

The impact of top-down spatial attention on laterality and hemispheric asymmetry in the human parietal cortex

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The human parietal cortex exhibits a preference for contralaterally presented visual stimuli (i.e., laterality) as well as an asymmetry between the two hemispheres with the left parietal cortex showing greater laterality than the right. Using visual short-term memory and perceptual tasks and varying target location predictability, this study examined whether hemispheric laterality and asymmetry are fixed characteristics of the human parietal cortex or whether they are dynamic and modulated by the deployment of top-down attention to the target present hemifield. Two parietal regions were examined here that have previously been shown to be involved in visual object individuation and identification and are located in the inferior and superior intraparietal sulcus (IPS), respectively. Across three experiments, significant laterality was found in both parietal regions regardless of attentional modulation with laterality being greater in the inferior than superior IPS, consistent with their roles in object individuation and identification, respectively. Although the deployment of top-down attention had no effect on the superior IPS, it significantly increased laterality in the inferior IPS. The deployment of top-down spatial attention can thus amplify the strength of laterality in the inferior IPS. Hemispheric asymmetry, on the other hand, was absent in both brain regions and only emerged in the inferior but not the superior IPS with the deployment of top-down attention. Interestingly, the strength of hemispheric asymmetry significantly correlated with the strength of laterality in the inferior IPS. Hemispheric asymmetry thus seems to only emerge when there is a sufficient amount of laterality present in a brain region.

Introduction

The human parietal cortex exhibits a strong laterality effect, showing greater activation to contralaterally than ipsilaterally presented visual stimuli (Silver &

Kastner, 2009). Meanwhile, an imbalance or asymmetry between the left and right parietal lobes has also been observed as right parietal damage is more common than left parietal damage in neglect patients (Pouget & Driver, 2000; Stone, Patel, Greenwood, & Halligan, 1992; Vallar, 1998; Vallar & Perani, 1986). One theory argues that the right parietal lobe controls the deployment of attention to both visual hemifields whereas the left parietal lobe does so only to the contralateral hemifield (Heilman & Van Den Abell, 1980; Mesulam, 1981, 1999). Another theory argues that both the right and the left parietal lobes control the deployment of attention to the contralateral hemifield, but hemispheric asymmetry exists such that the laterality effect is greater in the left than in the right parietal lobe (Kinsbourne, 1977; Szczepanski, Konen, & Kastner, 2010).

The parietal cortex may be engaged in attention-related processing in a number of different ways. Observers can be cued to attend to the whole field with stimuli presented unpredictably in either the left or the right hemifield or cued to attend to a specific hemifield with stimuli only shown in the cued hemifield. In the former case, top-down spatial attention is not biased to either hemifield until it is directed by the bottom-up visual input. In the latter case, top-down attention is biased to one hemifield in advance. Despite differences in how top-down attention is deployed in these two scenarios, little effort has been made to understand whether hemispheric laterality and asymmetry are fixed characteristics of the human parietal cortex or dynamically modulated by the manner in which spatial attention is deployed.

Using a visual short-term memory (VSTM) paradigm, Xu and Chun (2006) reported that although fMRI responses from a region expanding the inferior intraparietal sulcus (IPS; henceforward referred to as the inferior IPS) track the number of items shown (up

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to four) regardless of item complexity, those from a region expanding the superior IPS (henceforward referred to as the superior IPS) tracked the total amount of visual information encoded in VSTM. Xu and Chun (2006) argued that the inferior IPS individuates and selects objects via their locations, and the superior IPS encodes the detailed task-relevant feature information from the selected objects (see Xu & Chun, 2009; see also Bettencourt, Michalka, & Somers, 2011; Bettencourt & Somers, 2009; Jeong & Xu, 2013; Xu, 2008, 2009, 2010; Xu & Chun, 2007). However, it is unclear how hemispheric laterality and asymmetry would affect visual object representation in these two parietal regions because responses from the right and left hemispheres were averaged together in previous studies.

The present study aimed to address these unresolved issues by examining hemispheric laterality and asymmetry in the inferior and superior IPS while manipulating the amount of top-down attentional bias. This was done by cuing participants to pay attention to either both hemifields or to just one hemifield. Given location-based encoding in the inferior IPS and feature-based encoding in the superior IPS, the inferior IPS was expected to show greater laterality than the superior IPS. These functional differences further predict that manipulating the top-down attentional bias would have different effects on laterality and hemispheric asymmetry in the inferior and superior IPS.

