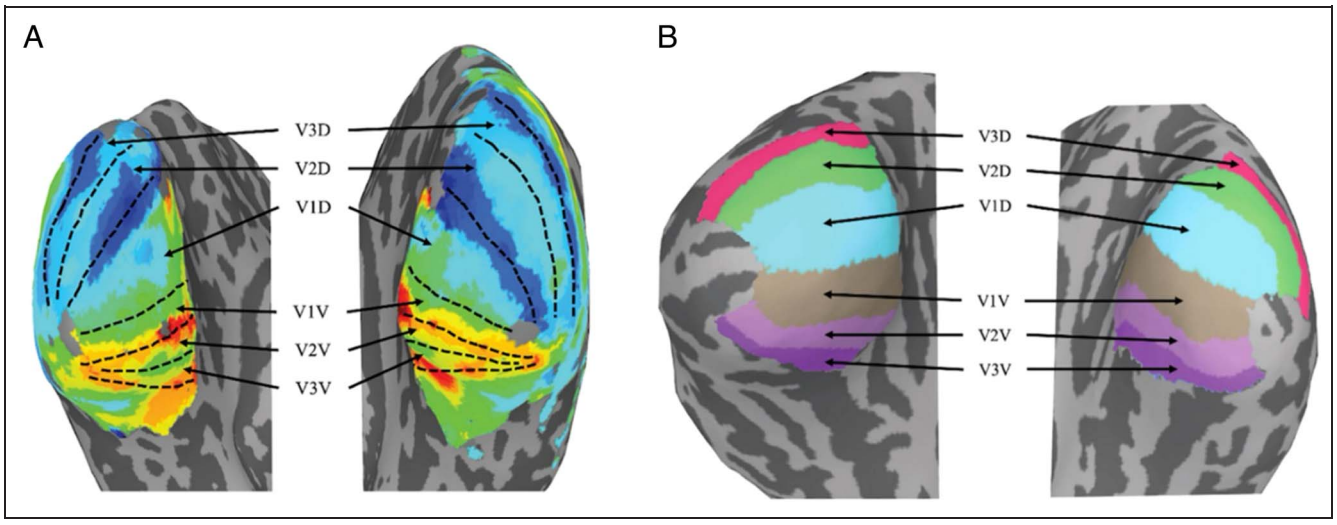

Figure 4. Topographic regions used to define ROIs for Experiments 1 and 2. (A) Retinotopy for a sample participant in Experiment 1 and (B) atlas-defined topographic areas for a sample participant in Experiment 2. Each region has a representation of one quadrant of the visual field. This allows for the dissociation of the critical locations of the task (i.e., cued location, uncued-same-object location, uncued-other-object location).

our four quadrants, for further analysis. This procedure was repeated for all 20 participants.

Analysis

General Linear Model

For each participant, we applied a volume-based general linear model (Friston et al., 1995) to estimate the response within each voxel to valid trials (i.e., cue and target both appeared at the same location) coded as a function of where in the visual field the cue and target appeared. Fixed-shape canonical hemodynamic response functions time-locked to the beginning of each trial were used as regressors for each of the four conditions (generalized additive model: $h(t) = t\,p\,\exp(t/q)$ in AFNI's *3dDeconvolve* function). Separate models were run for the four 100% valid runs and the four runs that contained invalid trials. Responses to invalid trials were excluded from all analyses as were trials in which the participant indicated that they had broken fixation.

To get the final beta weight values for each condition, which represent percent signal change in participant's BOLD response to being cued within each quadrant of the visual field, we regressed out the six-parameter head motion estimates, quadratic and linear drifts within each run, and baseline shifts between each run as nuisance variables. Thus, for each experiment, we obtained eight distinct beta weights per participant corresponding to the response to valid trials in which cues were presented in each quadrant in either the 100% valid runs or those with invalid trails.

Defining ROIs

In Experiment 1, ROIs for statistical analyses were based on those voxels within each cortical area (i.e., left hemisphere V1v) that were most active across the experiment irrespective of condition. This was done to maximize the likelihood that the voxels being examined corresponded to the ends of the rectangles. We applied a median threshold so that the top-half most active voxels within each retinotopically defined were included in subsequent analyses. In Experiment 2, this was accomplished by using the localizer data such that the top-half most active voxels in response to the localizer (median threshold) were selected for each atlas-defined retinotopic area and used in subsequent analyses. We note that the use of median thresholds is liberal, in that by considering 50% of all voxels within a given quadrant representations, we are certainly including many voxels whose maximal sensitivity corresponds to locations within the quadrant outside of the cued end of the rectangle. Such voxels are unlikely to be modulated by the attentional demands of the task and, as such, would be expected to add noise to the analysis. Thus, the use of this liberal threshold lends itself to a more conservative approach to the data overall.

