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The search for the neural mechanisms of the set size effect

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Abstract

The set size effect in visual search refers to the linear increase in response time (RT) or decrease in accuracy as the number of distractors increases. Previous human and monkey studies have reported a correlation between set size and neural activity in the frontal eye field (FEF) and intraparietal sulcus (IPS). In a recent functional magnetic resonance imaging study, we did not observe a set size effect in the superior precentral sulcus (sPCS, thought to be the human homolog of the FEF) and IPS in an oculomotor visual search task (Ikkai *et al.*, 2011). Our task used placeholders in the search array, along with the target and distractors, in order to equate the amount of retinal stimulation for each set size. We here attempted to reconcile these differences with the results from a follow-up experiment in which the same oculomotor visual search task was used, but without placeholders. A strong behavioral set size effect was observed in both studies, with very similar saccadic RTs and slopes between RT and set size. However, a set size effect was now observed in the sPCS and IPS. We comment on this finding and discuss the role of these neural areas in visual search.

Introduction

The visual world is a cornucopia of clutter from which the attention system must select relevant information. For decades, visual search tasks have been used to explore the principles and mechanisms of visual perception and visual attention (Treisman & Gelade, 1980; Chelazzi, 1999; Wolfe & Horowitz, 2004). In a typical visual search task, subjects detect a target that is embedded within an array of distractors. Increasing the number of distractors tends to produce a higher response time (RT) and lower accuracy, a finding known as the set size effect (Carrasco & Yeshurun, 1998; Wolfe *et al.*, 1998; McElree & Carrasco, 1999). The set size effect is associated with automatic 'pre-attentive' processing, various attentional mechanisms, and conscious search for the target (Treisman, 1991; Wolfe & Horowitz, 2004).

Research on the neural basis of the set size effect is challenging, because a change in set size may modify the perceptual and cognitive demands of a task. For example, a change in set size may vary the amount of visual information in the display, thereby altering brain activity in low-level visual areas; or it may differentially engage attentional areas, such as the posterior parietal cortex (PPC) (Robinson *et al.*, 1995; Corbetta & Shulman, 2002; Jerde *et al.*, 2008); or it may vary the number of potential targets for attention and action, thereby changing the demands on target selection; and so on. It is thus not surprising that neuroimaging studies have reported a set size effect in different brain regions (e.g. occipital, parietal and prefrontal cortices) (Leonards *et al.*, 2000; Muller *et al.*, 2003; Anderson *et al.*, 2007). In monkey electrophysiological studies, the firing rate of neurons in the frontal eye field (FEF) (Cohen *et al.*, 2009a) and the lateral intraparietal area (LIP) (Balan *et al.*, 2008) declines as set size increases. This finding is thought to reflect an increase in competitive interactions among neurons for which the potential targets lie in their receptive fields (RFs) (Kastner *et al.*, 2001; Schall *et al.*, 2004; Cohen *et al.*, 2010).

Using rapid event-related functional magnetic resonance imaging (fMRI), we recently found that regions in the prefrontal cortex and PPC did not show a set size effect in an oculomotor visual search task (Ikkai *et al.*, 2011), a finding that seems to be at odds with other studies (Balan *et al.*, 2008; Cohen *et al.*, 2009a). Importantly, our saccadic RT (SRT) data showed a robust set size effect, namely a linear increase in SRT as the target/distractor ratio increased (Fig. 2A). Furthermore, we observed a robust set size effect in occipital and temporal regions, indicating that our experiment taxed perceptual processing; moreover, SRT correlated with blood oxygen level-dependent (BOLD) activity in the occipital, parietal and prefrontal cortices (Fig. 3A), indicating that neural activation reflected the demands of the task. One key difference between the visual search task used in Ikkai *et al.* (2011) and those used in other studies was the use of placeholders in the stimulus array (Fig. 1A). Our rationale for using placeholders was to avoid the potential confounds of manipulating set size by merely changing the number of distractors and not controlling for retinal stimulation, as mentioned above.