In Experiments 1 and 2, using an event-related fMRI design, participants encoded unilaterally presented target shapes into their VSTM. Both parietal regions showed a preference to the contralateral visual input (i.e., laterality) regardless of whether the target-appearing hemifield was cued in advance or not. Laterality was greater in the inferior than superior IPS, consistent with their roles in object individuation and identification, respectively. When target shapes appeared unpredictably in either the left or right hemifield in Experiment 1, no hemispheric asymmetry was present in either parietal region. However, when the target-present hemifield was cued in advance in Experiment 2, laterality increased in the inferior but not superior IPS. Correspondingly, hemispheric asymmetry emerged in the inferior IPS but not in the superior IPS. To replicate and extend these findings, in Experiment 3, in both a VSTM and a perceptual task, top-down attentional bias was strengthened by using a block fMRI design and making the hemifield in which the targets appeared consistent within a block of trials. In both tasks, laterality was again found in both parietal regions with greater laterality in the inferior than superior IPS. Using a block design in Experiment 3 also increased laterality in the inferior IPS compared to Experiment 1 but not in the superior IPS. As in Experiment 2, hemispheric asymmetry was only present

in the inferior but not superior IPS in both tasks. Together, these results show that although the strength of laterality could be modulated by the deployment of top-down attention in certain brain regions, it nevertheless is consistently present across distinctive IPS regions under different attentional modulations and tasks. Hemispheric asymmetry, on the other hand, seems to only emerge in specific parietal regions when the deployment of top-down spatial attention increases laterality sufficiently.

Materials and methods

Participants

Eleven (six females), nine (four females), and 12 (five females) participants took part in Experiments 1, 2, and 3, respectively. Three participants took part in more than one experiment with at least 6 months apart between the experiments (one in Experiments 1 and 3; one in Experiments 2 and 3; and one of the authors, S. K. J., in all three experiments).

All participants were between the ages of 18 and 35 and right-handed and had normal or corrected-to-normal visual acuity. They were recruited from the Harvard University community with informed consent and received payment for their participation in the experiments. The experiments were approved by the Committee on the Use of Human Subjects at Harvard University and conducted according to the Declaration of Helsinki.

Two additional participants were tested in Experiment 1 but were excluded from further analysis due to excessive head motion (greater than 3 mm) and a failure to localize regions of interest (ROIs) in both hemispheres. Three additional participants were tested but excluded in Experiment 2 due to the following reasons: One participant's ROIs could not be localized in both hemispheres, and the other two participants failed to maintain proper fixation during the task.¹ One additional participant was tested in Experiment 3 but was excluded due to a failure to obtain above fixation-level fMRI activations from the experimental conditions.

Design and procedure

Main experiments

Experiment 1 was designed to measure hemispheric laterality and asymmetry in a VSTM paradigm when top-down spatial attention was not biased to a specific hemifield. Using an event-related fMRI design in which participants attended simultaneously to both the left

and the right hemifields, they were asked to remember in a sample display either two or four black target shapes presented briefly in one of the hemifields. The hemifield in which the target shapes would appear in a given trial followed a pseudorandom order and thus could not be predicted by the participants, forcing them to attend simultaneously to both hemifields. To further encourage participants to attend to both hemifields simultaneously, filler trials were included in which two or four black target shapes appeared in both hemifields (either one or two targets in each hemifield for set size two and four displays, respectively). These filler trials were not included in the final analysis. After a brief delay, participants judged in a test display whether a test shape shown at fixation matched one of the remembered target shapes by pressing the appropriate response button with either their right index or middle finger. The test shape was presented at fixation to discourage participants from continuously attending to the target-present hemifield during the delay period. A match occurred in 50% of the trials (see Figure 1A for an illustration of an example trial).

All stimuli appeared on a light gray background. Eight different target shapes were used (Xu & Chun, 2006). Each shape subtended approximately $2.74^\circ \times 2.74^\circ$, and the distance between the fixation and the center of each shape was 5.3° . The size of the entire display was $11.8^\circ \times 11.8^\circ$. Nine placeholders, marking all the possible target locations and the central fixation, appeared throughout each trial (see Figure 1A).