Sorting of Responses According to Condition Based on Cue-target Location

Figure 5 illustrates how we sorted the responses within each quadrant according to whether they correspond to valid, invalid-same object, or invalid-other object conditions. Figure 5A illustrates how each ROI corresponds to a quadrant in the visual field. For example, the top left quadrant of the visual field corresponds with topographic right hemisphere ventral ROIs, the bottom left quadrant corresponds with right hemisphere dorsal ROIs, and so on. We sorted and compared responses in each ROI according to where the cue occurred. For example, in Experiment 1, responses in voxels within the right hemisphere ventral ROIs to trials in which the upper left quadrant was cued were classified as "Cued" or the response at the valid location (Figure 5B-left). Similarly, the responses

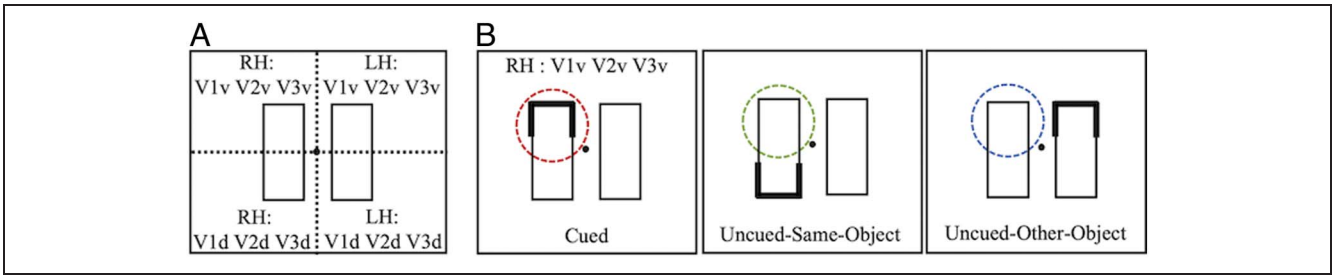

Figure 5. Condition-based sorting of BOLD responses for analysis. (A) As illustrated, each quadrant of the visual field is represented within specific regions of visual cortex. (B) An example of how responses from given visual areas are sorted according to specific task conditions: B-left: When the upper left quadrant is cued, the representations within ventral areas in the right hemisphere (dashed circle) correspond to the cued location. B-middle: When the lower left quadrant is cued, these same right-hemisphere, ventral areas represent the uncued-same-object location. B-right: Finally, when the upper-right quadrant is cued, these same areas represent the uncued-other-object location. Across the experiment, such assignments were used for the cortical representations of all four quadrants of the visual field.

in these same voxels to trials in which the lower left quadrant was cued were classified as "Uncued-Same-Object" (Figure 5B-middle). Responses in these same voxels to trials in which the upper right quadrant was cued were thus classified as "Uncued-Other-Object" (Figure 5B-right). This process was repeated in each hemisphere for each of the six ROIs. This procedure was essentially the same for Experiment 2 only taking into consideration the horizontal layout of the rectangles.

fMRI Analysis of Cued versus Uncued Locations

In both Experiments, there are two good reasons to expect that the BOLD signal response within voxels corresponding to the cued location would be greater than the responses within voxels corresponding to the two uncued locations. For one, there are two small visual transients that occur at the cued location (cue and probe). For another, to perform the task, participants are very likely to deploy covert attention to the cued location. To verify this expected result, we extracted the response within a given voxel to the cued location and the average response to the two uncued locations within the same voxel. These responses were then independently averaged across all voxels within the ROI and then averaged across the four ROIs corresponding to the entire visual field representation (i.e., V1). This process was performed for each participant separately for V1, V2, and V3 in the 100% valid runs and for V1, V2, and V3 in the runs containing invalid trials. In each experiment, the specific voxel selection/condition sorting took into consideration the vertical/horizontal layout of the rectangles.

fMRI Analysis of Uncued-same versus Uncued-other Locations

In both experiments, the critical comparison is between the BOLD signal responses corresponding to the two uncued locations. It is the behavioral differences observed between these locations that commonly serve as the operational definition of OBA and difference in BOLD response that defines a neural correlate of OBA. To make this critical comparison, we followed an analogous procedure to that described above, except that within each voxel, we extracted the uncued-same-object response and the uncued-other-object response. Again, this process took into consideration the layout of the rectangles and was performed for each participant separately for V1, V2, and V3 in the 100% valid runs and for V1, V2, and V3 in the runs containing invalid trials.