However, the use of placeholders may also have equated the number of potential targets across set sizes. That is, despite the clear existence of a set size effect at the behavioral level and in the extrastriate visual cortex, the presence of placeholders meant that 12 potential targets were present for each set size (Fig. 1A). We hypothesized that this search array might have been responsible for

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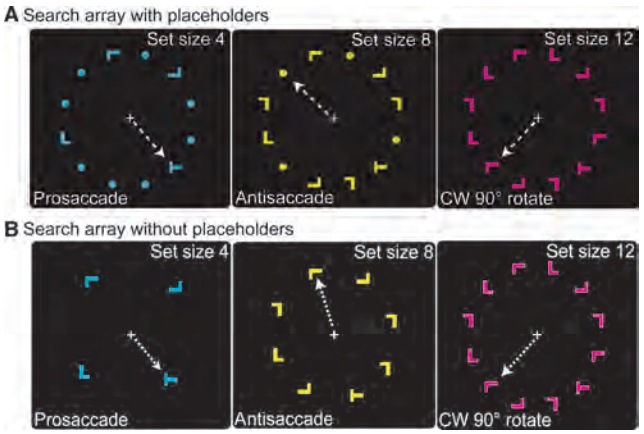

FIG. 1. Visuomotor search task, example trials. Subjects fixated a white cross during a variable inter-trial interval (3–11 s) that served as a baseline. Upon presentation of the search array, subjects covertly searched for the letter T among letter L distractors. The left, middle and right panels show examples of trials in which there were four-item, eight-item and 12-item search arrays. The left, middle and right panels show examples of trials in which subjects looked towards the target (prosaccade), away from the target (antisaccade), or rotated 90° clockwise from the target. The color of the search array indicated which saccade transformation to apply. Although the color-transformation assignment was counterbalanced across subjects, in this example, cyan, yellow and magenta instructed a prosaccade, antisaccade or rotation saccade, respectively (indicated by the white dotted arrow, which was invisible to subjects). Two versions of the task are depicted – one with placeholders that equate the amount of retinal stimulation (a) as used in Ikkai *et al.* (2011); and one without placeholders (b), as used in the present study. CW, clockwise.

the lack of a set size effect in the prefrontal cortex and PPC reported in Ikkai *et al.* (2011). In the present follow-up experiment, we modified the search array by removing the placeholders, and scanned subjects using the same experimental and statistical procedures as in Ikkai *et al.* (2011). Set size 4 now contained only four items, set size 8 contained only eight items, and set size 12 contained 12 items (Fig. 1B); thus, the number of distractors and the amount of retinal stimulation varied across set sizes. We then re-examined whether activation in the superior precentral sulcus (sPCS) and intraparietal sulcus (IPS) was related to set size.

Materials and methods

Aside from the lack of placeholders used here, the visual search task, imaging procedures and analyses were essentially identical to those used in our previous study (Ikkai *et al.*, 2011). Four neurologically healthy subjects (three males, all right-handed, aged 24–40 years) were recruited for participation and paid for their time. Subjects gave written informed consent, and all procedures were in compliance with the safety guidelines for fMRI research and approved by the human subjects Institutional Review Board at New York University.

Behavioral procedures and factorial design

The experimental stimuli were controlled by E-PRIME (Psychology Software Tools, Pittsburgh, PA, USA) and projected (Eiki LC-XG100) into the bore of the scanner on a screen that was viewed by the subjects through an angled mirror. Subjects fixated a central white cross against a black background until a search array was presented. Examples of three of the nine possible search array displays are shown in Fig. 1B. Search arrays consisted of one target (letter T) and three, seven or 11 distractors (letter L). Both stimuli were 0.64° of visual angle high and wide, and presented within an invisible annulus with an outer radius of 5.75° of visual angle. Search arrays were visible for 3 s, while subjects covertly searched for the target (that is, gaze remained at fixation). Target and distractors could be presented in any of three colors (yellow, magenta, and cyan), and in any of four orientations (0°, 90°, 180°, and 270°). A variable inter-trial interval (3, 5, 7, 9 or 11) was used between search trials.