Experiment 1 contained a total of nine stimulus conditions. There were four display conditions for set size two and four for set size four plus the fixation condition. The four-display conditions for each set size were (a) targets shown at the left hemifield, (b) targets shown at the right hemifield, (c) targets shown bilaterally at the upper visual field, and (d) targets shown bilaterally at the lower visual field. Conditions c and d were filler trials and were excluded from further data analysis. Trials from different stimulus conditions were intermixed within each run, following a balanced trial history design (see Kourtzi & Kanwisher, 2000; Todd & Marois, 2004; Xu & Chun, 2006). Each trial lasted 6 s and contained a fixation display (1000 ms), a sample display (200 ms), a blank display (1000 ms), a test display/response period (1800 ms), and a feedback display (2000 ms). There were 83 trials in each run with nine trials for each stimulus condition and two additional filler trials. These additional filler trials were included at the beginning and end of each run to balance the trial history of the first and last trials, respectively (see Todd & Marois, 2004; Xu & Chun, 2006). These filler trials were also excluded from data analysis. Each participant completed two or three runs with each run lasting 8 min 27 s. Eye movements were

not monitored in Experiment 1 as sample displays were shown very briefly (200 ms) and unpredictably in either or both hemifields, making systematically biased eye movement pattern across the different conditions unlikely.

Experiment 2 was designed to test whether hemispheric asymmetry emerges when top-down attention is deployed to a specific hemifield in advance. As in Experiment 1, target shapes appeared either in the left or right hemifield in a pseudorandom order in an event-related design. But unlike in Experiment 1, here a cue was presented at the beginning of each trial to instruct the participants to attend to either the left or right hemifield (Figure 1B). The cue was a blue triangle (subtended approximately $2.74^\circ \times 2.74^\circ$) appearing briefly twice at fixation before the presentation of the targets (see Figure 1B).

In each trial, participants encoded from a sample display three black target shapes appearing in the attended hemifield. After a short delay, they saw three shapes in a test display and judged whether these test shapes matched the target shapes shown at the same locations by pressing an appropriate response key with either their right index or middle finger. By presenting the test shapes in the target-appearing hemifield, the participants were encouraged to sustain their top-down spatial attention to the target-present hemifield throughout the trial. A match occurred in 50% of the trials. In the nonmatch trials, a new shape not shown in the sample display appeared in the test display. Seven placeholders, marking all the possible target locations and the central fixation location, were shown throughout each trial (Figure 1B).

Each trial lasted 6 s and contained a fixation period (625 ms), a first cue (125 ms), a blank display (125 ms), a second cue (125 ms), a blank display (1000 ms), a sample display (200 ms), a blank display (1000 ms), a test display/response period (1800 ms), and a feedback display (1000 ms). There were 27 trials in each run with 10 attending-left and 10 attending-right trials, five fixation trials, and two filler trials for trial history balancing purposes. Filler trials were excluded as in Experiment 1. Each participant completed five runs with each run lasting 2 min 51 s.

Experiment 3 was designed to measure hemispheric laterality and asymmetry in both a VSTM and a perceptual paradigm using an fMRI block design in which participants were cued to attend the same hemifield throughout a block of trials. In half of the runs of Experiment 3, participants performed a VSTM task similar to that of Experiment 2 but with trials in which targets appeared in the same hemifield grouped together into blocks. Each such block of trials lasted 38 s and contained a 4-s fixation period, a 2-s instruction screen cuing participants the hemifield to