RESULTS

Excluded Trials

Trials were excluded from subsequent analysis if participants indicated that they lost fixation during the trial or if they did not make a response during the intertrial interval. In Experiment 1, we excluded, on average, 6.67 (4.17%) ± 1.56 (0.98%) trials from the first four valid functional runs, and 3.67 (2.29%) ± 1.17 (0.73%) trials from the valid trials only in the last four invalid functional runs. In Experiment 2, we excluded, on average, 4.95 (3.09%) ± 1.558 (0.97%) trials from the first four valid runs and 9.05 (5.66%) ± 2.735 (1.71%) valid trials from the last four invalid functional runs.

Results of Cued versus Uncued Location Analyses

As mentioned above in the Methods section, in both experiments, there are two good reasons to expect that the BOLD signal response within voxels corresponding to the cued location would be greater than the responses within voxels corresponding to the two uncued locations. For one, there are two small visual transients that occur at the cued location (cue and probe). For another, to perform the task participants, we are very likely to deploy covert attention to the cued location.

Experiment 1

For V1, V2, and V3 we performed a 2 × 2 repeated-measures ANOVA with factors of Cue (cued location,

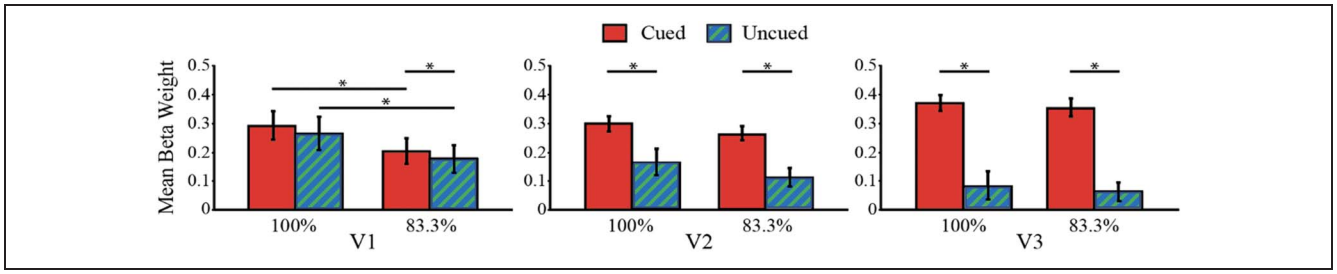

Figure 6. Cued versus uncued analysis for Experiment 1. Consistent with effects commonly reported for spatial attention, the BOLD response in ROIs corresponding to the cued location is larger than uncued locations. In all cases except for V1 in the 100% valid runs, this difference was statistically significant. Error bars indicate the standard error of the mean, *$p < .05$ uncorrected.

uncued location) and Validity (100% valid, 83.3% valid). Uncued location was the average of uncued-same-object location and uncued-other-object location. Reported p values are uncorrected.

In V1 (Figure 6, Graph 1), we found a significant main effect of Cue, $F(1, 8) = 6.41$, $p = .035$, $\eta_p^2 = .445$, and Validity, $F(1, 8) = 6.778$, $p = .031$, $\eta_p^2 = .459$, such that the BOLD signal response to the cued location was greater than the uncued and the overall BOLD response to the 100% valid runs was greater than that to the 83.3% valid runs. There was no significant interaction between Cue and Validity, $F(1, 8) < 0.001$, $p = .977$, $\eta_p^2 < .001$). Post hoc t tests revealed a significant difference between BOLD responses to the cued and uncued locations in the 83.3% valid runs, $t(8) = 3.34$, $p = .01$, and a difference in the 100% valid runs that did not reach statistical significance, $t(8) = 1.88$, $p = .098$. For comparisons of validity, the BOLD responses in the 100% valid runs were significantly greater than those in the 83.3% valid runs for both the cued, $t(8) = 2.56$, $p = .034$, and uncued, $t(8) = 2.6$, $p = .031$, locations.

A similar pattern of results was observed in V2 (Figure 6, Graph 2). Again, we observed a significant main effect for Cue, $F(1, 8) = 33.924$, $p < .001$, $\eta_p^2 = .809$, but not validity, $F(1, 8) = 4.161$, $p = .076$, $\eta_p^2 = .342$. Again, there was no significant interaction between Cue and Validity, $F(1, 8) = 2.53$, $p = .15$, $\eta_p^2 = .24$. Post hoc t tests revealed significant differences between the responses in cued versus uncued locations for both the 100% valid runs, $t(8) = 4.59$, $p = .002$, and 83.3% valid runs, $t(8) = 7.40$, $p < .001$.