A fully crossed factorial design with two factors, set size and saccade transformation, each with three levels, yielded a total of nine trial types. To manipulate set size, search arrays consisted of four, eight or 12 letter items. To manipulate saccade transformation, the color of the search array specified the saccade transformation (Fig. 1) – the color instructed subjects to make a saccade to the target (prosaccade), 180° opposite from the target (antisaccade), or rotated clockwise or counterclockwise 90° from the target (rotated saccade). The color–saccade transformation assignment was counterbalanced across subjects, and the order of trial types was pseudo-randomized. The location of the target and the color of the search array were pseudo-randomized so that neither the search nor saccade target appeared in the same place on more than two trials in a row, and the same color did not repeat on more than two trials. Each scanning session consisted of eight blocks of four trials per condition, yielding a total of 36 trials per block and a total of 32 trials per condition in a scanning session.

It is important to note that the factorial design allowed us to directly assess whether an interaction existed between the two factors, namely set size and saccade transformation. For set size, the three levels were four, eight or 12 items in the search array; for saccade transformation, the three levels were prosaccade, antisaccade, and rotated saccade. An interaction between set size and saccade transformation would occur if the differences on one factor depended on the level of the other factor. Critically, the two factors did not interact at the behavioral and neural levels, as measured in the statistical analyses (see Results). The lack of an interaction meant that the effects of set size could be meaningfully assessed independently of the levels of saccade transformation.

Oculomotor procedures

Eye position was monitored in the scanner at 60 Hz with an infrared videographic camera equipped with a telephoto lens (ASL 504LRO; Applied Sciences Laboratories, Bedford, MA, USA; modified with a Sony HAD CCD) that focused on the right eye viewed from the flat surface mirror mounted inside the radiofrequency coil. Nine-point calibrations were performed at the beginning of the session and between blocks when necessary. Eye-movement data were transformed to degrees of visual angle, calibrated using a third-order polynomial algorithm that fits eye positions to known spatial positions, and scored offline with in-house software (GRAPES). Any trials with unwanted/incorrect saccades were discarded (e.g. overt search, corrective saccade, and saccade to wrong item). Only trials in which the first saccade landed on the correct target and remained there until the search array offset were analyzed further. Saccadic RTs were estimated with semi-automatic routines that relied on the velocity of the eye reaching about 30°/s to determine the onset of saccades. The data were also inspected visually, trial by trial, and corrections were made if necessary.

fMRI procedures

fMRI data were collected with a 3-T head-only scanner (Allegra; Siemens, Erlangen, Germany) at the Center for Brain Imaging at New

York University. Images were acquired with custom radiofrequency coils (NM-011 transmit head-coil and NMSC-021 four-channel phased array receive coil; NOVA Medical, Wakefield, MA, USA) placed over the lateral frontal and parietal cortices. During each fMRI scan, a series of volumes was acquired with a T2*-sensitive echo planar imaging pulse sequence (repetition time, 2000 ms; echo time, 30 ms; flip angle, 80°; 36 slices; 3 × 3 × 3-mm voxels; 192 × 192-mm field of view). High-resolution (1-mm isotropic voxels) MP-RAGE three-dimensional T1-weighted scans were acquired for anatomical registration, segmentation, and display.

BOLD activity analytic procedures

Post hoc image registration was used to correct for residual head motion [MCFLIRT (motion correction with the Linear Image Registration Tool from Oxford University's Center for Functional MRI of the Brain)] (Jenkinson *et al.*, 2002). Additional preprocessing of the fMRI data was as follows. First, the time series of each voxel was bandpassed (0.05–0.25 Hz) to compensate for the slow drift typical in fMRI measurements (Zarahn *et al.*, 1997), and divided by its mean intensity to convert to percentage signal modulation and compensate for the decrease in mean image intensity with distance from the receive coil. The fMRI response was modeled with an impulse time-locked to the onset of the search array convolved with a canonical hemodynamic response function (Polonsky *et al.*, 2000). Each level of both factors (e.g. set size 4–prosaccade, set size 4–antisaccade, set size 12–rotated saccade) were modeled separately in the design matrix and entered into a modified general linear model (Worsley & Friston, 1995) for statistical analysis with VoxBo (http://www.voxbo.org). For each subject, Caret (http://brainmap.wustl.edu/caret) was used for anatomical segmentation, gray–white matter surface generation, flattening, and multi-fiducial deformation mapping to the PALS atlas (Van Essen, 2005). To examine the relationship between RT and the BOLD activity signal, statistical maps were computed that reflected correlations between evoked BOLD activity and SRT on a trial-by-trial basis. To do this, excluding incorrect trials, RT (convolved with a hemodynamic response function) was regressed against BOLD activity time-courses.