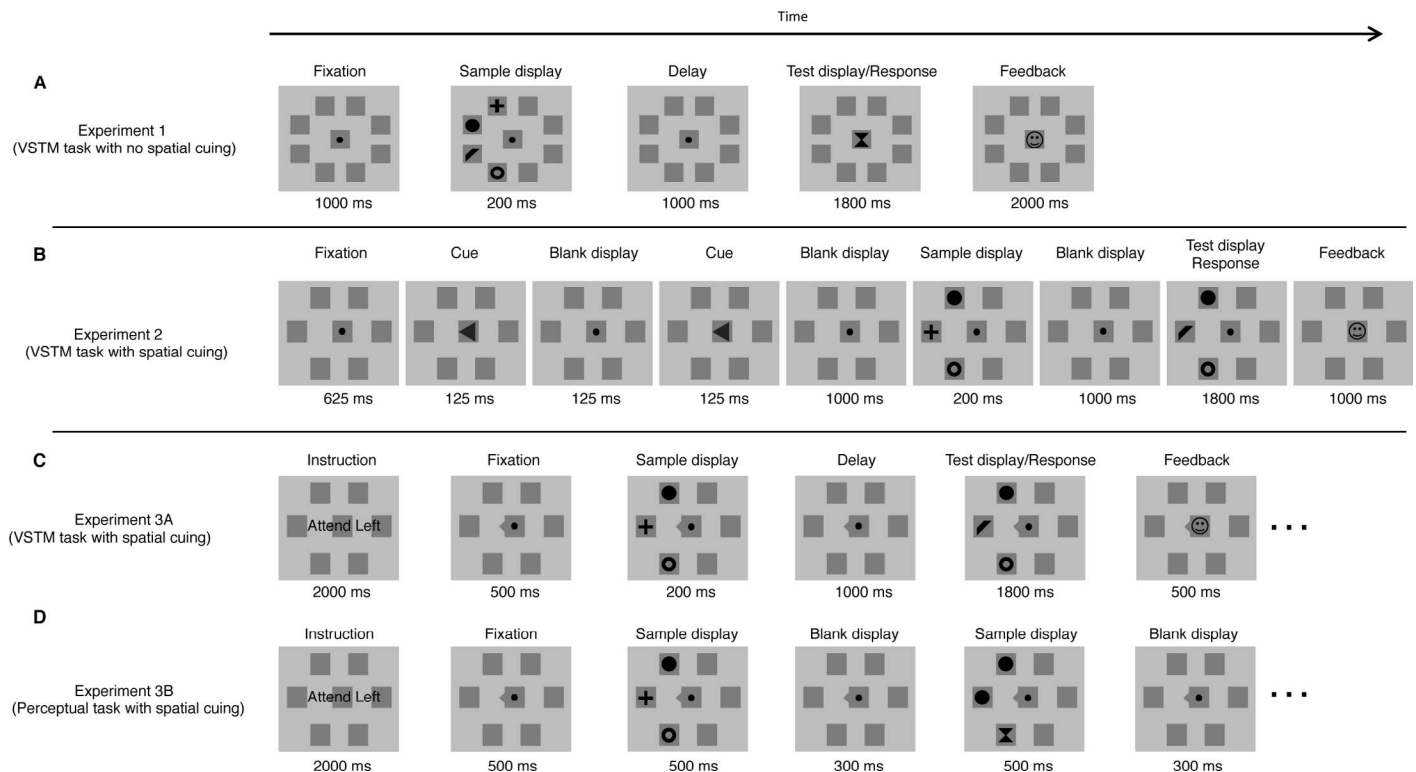


Figure 1. (A) An example trial from Experiment 1 with a VSTM task and no spatial cuing. In each trial, participants saw two or four target shapes appearing briefly in either the left or right hemifield in an unpredictable manner. After a short delay, participants judged whether the test shape shown at fixation matched one of the target shapes. A match occurred in half of the trials. (B) An example trial from Experiment 2 with a VSTM task and spatial cuing. In each trial, participants first saw two cues flashing briefly, cuing them to a specific hemifield. They then saw three target shapes appearing in the cued hemifield. After a short delay, they judged whether the three test shapes shown were identical to the target shapes shown at the same location. In change trials, one of the test shapes was replaced by a new shape. A change occurred in half of the trials. (C) An example trial from Experiment 3A with a VSTM task and spatial cuing. The hemifield that contained the three target shapes was fixed for a block of trials and was cued at the beginning of each block. To ensure proper location cuing, a small triangle near the fixation cuing the target-present hemifield was also shown throughout a given block of trials. (D) An example trial from Experiment 3B with a perceptual task and spatial cuing. As in (C), the hemifield in which the target shapes appeared was fixed for a block of trials and was cued throughout the block by a small triangle near the fixation. In each block of trials, participants monitored a sequential presentation of trials each containing three shapes and detected trials in which two of the three shapes were identical. This occurred in 10% of the trials.