Again, a similar, if not even more compelling pattern of results is observed in V3 (Figure 6, Graph 3). As seen at V1 and V2, we found a significant main effect of Cue, $F(1, 8) = 65.982$, $p < .001$, $\eta_p^2 = .892$; no main effect of Validity, $F(1, 8) = 0.111$, $p = .748$, $\eta_p^2 = .014$; and no interaction between Cue and Validity, $F(1, 8) = 0.111$, $p = .748$, $\eta_p^2 = .014$. Post hoc t tests revealed significantly greater BOLD responses in cued versus uncued locations for both 100% valid runs, $t(8) = 6.98$, $p < .001$, and 83.3% valid runs, $t(8) = 9.28$, $p < .001$.

Experiment 2

As in Experiment 1, for V1, V2, and V3, we performed a 2 × 2 repeated-measures ANOVA with factors of Cue (cued location, uncued location) and Validity (100% valid, 71.4% valid), where the uncued location was the average of uncued-same-object location and uncued-other-object location. Similar to Experiment 1, patterns of results across early visual cortex (V1, V2, V3) in Experiment 2 again are consistent with spatial attention effects found in literature (Kastner & Pinsk, 2004).

In V1 (Figure 7, Graph 1), we found a significant main effect of Cue, $F(1, 19) = 61.294$, $p < .001$, $\eta_p^2 = .763$, but not Validity, $F(1, 19) = 0.609$, $p = .445$, $\eta_p^2 = .031$. The interaction between Cue and Validity was not significant,

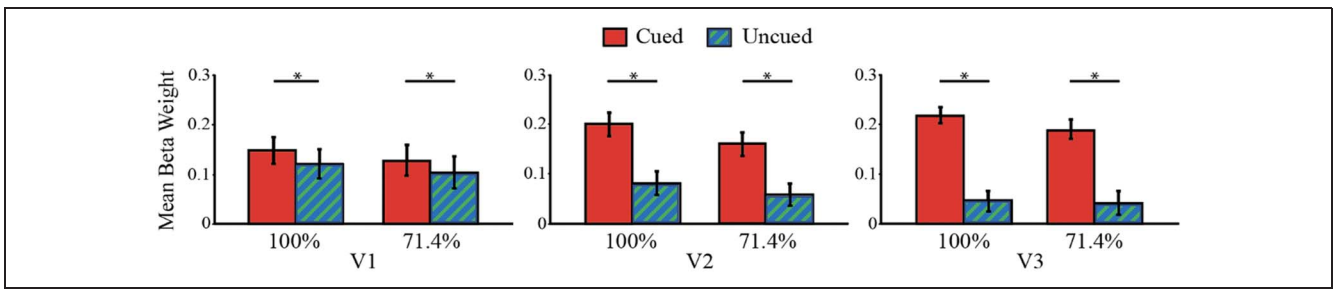

Figure 7. Cued versus uncued analysis for Experiment 2. We see a similar pattern for the larger BOLD response in ROIs corresponding to the cued location than uncued locations in Experiment 2 as we did in Experiment 1. This time, in all cases, this difference was statistically significant. Error bars indicate the standard error of the mean, *$p < .05$ uncorrected.

$F(1, 19) = 0.183, p = .673, \eta_p^2 = .01$. Our post hoc t tests revealed significantly greater BOLD responses in cued versus uncued locations for 100% valid runs, $t(19) = 7.09, p < .001$, and 71.4% valid runs, $t(19) = 5.04, p < .001$.

Consistent with results in V1, in V2 (Figure 7, Graph 2), we found the main effect of Cue, $F(1, 19) = 165.627$, $p < .001$, $\eta_p^2 = .897$, to be significant, but not Validity, $F(1, 19) = 2.61, p = .123, \eta_p^2 = .121$. Unlike V1, we found the interaction, $F(1, 19) = 8.116, p = .01, \eta_p^2 = .299$, in V2 to be significant. Our post hoc comparisons revealed that both the BOLD responses for cued versus uncued locations for 100% valid runs, $t(19) = 13.8, p < .001$, and 71.4% valid runs, $t(19) = 10.7, p < .001$, were significant.

In V3 (Figure 7, Graph 3), we found similar results, a significant main effect of Cue, $F(1, 19) = 101.615, p < .001, \eta_p^2 = .842$; nonsignificant main effect of Validity, $F(1, 19) = 1.286, p = .274, \eta_p^2 = .063$; and a significant interaction between Cue and Validity, $F(1, 19) = 10.181, p = .005, \eta_p^2 = .349$. Our post hoc t tests showed a significant effect for BOLD responses for both the cued versus uncued location for 100% valid runs, $t(19) = 11.8, p < .001$, and 71.4% valid runs, $t(19) = 8.24, p < .001$.