Time-series analytic procedures

Region of interest (ROI)-based analyses were used to examine the time-courses of BOLD activity signal change. First, on each subject's high-resolution anatomical scans, the gray matter was traced along ROIs. ROIs included the sPCS (along the precentral sulcus and lateral to the junction with the superior frontal sulcus); the IPS (from the junction with the postcentral sulcus to the junction with the parieto-occipital sulcus); and an extrastriate region along the collateral sulcus, here called the VIS, that showed a set size effect in Ikkai *et al.* (2011) and Leonards *et al.* (2000). Within each ROI, an *F*-test was used to select 20 voxels (540 mm^3) with the strongest overall task effect; these voxels showed a consistent deviation from baseline during the task. The selection was unbiased by activation (could be negative or positive relative to baseline) or trial type (none of the factor–level combinations were given unique weight). BOLD activity data were converted into percentage signal change, and time-courses time-locked to the onset of the search array were deconvolved with AFNI (http://afni.nimh.nih.gov/afni), with no hemodynamic response assumed. The estimated impulse response functions were averaged across voxels within an ROI and averaged across subjects from analogous ROIs to visualize time-series. Error bars are standard deviations between subjects at each time point. For an individual subject, the average of three repetition times around the peak of the impulse response function (time points 4, 6 and 8 s) from each condition was extracted from each ROI and used as a dependent variable in statistical analyses of the time-courses.

Results

Behavioral results

Remarkably, the behavioral measures were almost identical, regardless of whether placeholders were used or not. Across trial types, subjects were, on average, 82% accurate without placeholders, as compared with 86% accurate with them (Ikkai *et al.*, 2011). A repeated measures ANOVA of accuracy revealed a marginally significant effect of set size ($F_{2,6} = 4.77$, $P = 0.06$), but no significant effect for saccade transformation ($F_{2,6} = 0.79$, $P = 0.50$), and the interaction between the two was not significant ($F_{4,12} = 0.17$, $P = 0.95$). A repeated measures ANOVA of SRT revealed significant effects of set size ($F_{2,6} = 48.90$, $P = 0.00019$) and saccade transformation ($F_{2,6} = 8.0$, $P = 0.02$), and the interaction between the two was not significant ($F_{4,12} = 1.3$, $P = 0.31$). As predicted, subject performance was better when the set size was smaller, and when the saccade transformation was simpler (Table 1). Figure 2A and B shows the average SRT of all subjects. The slope of the set size effect was very similar regardless of placeholders (45.5 ms/item with placeholders vs. 40.2 ms/item without placeholders) (Fig. 2D). The magnitude of this set size effect is comparable with that found in behavioral studies (Carrasco & Yeshurun, 1998; Horowitz & Wolfe, 1998; Wolfe, 2010). The results for set size 12 were identical in the two studies, because no placeholders were used in either version. Overall, behaviorally, the only difference between the two versions was a slightly steeper slope (5.3 ms/item) when placeholders were not used (Fig. 2D). One can appreciate this by comparing the slightly shifted cumulative distributions shown in

Table 1. Behavioral data

	Set size	Prosaccade	Antisaccade	Rotated saccade	Mean
Accuracy (%)	4	92.6 (7.6)	91.1 (6.5)	88.7 (3.8)	90.8
Accuracy (%)	8	89.6 (10.0)	76.8 (15.9)	77.8 (21.0)	81.4
Accuracy (%)	12	78.8 (10.9)	70.6 (5.1)	74.3 (17.8)	74.6
Accuracy (%)	Mean	87.0 (7.3)	79.5 (10.5)	80.3 (7.5)	82.3
RT (ms)	4	799.4 (212.1)	1021.1 (315.7)	1227.7 (407.8)	1012.1 (364.6)
RT (ms)	8	970.2 (345.5)	1147.9 (385.8)	1297.4 (422.4)	1133.3 (406.5)
RT (ms)	12	1225.8 (441.9)	1414.9 (461.2)	1494.7 (450.4)	1376.2 (463.6)
RT (ms)	Mean	985.0 (380.2)	1180.2 (418.1)	1332.9 (439.2)	1162.3 (436.5)

Values are means (standard deviation); $N = 4$ subjects.