attend to (either “attend left” or “attend right”), and a 32-s stimulus presentation period containing eight trials. Each trial lasted 4 s and contained a fixation period (500 ms), a sample display (200 ms), a blank display (1000 ms), a test display/response period (1800 ms), and a feedback display (500 ms). To further remind the participants the hemifield that they should be attending to within a block of trials, a small triangle pointing to the attended hemifield was also present near fixation throughout the block (see Figure 1C). Each run contained four blocks each of “attend left” and “attend right” conditions. In addition to the stimulus blocks, a 30-s fixation block was included in the middle of each run to allow the measurement of baseline fMRI responses needed for calculating the percentage of signal change evoked by the stimulus blocks.

In the other half of the runs of Experiment 3, participants performed a perceptual task with the same block design. Within each block of trials, they viewed 40 sequentially presented trials each containing three shapes appearing in the attended hemifield and pressed a response button whenever two of the three shapes were identical in a given trial (Figure 1D). This occurred in 10% of the trials. Each trial appeared for 500 ms and was followed by a blank display of 300 ms. Other aspects of this experiment were identical to that of the VSTM task in Experiment 3. Each run in Experiment 3 lasted 5 min 42 s with three runs for the VSTM task and three for the perceptual task.

In Experiments 2 and 3, eye movements were monitored with an EyeLink 1000 eye tracker to ensure

that participants maintained proper central fixation throughout the experiment.

Localizer experiments

To define the inferior and superior IPS ROIs, two independent localizer experiments were conducted. To ensure that the ROIs localized were involved in processing the specific visual stimuli used in the main experiments, the same shapes from the main experiment appeared in all the ROI localizers described below in the same size and eccentricity as they did in the main experiments.

To localize the superior IPS that closely tracks the amount of visual information retained in VSTM, a shape VSTM experiment similar to that of Xu and Chun (2006) was conducted. Specifically, participants were asked to remember one, two, three, four, or six black object shapes presented briefly around the central fixation. After a short delay, a test shape appeared at fixation and required participants to make a match/mismatch judgment. A match occurred in 50% of the trials. Each trial lasted 6 s and contained the following: a fixation period (1000 ms), a sample display (200 ms), a delay period (1000 ms), a test shape display/response period (2500 ms), and a feedback display (1300 ms). With a counterbalanced trial history design, 12 stimulus trials for each set size and 12 fixation trials in which only a fixation dot was present during the 6-s trial period were included in each run. Three filler trials were included at the beginning and end of each run for practice and trial history balancing purposes. These filler trials were excluded from data analysis. Each participant completed two runs, each lasting 7 min and 42 s.

To define the inferior IPS, as in Xu and Chun (2006), participants saw blocks of shape and noise images. The shape images were similar to the set size six sample displays that appeared in the superior IPS localizer. Each block lasted 16 s and contained either 20 shape or 20 noise images with each appearing for 500 ms and followed by a 300-ms blank display. To ensure that participants attended the displays, they were asked to detect a slight spatial jitter that occurred randomly once in every 10 images. Each run contained eight shape and eight noise image blocks. Each participant was tested with two runs with each run lasting 4 min and 40 s.

fMRI methods

fMRI data were acquired from a Siemens Tim Trio 3T scanner at the Harvard Center for Brain Science in Cambridge, Massachusetts. Participants viewed images back-projected onto a screen at the rear of the scanner

bore through an angled mirror mounted on the head coil. All experiments were controlled by an Apple MacBook Pro laptop running Matlab with Psychtoolbox extensions (Brainard, 1997). Behavioral responses from the participants during the imaging session were recorded through a button box connected to the laptop. Anatomical images were acquired using standard protocols. For both the localizer runs and the main experimental runs, 24 5-mm-thick slices (3 mm × 3 mm in plane, 0 mm skip, matrix size 72 × 72) parallel to the anterior commissure-posterior commissure line were acquired using a gradient echo pulse sequence (TR of 1500 ms, TE of 29 ms, flip angle of 90° for Experiments 1 and 2 and the superior IPS localizer; TR of 2000 ms, TE of 30 ms, flip angle of 85° for Experiments 3A and 3B and the inferior IPS localizer).

fMRI data were analyzed using BrainVoyager QX (www.brainvoyager.com). Three-dimensional motion correction, slice acquisition time correction, linear trend removal, and Talairach space transformation were conducted during data preprocessing (Talairach & Tournoux, 1988).