Results of Uncued-same- versus Uncued-other-object Analysis

Experiment 1

In each visual area V1, V2, and V3, we computed a 2 × 2 repeated-measures ANOVA with factors of Uncued-Location (uncued-same-object, uncued-other-object) and Validity (100% valid, 83.3% valid). Reported p values are uncorrected.

In V1 (Figure 8, Graph 1), we only found a significant main effect of Validity, $F(1, 8) = 6.785, p = .031, \eta_p^2 = .459$, but not the main effect of Uncued-Location, $F(1, 8) = 0.228, p = .646, \eta_p^2 = .028$, nor interaction between Uncued-Location and Validity, $F(1, 8) = 0.695, p = .429, \eta_p^2 = .08$. Post hoc t tests revealed a significant difference between the uncued-same-object location in the 100% valid versus 83.3% valid runs, $t(8) = 2.72, p = .026$, and uncued-other-object location in 100% valid versus the 83.3% valid runs, $t(8) = 2.42, p = .042$.

We found a similar pattern of results in V2 (Figure 8, Graph 2). We found a significant main effect of Validity, $F(1, 8) = 5.379, p = .049, \eta_p^2 = .402$, but not Uncued-Location, $F(1, 8) = 0.619, p = .454, \eta_p^2 = .072$. The analysis did reveal a significant interaction between Uncued-Location and Validity, $F(1, 8) = 8.148, p = .021, \eta_p^2 = .505$. Post hoc t tests showed a significant difference in BOLD in uncued-same-object location in the 100% valid versus 83.3% valid runs, $t(8) = 2.63, p = .03$, but not the uncued-other-object location in 100% valid versus the 83.3% valid runs, $t(8) = 1.83, p = .105$. Despite the significant interaction between uncued-location and validity, none of the observed differences are consistent with a neural correlate of OBA.

The results observed in V3, however, are fundamentally different and are indicative of a neural correlate of OBA (Figure 8, Graph 3). In V3, the analysis revealed a significant main effect of Uncued-Location, $F(1, 8) = 10.640, p = .011, \eta_p^2 = .571$. Neither the main effect of Validity, $F(1, 8) = 0.685, p = .432, \eta_p^2 = .079$, nor the interaction of Uncued-Location and Validity, $F(1, 8) = 1.113, p = .332, \eta_p^2 = .122$, was significant. A 2 × 2 repeated-measures Bayesian ANOVA (Quintana & Williams, 2018; Lee & Wagenmakers, 2014; Jeffreys, 1961) found evidence in favor of the null hypothesis that there is no interaction between Cue and Location: BF01 = 2.521. Post hoc t tests results showed a BOLD response in uncued-same-object location and uncued-other-object location in the 100% valid runs, $t(8) = 3.09, p = .015$, and the 83.3% valid runs, $t(8) = 2.83, p = .022$, to be significant.

Experiment 2

In V1, V2, and V3, we again computed a 2 × 2 repeated-measures ANOVA with factors of Uncued-Location (uncued-same-object, uncued-other-object) and Validity (100% valid, 71.4% valid). Reported p values are uncorrected.

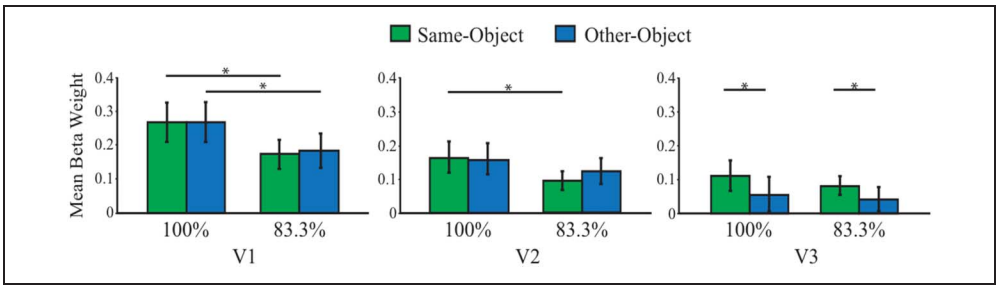

Figure 8. Uncued-same- versus uncued-other-object analysis for Experiment 1. In V3, the BOLD signal response corresponding to the uncued-same-object locations is significantly larger than that in the uncued-other-object locations. Importantly, this effect was observed in both the 100% valid and 83.3% valid runs and there was no significant interaction between Location and Validity. The finding in the 100% valid case supports the hypothesis that OBA is not wholly dependent on the presence of invalid trials encountered over the course of an experiment. Error bars indicate the standard error of the mean, *$p < .05$ uncorrected.