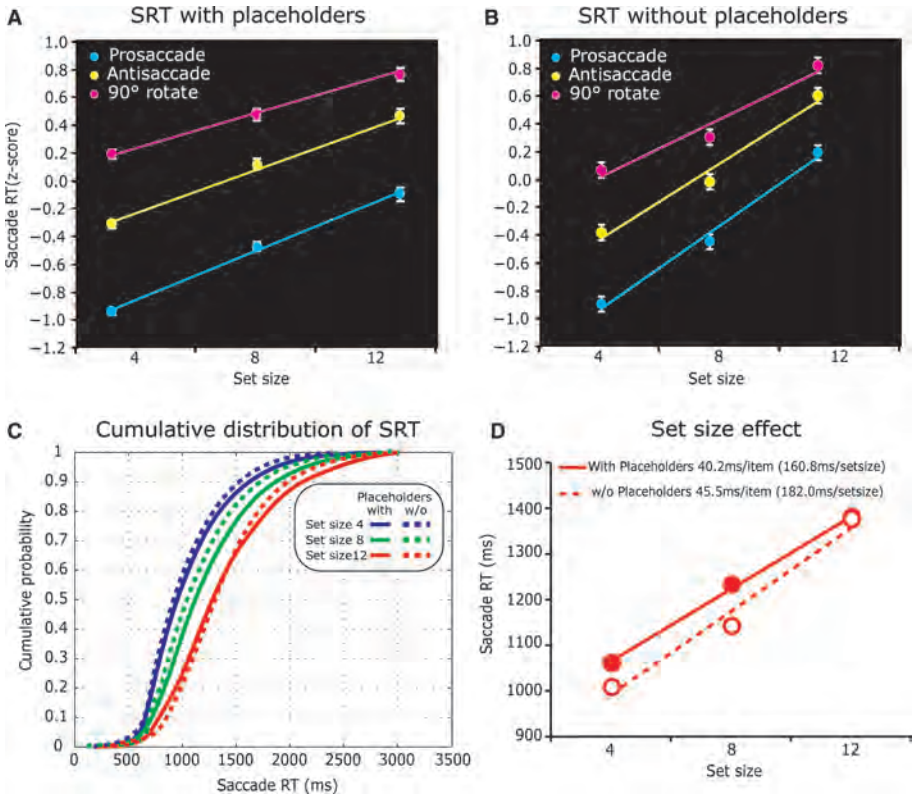

FIG. 2. Behavioral data. The average SRT data across all subjects in (A) the placeholder (N = 18) and (B) no placeholder (N = 4) conditions. Each subject's SRT was converted into z-scores before averaging. Error bars are standard errors of the mean. Note the positive linear increase in SRT as a function of set size and saccade transformation. (C) Cumulative distributions of SRT for each set size. The search array comes on at t = 0. Solid lines indicate SRTs from the experiment with placeholders, and dotted lines indicate SRTs from the experiment without placeholders. SRTs for smaller set sizes are faster and the distributions for each set size are similar, regardless of the use of placeholders. (D) Set size effect on SRT can be discerned from the positive slopes. Set size slopes are similar with placeholders (solid) and without them (dashed).

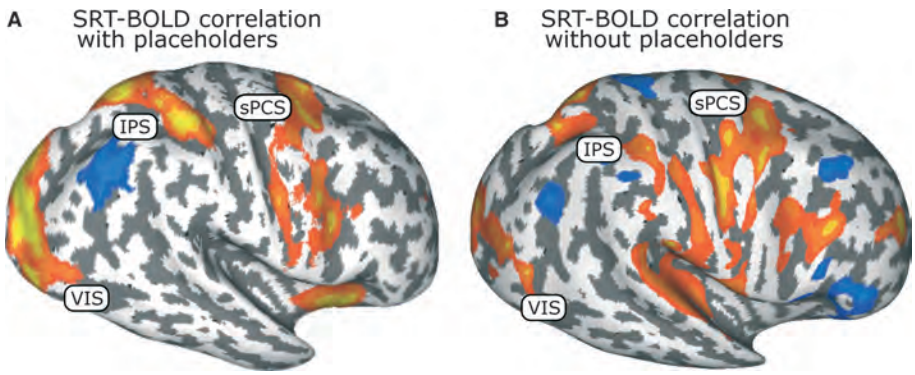

FIG. 3. Cortical regions in which BOLD activity correlated with SRT (A) with placeholders (N = 18) and (B) without them (N = 4). Warm colors show that the region's BOLD activity signal increased as the SRT increased, whereas cool colors show that the BOLD activity signal decreased as the SRT increased.