Defining ROIs

To define the superior IPS ROI in each participant as was done previously (Todd & Marois, 2004; Xu & Chun, 2006), fMRI data from the superior IPS localizer were analyzed using multiple regressions with the regression coefficient for each VSTM set size weighted by that participant's behavioral VSTM capacity for that set size (calculated with Cowan's K formula, see Cowan, 2001). The superior IPS was defined as voxels in the superior IPS region showing a significant activation in the regression analysis (false discovery rate [FDR] $q < .05$, corrected for serial correlation) and whose Talairach coordinates matched those reported in Todd and Marois (2004). The inferior IPS ROI was defined as voxels in the inferior IPS region showing higher activations to the shape than to the noise displays (FDR $q < .05$, corrected for serial correlation) and whose Talairach coordinates matched those reported in Xu and Chun (2006). The average numbers of voxels in the inferior and superior IPS from each of the experiments are listed in Table 1. The numbers of inferior and superior IPS voxels in each experiment were not significantly different from each other ($t_s < 1$, $p_s > 0.44$).

Using tasks involving covert attention, delayed saccade, or passive viewing and presenting visual stimulation at predictable locations, multiple topographic maps representing the contralateral hemifield have been reported along the human IPS (Schluppeck, Curtis, Glimcher, & Heeger, 2006; Schluppeck, Glimcher, & Heeger, 2005; M. I. Sereno, Pitzalis, & Martinez, 2001; Silver & Kastner, 2009; Swisher,

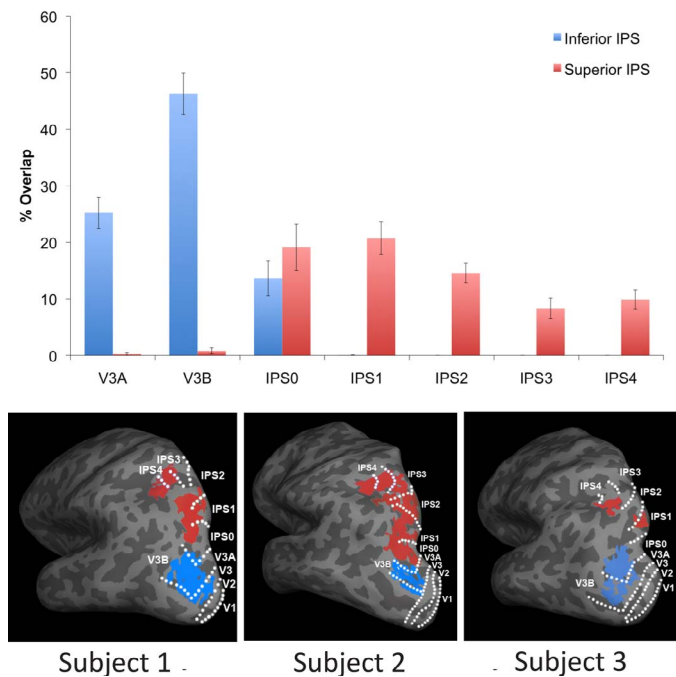


Figure 2. The amount of anatomical overlap between the inferior/superior IPS regions and the IPS topographic regions in the average of all participants (upper) and in three representative participants (lower). The inferior IPS had the greatest overlap with V3B and the superior IPS had the greatest overlap with IPS0, IPS1, and IPS2. Error bars indicate standard errors of the mean. Figure adapted from Bettencourt & Xu, 2016b.

Halko, Merabet, McMains, & Somers, 2007). Findings from our lab showed that the inferior IPS overlapped with V3A, V3B, and IPS0 (85% total with all the topographic areas), and the superior IPS overlapped with IPS1 to IPS 4 (74% total with all the topographic areas) (Bettencourt & Xu, 2011, 2016b, see Figure 2). Thus, whereas the superior IPS seems to be limited to the parietal lobe, the inferior IPS spans both parietal and occipital lobes and is located at the junction of the IPS and the transverse occipital sulcus.