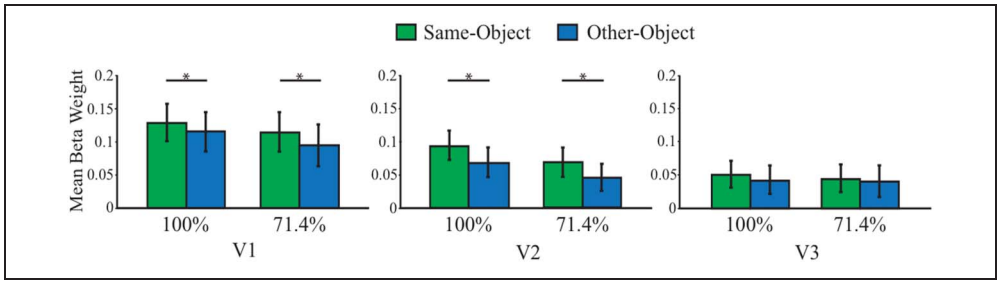

Figure 9. Uncued-same- versus uncued-other-object analysis for Experiment 2. In V1 and V2 the BOLD response corresponding to the uncued-same-object locations is significantly larger than that in the uncued-other-object locations. Importantly, this effect was observed in both the 100% valid and 71.4% valid runs and there was no significant interaction between location and validity. As in Experiment 1, the findings in the 100% valid cases once again support the hypothesis that OBA is not wholly dependent on the presence of invalid trials encountered over the course of an experiment. Error bars indicate the standard error of the mean, $*p < .05$ uncorrected.

In V1 (Figure 9, Graph 1), the main effect of Uncued-Location was significant, $F(1, 19) = 10.564$, $p = .004$, $\eta_p^2 = .357$. We did not find a significant main effect of Validity, $F(1, 19) = 0.527$, $p = .477$, $\eta_p^2 = .027$, nor interaction, $F(1, 19) = 0.379$, $p = .545$, $\eta_p^2 = .02$ (BF01 = 3.471: moderate evidence in favor of the null hypothesis). Our post hoc t tests showed a significant difference between the uncued-same-object versus uncued-other-object location in the 100% valid runs, $t(19) = 2.25$, $p = .037$, and the 71.4% valid runs, $t(19) = 2.49$, $p = .022$.

We found similar results in V2 as in V1 (Figure 9, Graph 2). Again, we found a significant main effect of Uncued-Location, $F(1, 19) = 21.017$, $p < .001$, $\eta_p^2 = .525$, but not a significant main effect of Validity, $F(1, 19) = 1.356$, $p = .259$, $\eta_p^2 = .067$, nor interaction, $F(1, 19) = 0.053$, $p = .82$, $\eta_p^2 = .003$ (BF01 = 4.712: moderate evidence in favor of the null hypothesis). Post hoc comparisons indicated a significant difference between the uncued-same-object location and uncued-other-object location in the 100% valid runs, $t(19) = 3.93$, $p < .001$, and the 71.4% valid runs, $t(19) = 2.99$, $p < .01$.

Although the overall pattern of result in V3 (Figure 9, Graph 3) is similar to that observed in V1 and V2, no significant effects of Uncued-Location and Validity were revealed: Main effect of Uncued-Location, $F(1, 19) = 1.326$, $p = .264$, $\eta_p^2 = .065$; main effect of Validity, $F(1, 19) = 0.063$, $p = .805$, $\eta_p^2 = .003$; and the interaction between Uncued-Location and Validity, $F(1, 19) = 0.170$, $p = .685$, $\eta_p^2 = .009$.

DISCUSSION

By using fMRI to probe the BOLD response to the uncued same and other object locations in the classic two-rectangle paradigm, we were able to observe that participants allocated attention similarly whether the runs contained invalid trials or not. Generally, our results showed that OBA is not wholly dependent on the presence of invalid trials. Notably, for both experiments, we found evidence that the observed OBA effect was no different in the 100% valid runs compared with the runs with invalid trials. This shows us that the manifestation of relative neural enhancement at task-irrelevant locations, although small, is not driven by the mere presence of invalid trials. Why this is the case is open to speculation but speaks to OBA being a cognitive process that fundamentally lies at the intersection of space-based attention and the formation and/or maintenance of object representations. It may be the case that from a neural perspective, the basis for the behavioral effect operationally defined as OBA in the two-rectangle paradigm is in fact the same as the neural representation of the cued object itself. Also unanswered is the question of whether objects formed through different configural processes interact with attention in the same way. For example, the rectangles used here are formed through bounded regions, but object can be defined by a host of perceptual grouping principles.