Fig. 2C. Importantly, as the two main effects (set size and saccade transformation) did not interact, it is straightforward to interpret the effects of increasing the set size.

Imaging results – correlation of BOLD activity signal with RT

As in Ikkai *et al.* (2011), we replicated positive correlations between behavioral SRTs and bilateral activation in the sPCS and IPS, as well as extensive activation in occipital cortex (Fig. 3), indicating a strong coupling of neural activation with task performance. Positive correlations may reflect the greater neural activity (duration or magnitude) associated with the more demanding level of the factor (e.g. set size – set size 12 > set size 8 > set size 4), which resulted in longer SRTs.

Imaging results – ROI time-series analyses

Recall that when placeholders were used in Ikkai *et al.* (2011), BOLD activity in the sPCS and IPS did not correlate with set size; rather, it only correlated with the saccade transformation (Fig. 4, left). Using

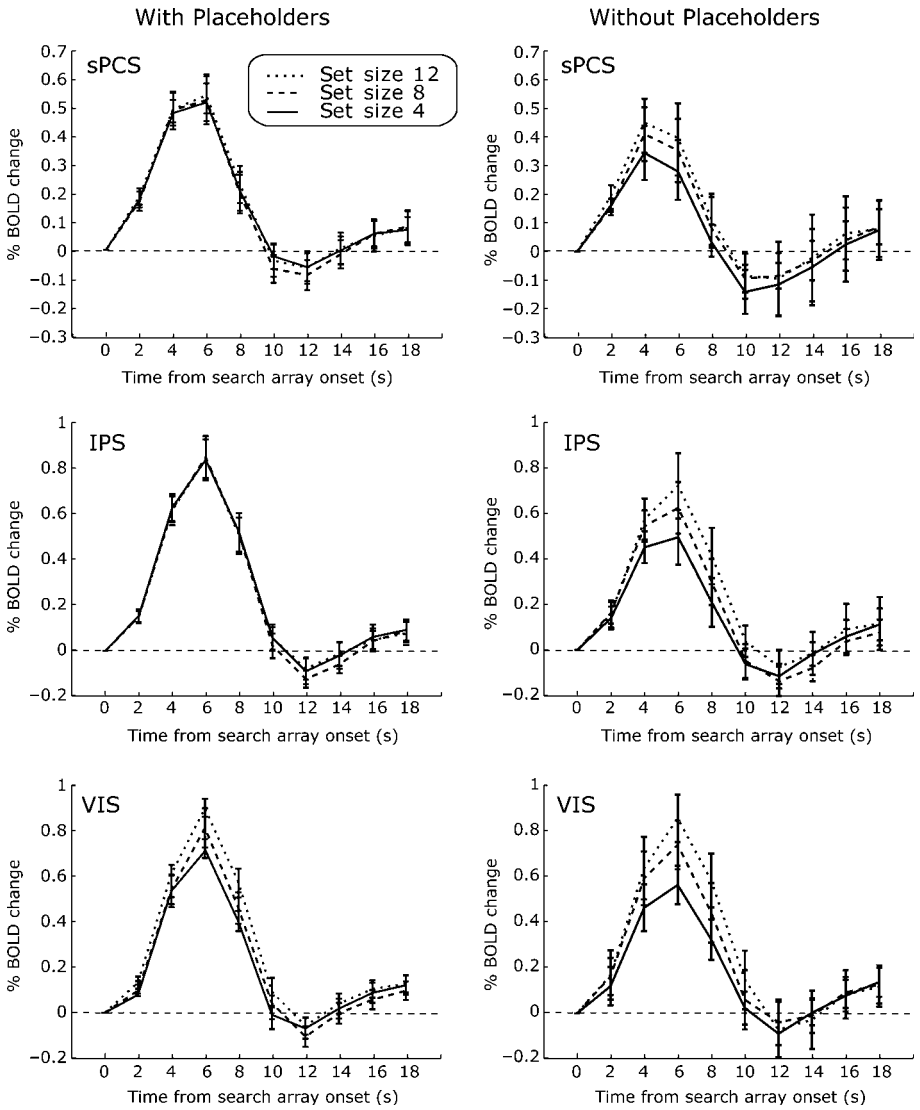

FIG. 4. Deconvolved time-series from the search task with placeholders (left, $N = 18$) and without placeholders (right, $N = 4$). The search array came on at $t = 0$. The plots represent means ± 1 standard deviation across subjects. When placeholders were used, only portions of the visual cortex showed an effect of set size. When placeholders were not used, the sPCS and IPS showed an effect of set size. A set size effect was defined as an area that showed a linear increase in BOLD activity with an increase in set size.

these same procedures, we plotted the subject-averaged time-series from ROIs time-locked to the onset of the search array. The BOLD activity in all ROIs did not show a significant interaction between set size and saccade transformation in either study, again simplifying the interpretation of the main effect of set size. The IPS, sPCS and VIS ROIs showed a significant or nearly significant linear increase in the BOLD activity signal, and strong effect sizes, as the set size increased – right and left IPS combined, $F_{1,3} = 13.23$, $P = 0.036$, effect size = 0.82; left IPS, $F_{1,3} = 13.69$, $P = 0.03$, effect size = 0.82; right IPS, $F_{1,3} = 9.40$, $P = 0.05$, effect size = 0.76; left and right sPCS combined. $F_{1,3} = 8.98$, $P = 0.06$, effect size = 0.75; left sPCS, $F_{1,3} = 12.02$, $P = 0.04$, effect size = 0.80; right sPCS, $F_{1,3} = 2.99$, $P = 0.18$, effect size = 0.50; left and right VIS combined, $F_{1,3} = 31.53$, $P = 0.01$, effect size = 0.91; left VIS, $F_{1,3} = 40.74$, $P = 0.01$, effect size = 0.93; right VIS, $F_{1,3} = 15.26$, $P = 0.03$, effect size = 0.84. In summary, the activity in the sPCS, IPS and VIS correlated with overall SRT in both task versions. The sPCS and IPS only showed a set size effect when placeholders were not used. Finally, the VIS showed a set size effect regardless of whether placeholders were used or not.