The inferior and superior IPS are defined as regions in the inferior and superior parts of the IPS, respectively. These regions are referred to as the inferior and superior IPS only for simplicity by their approximate anatomical locations. Although these two regions could be given more specific functional names, given the involvement of the human parietal cortex across a number of different cognitive tasks, naming parietal regions by the specific functions they play in a

specific task context could be rather limited and potentially misleading. Perhaps realizing this, except for a few action-defined parietal regions, the general literature on the human parietal cortex has labeled functional regions by their approximate anatomical locations rather than by the specific cognitive functions identified. Our naming of the two parietal regions simply followed this tradition. One advantage of this naming tradition is that it could facilitate comparisons across studies and tasks.

Main analyses

To examine fMRI responses from the main experiments, time course data from each participant in the main experiments were extracted from independently localized and participant-specific inferior IPS and superior IPS ROIs in each hemisphere. In Experiments 1 and 2, eight TRs of raw fMRI responses were extracted from each trial onset (totaling 12 s to account for both the rise and fall of the fMRI responses) and then averaged for all trials of the same stimulus condition to obtain the average time course for that condition. To compute the percentage of signal change of a stimulus condition, the raw time course of the fixation condition was first subtracted from that of the stimulus condition at each time point. The resulting values were then divided by the corresponding values of the fixation condition at each time point (see Kourtzi & Kanwisher, 2000; Todd & Marois, 2004; Xu & Chun, 2006). After obtaining the percentage of signal change time course for each stimulus condition, the peak response amplitude of each stimulus condition in each hemisphere was selected to calculate hemispheric laterality and asymmetry for each participant. The results were then pulled together across participants to generate group averages and enable the performance of statistical tests at the group level.

In Experiment 3, elevated fMRI responses starting at 6 s after the onset of the stimulus block (to account for hemodynamic response lag) and extending 30 s (15 TRs total) were averaged to generate a raw response for each stimulus block. Responses were then averaged across blocks containing the same stimulus condition to generate an average raw response value for each stimulus condition. The percentage of signal change for each stimulus condition was calculated by subtracting from the averaged raw response the lowest value in the long fixation block and then dividing by that value.

	Experiment 1	Experiment 2	Experiment 3
Inferior IPS	143.09 ± 80.63	198.22 ± 71.15	112.83 ± 79.06
Superior IPS	151.72 ± 69.10	204.55 ± 77.39	102.41 ± 74.72

Table 1. The average number of voxels in inferior and superior IPS from each of the experiment (mean ± SD).

To quantify the amount of laterality in each ROI in each hemisphere as was done previously (Sheremata, Bettencourt, & Somers, 2010; Szczepanski et al., 2010), a laterality index was calculated. This was defined as the difference between the contralateral and ipsilateral activations divided by the sum of these two activations. If a brain region responds only to the contralateral but not at all to the ipsilateral stimulus presentations, it would have a laterality index of one. Conversely, if a brain region responds equally strongly to both the contralateral and ipsilateral presentations, it would have a laterality index of zero. Because the laterality index is normalized over response amplitudes, it enabled comparisons between different brain regions and between experiments with different overall response amplitudes.

Results

Experiment 1: VSTM task with no spatial cuing in an event-related design

In Experiment 1, participants were asked to encode in a sample display either two or four target shapes presented briefly (200 ms) in either hemifield. After a short delay (1 s), they judged whether or not a centrally presented test shape matched one of the remembered target shapes. Because target shapes could appear in either hemifield in an unpredictable manner, to ensure successful task performance, participants needed to attend simultaneously to both hemifields at all times. With this VSTM design, this experiment examined whether parietal regions involved in object individuation and identification (the inferior and superior IPS, respectively, see Xu and Chun, 2009) show a preference to contralaterally presented visual input (i.e., laterality) and whether this preference is greater in the left than in the right hemisphere (i.e., hemispheric asymmetry).

Behavioral results

From the behavioral data collected during the imaging session, Cowan's K (Cowan, 2001) was calculated to estimate behavioral VSTM capacity when either two or four target shapes were presented. Average K values were (left and right mean \pm SD): 1.8 ± 0.29 and 1.78 ± 0.22 for set size two and 2.2 ± 1.16 and 2.44 ± 1.08 for set size four. There was no difference between the attend-left and attend-right trials in either set size ($t_s < 1$, $p_s > 0.43$), and the attended hemifield did not interact with set size ($F < 1$, $p > 0.44$).