For Experiment 1, we utilized the vertical-only configuration of the classic two-rectangle paradigm (Egly et al., 1994). We compared the BOLD response for the cued versus uncued locations in runs with and without invalid trials and were able to observe a fairly consistent difference in allocation of attention to spatial location, which mirrors other classic findings in literature (Kastner & Pinsk, 2004). This finding indicated that the cue was successful in guiding our participants' attention. Critical to our hypothesis, we also compared the BOLD response to same versus other object location in runs with and without invalid trials. Like previous studies of the neural correlates of OBA (Ekman et al., 2020; Shomstein & Behrmann, 2006; Müller & Kleinschmidt, 2003), we found greater BOLD activation in the same versus other object conditions within early retinotopic visual cortex.

We want to highlight that the results in V3 in Experiment 1 are quite remarkable in that they reflect differential modulations of BOLD signals in areas of visual cortex (quadrants of V3) that did not receive time-locked visual stimulation in a context (100% valid runs) in which there is no endogenous rationale for differentially deploying spatial attention. However, it is important to note a key confounding difference between the uncued-same-object and uncued-other-object conditions. Given the vertically oriented configuration of the rectangles, the invalid-

same-object location in the visual field is always in the same hemifield as the cued-location and the invalid-other-object location is always in the opposite hemifield. There is evidence in the literature for hemifield asymmetries in the intrinsic spread of attention in response to a cued location (Hughes & Zimba, 1985). As such, the pattern of results observed here could reflect a neural correlate of this asymmetry rather than OBA per se. It is thus critical to turn our attention to the results obtained in response to the horizontal configuration used in Experiment 2, in which the relationship between hemifields and uncued-locations is reversed.

We speculated that the pattern of results in Experiment 1 could be due to a potential hemisphere confound caused by the configuration of our objects. Because the rectangles were always oriented vertically in Experiment 1, this resulted in the same object location being in the same hemisphere as the cued location. This could have led to a BOLD signal benefit at the same object location compared with the other object location due to the position rather than OBA effects, as supported by others: same hemisphere benefit versus other hemisphere inhibition (Hughes & Zimba, 1985), imbalance across shifts of attention across meridians (Greenberg et al., 2014), and more specifically due to target versus object placement (Al-Janabi & Greenberg, 2016). Although Barnas and Greenberg (2016, 2019, 2024) found a behavioral advantage for horizontal meridian shifts over vertical shifts, which led them to conclude that effects of OBA are not evenly distributed across objects, how such an asymmetry might manifest in the BOLD signal is unclear. To ensure that our finding was not due to hemisphere asymmetry, we ran Experiment 2, in which the rectangles were presented in the horizontal configuration. We were able to replicate our result by observing neural correlates of OBA in the 100% valid runs as well as in the runs with reduced validity in early visual areas V1 and V2.

We would once again like to highlight that the results obtained in Experiment 2 are quite remarkable in that they again reflect differential modulations of BOLD signals in areas of visual cortex (quadrants of V1 and V2) that did not receive time-locked visual stimulation (100% valid trials). These areas fundamentally differed in their correspondence to being on the same or other object as the cued location. Furthermore, in the 100% valid runs, there was again no endogenous rationale for differentially deploying spatial attention and, moreover, the horizontal configuration accounts for potential hemifield asymmetries in the deployment of spatial attention. Taken together and in conjunction with the results of Experiment 1, this provides further support for the hypothesis that OBA is not solely dependent on the presence of invalid trials.

We have no a priori explanation for why our pattern of results did not reach significance in V3 in Experiment 2, as compared with Experiment 1. We speculate that this could be due to the use of a probabilistic atlas (Wang et al., 2015) in Experiment 2, versus a more individualized retinotopy in Experiment 1, the conservative threshold used for voxel selection or that this may be related in some way to the behavioral asymmetries reported in the literature (Pilz, Roggeveen, Creighton, Bennett, & Sekuler, 2012). Importantly, the findings from our experiments lead us to conclude that OBA effects are not a mere by-product of cue validity in the classic two-rectangle paradigm.