Discussion

We report here that even when behavior was essentially indistinguishable, BOLD activity in the sPCS and IPS differed remarkably during visual search, depending on whether placeholders were used to equate for retinal stimulation. It would be easy to disregard these effects if the behavior were not so similar. Moreover, overall SRTs correlated with BOLD activity in the sPCS and IPS, regardless of whether placeholders were used. Therefore, the lack of a set size effect in the frontal and parietal cortices when placeholders were used (Ikkai *et al.*, 2011) cannot be attributed to either a restriction in the range of SRTs for the placeholder condition (Fig. 2) or a lack of association with behavior (Fig. 3). So how do we make sense of these findings?

First, when no placeholders were used in the current study, the results could simply be attributable to the increased amount of retinal

stimulation with increasing set sizes. Indeed, both the sPCS and IPS contain neurons that increase in activity when irrelevant stimuli are placed within their RFs (Mohler *et al.*, 1973; Bisley *et al.*, 2004; Ipata *et al.*, 2009). Second, the use of placeholders (Ikkai *et al.*, 2011) not only equated retinal stimulation, but for the sPCS and IPS, it may have equated the number of potential saccade goals across set sizes. That is, with the use of placeholders, set sizes 4, 8 and 12 all had the same number of potential saccade goals, namely 12 (Fig. 1A). Thus, one would not necessarily expect to find a set size effect in brain areas that select among saccade goals, such as the FEF and LIP (Schall & Hanes, 1993; Bichot & Schall, 2002; Ipata *et al.*, 2006; Thomas & Pare, 2007; Ipata *et al.*, 2009), because the number of potential saccade goals was identical across set sizes when placeholders were used. Third, the brain as a whole may not have treated the placeholders used in Ikkai *et al.* (2011) as equivalent to the L distractors, as a strong set size effect was observed at the behavioral level (Fig. 2) and in the extrastriate visual cortex (Fig. 4). Target identification during visual search is based on feature discrimination, which probably depends on computations performed in the extrastriate cortex (Gregoriou *et al.*, 2009a), and not human homologs of the monkey FEF or LIP, which do not seem to have feature selectivity.

Recent monkey electrophysiology studies have examined the role of the FEF (Cohen *et al.*, 2009a) and LIP (Balan *et al.*, 2008) on the set size effect during visual search. As set size increased, monkeys took more time to find the target, and the peak firing rate of neurons in both the FEF and LIP decreased in proportion to the longer RT. The most likely mechanism for this effect is the interplay between competitive and cooperative interactions among neurons in locating the search target (Schall *et al.*, 2004; Cohen *et al.*, 2010). Interestingly, the target selection time (TST), which is the time when a neuron's activity distinguishes between when the target is in its RF and when a distractor is in the RF (Cohen *et al.*, 2009a), was reported to increase in the FEF as the set size increased (Cohen *et al.*, 2009a), but not in the LIP (Balan *et al.*, 2008). The relationship of TST to set size is a matter of ongoing discussion (Balan & Gottlieb, 2009; Cohen *et al.*, 2009b). We speculate that if those researchers had used placeholders, the TSTs across set size may have collapsed or, at the very least, narrowed and delayed. One important clarification that should be made here is that target selection in this case does not refer to identifying the target's identity as such. Instead, it refers to identifying the location of the target. FEF and LIP neurons have poor feature selectivity, and could not distinguish between a T and L in their RFs. Therefore, the competitive interactions that lead to spatial selection are among neurons coding for different visual field locations that contain targets and distractors.

In our experiment without placeholders, the sPCS and IPS showed increasing BOLD activity with increasing set size. As fMRI best characterizes the population of neural activity in an area, this linear increase may reflect a greater number of neurons in active competition as the set size increases (Balan *et al.*, 2008; Cohen *et al.*, 2009a). Theoretically, the ongoing activity in the sPCS and IPS may form maps of prioritized space (Thompson & Bichot, 2005; Fecteau & Munoz, 2006; Gottlieb, 2007; Bisley & Goldberg, 2010). The locations of relevant stimuli and saccade goals may be represented in spatial topographic maps by the activation levels of neurons with RFs that contain the targets and distractors. If these maps are indeed agnostic for the features of stimuli whose locations are prioritized, this may explain why we failed to find a set size effect when placeholders were used. So what leads to spatial selection in the FEF and LIP? Consider that extrastriate cortical areas (e.g. V4) are able to discriminate between the visual features in the stimulus array (Chelazzi *et al.*, 2001; Bichot *et al.*, 2005), and we found correlations between BOLD activity and set size regardless of the use of placeholders. The output of these selective processes for visual features could bias activation in the frontal and parietal priority maps in favor of neurons with RFs that include the target. Visual search would then reflect the ongoing interactions between top-down inputs about the prioritized locations from areas such as the FEF and LIP to visual areas such as V4, and bottom-up inputs from V4 to the FEF as selective processing for visual features is used to identify the search target (Gregoriou *et al.*, 2009a,b).

We caution that our oculomotor search task is not a pure visual search task, as it involved a saccade transformation, for goals unrelated to the current discussion. Thus, our task is a hybrid of classic visual search tasks, with their demands on visual perception and visual attention, and response selection tasks, in which actions are selected among competing alternatives (Teichner & Krebs, 1974). Indeed, an interesting parallel can be drawn between the set size effect in visual search and Hick's law, which states that RT increases as a function of the number of response alternatives (Hick, 1952). Saccadic eye movements follow Hick's law (Lee *et al.*, 2005), and FEF (Lee & Keller, 2008) and IPS (Lee *et al.*, 2006) neurons are modulated by the number of alternatives in response selection. Given that perception and action are integrated in natural behavior, search tasks such as the one described here could be useful for investigating the neural basis of attention and action.

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Abbreviations

BOLD, blood oxygen level-dependent; FEF, frontal eye field; fMRI, functional magnetic resonance imaging; IPS, intraparietal sulcus; LIP, lateral intraparietal area; PPC, posterior parietal cortex; RF, receptive field; ROI, region of interest; RT, response time; sPCS, superior precentral sulcus; SRT, saccadic response time; TST, target selection time; VIS, an extrastriate region along the collateral sulcus.

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