Our results do not directly argue against the priority hypothesis as an explanation for many of the behavioral OBA effects found in literature (Nah & Shomstein, 2020; Shomstein & Yantis, 2004). This could be due to prior knowledge and lifetime experience of searching for things (guided search) or that prioritization operates in an additive fashion to an underlying non-prioritization-based mechanism (Shomstein & Yantis, 2004). Our results do suggest that in the absence of any task-specific priority given to noncued locations and no task-specific top–down reason why participants would attend to uncued locations on objects and given that the target would never appear there, the classic OBA difference in response is still observed for locations on the same object versus other object.

In our recent article (Cavanagh et al., 2023), we speculated how objects are formed and maintained in the brain. To attend to a location in space, some form of preattentive neural representation must exist to guide our attention to that specific location. This neural representation is what Rensink (2000) called a proto-object, which is a set of "volatile units" that are bound into a coherent object when we attend to it. Our findings would support this view that object representations exist even in the absence of directed attention, because our participants did not explicitly have to attend to uncued locations in the task. In the case of prioritization, in the 100% valid cue case, it is unclear why participants would dedicate attentional resources to the rest of the rectangle. However, we do not make the argument that this attentional enhancement to objects involves a dynamic spreading of attention, as some have suggested (Zhao et al., 2013; Chen & Cave, 2006, 2008; Richard et al., 2008). Our methods could not disentangle the time course of attention once participants attended to the cued location. We can only conclude that neural resources were dedicated disproportionately to a location on the same object versus on the other object.

Finally, our experiment utilized a hybrid exogenous–endogenous cue: rapid-transitory flash (exogenous) + 100% validity (endogenous). It remains unknown what would happen in the case of a purely endogenous cue, such as an arrow appearing in the center to volitionally direct participants to pay attention to specific locations. Goldsmith and Yeari (2003, 2012) discussed the differences in orienting to space and objects involved in cuing attention endogenously versus exogenously. In a purely endogenous cuing paradigm, participants first attend to the cue in the center; once the cue orients them where to next attend to next, they volitionally allocate their

attention to that location. This is starkly different from an exogenous cueing paradigm in which participants initially attend widely and then focus attention more discreetly to the location of the target automatically. Their experiments showed that OBA effects were observed when participants initially attended widely and then focused on the relevant location, as compared with participants beginning in the center and then shifting attention to the location of the target. However, such differences can be nuanced (Al-Janabi & Greenberg, 2016) and reasons for differences in OBA effects arising from endogenous and exogenous cueing have been debated in the field. Some studies have shown no OBA effects under endogenous cue (Macquistan, 1997), whereas others have shown mediated effects by priority (Shomstein & Yantis, 2002) and yet others have shown supportive evidence of OBA under endogenous cue (Al-Janabi & Greenberg, 2016; Şentürk, Greenberg, & Liu, 2016; Greenberg, 2009; Chen & Cave, 2008; Law & Abrams, 2002; Abrams & Law, 2000). We believe that future work should examine whether OBA effects like those reported here can be observed with purely endogenous central cueing in the absence of invalid trials.

Conclusion

In conclusion, in our two experiments, we set out to test whether OBA attentional enhancement is dependent on the presence of invalid trials. Results of Experiment 1 supported the hypothesis that OBA effects were independent of cue validity, and critically, the results were no different for fMRI runs, which did not contain invalid trials, as compared with runs that did. We replicated this finding in Experiment 2 and confirmed that the results found were not due to a potential hemisphere confound. In summary, our fMRI results address a potential confound that could have given rise to past OBA results. We find, however, that OBA appears to be a real phenomenon, rather than a consequence of invalid cueing.

Acknowledgments

We gratefully acknowledge Dr. Patrick Cavanagh for his generous support of this project. We also extend our sincere thanks to the anonymous reviewers for their constructive feedback, which significantly improved the quality of our manuscript. Additionally, we recognize the valuable research support provided by undergraduate research assistant Ineke Cordova during the data collection process for Experiment 2.

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Data Availability Statement

Data and analysis scripts will be made available to anyone who requests access by emailing the corresponding or last author.

Author Contributions

Taissa K. Lytchenko: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Marvin Maechler: Data curation; Methodology; Project administration; Writing—Review & editing. Nathan H. Heller: Data curation; Project administration; Writing—Review & editing. Sharif Saleki: Data curation; Project administration; Writing—Review & editing. Peter U. Tse: Conceptualization; Funding acquisition; Resources; Supervision; Writing—Review & editing. Gideon P. Caplovitz: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Visualization; Writing—Original draft; Writing—Review & editing.

Funding Information

National Science Foundation (https://dx.doi.org/10.13039/100000001), grant numbers: 1632738 and 1632849.

Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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