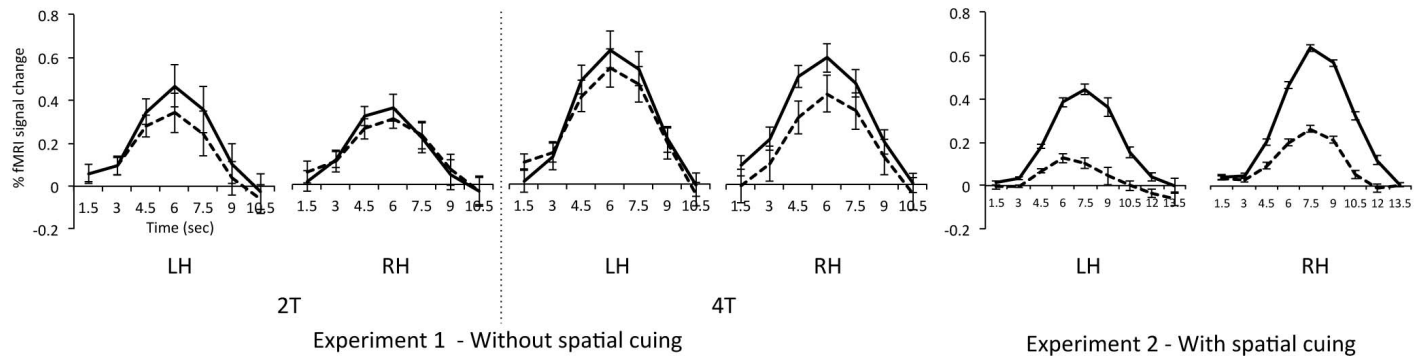
fMRI results

fMRI response amplitude measures: Time course of fMRI responses is plotted in Figure 3. To examine the presence of hemispheric laterality and asymmetry, we selected the peak responses of the time course (see Materials and methods) and carried out a four-way repeated-measures ANOVA on the fMRI responses obtained with region (inferior and superior IPS), hemisphere (left vs. right hemisphere ROI), hemifield (ipsilateral vs. contralateral stimulus presentation), and set size (two vs. four) as factors. This revealed a main effect of hemifield (laterality effect), $F(1, 10) = 64.49$, $p < 0.001$, with contralateral presentations showing higher responses than ipsilateral ones (Figure 4A, B). Hemispheric asymmetry, however, was not observed as there was neither a main effect of hemisphere, $F(1, 10) = 2.99$, $p = 0.11$, nor an interaction between hemisphere and hemifield, $F(1, 10) = 0.26$, $p = 0.61$. Detailed analyses within each ROI revealed that although hemispheric laterality was present in both ROIs ($F_s > 27.2$, $p_s < 0.001$), the two-way interaction between hemisphere and hemifield was not significant in either ROI ($F_s < 1.43$, $p_s > 0.25$), showing an absence of hemispheric asymmetry in both the inferior and superior IPS. Besides these effects, across the ROIs, there was also a main effect of region, $F(1, 10) = 72.0$, $p < 0.001$, with higher responses obtained in the superior IPS than in the inferior IPS, and a main effect of set size, $F(1, 10) = 11.07$, $p = 0.008$, with higher responses obtained with the larger set size.

Laterality index: Although no hemispheric asymmetry was found with direct fMRI response measures, to examine hemispheric asymmetry in greater detail, laterality indices were computed and compared between the left and right hemispheres (Figure 5A, B). Laterality index measures the difference between contralateral and ipsilateral responses with respect to the overall response amplitudes (see Materials and methods). It thus provides a more sensitive measure of laterality than measuring the absolute difference between the contralateral and ipsilateral responses.

As set size did not show any main effect nor interaction in either IPS ROI ($F_s < 1.03$, $p_s > 0.33$), laterality indices were averaged over the set size two and four conditions in further analyses. Consistent with results from fMRI response amplitude measures, a two-way repeated-measures ANOVA with region and hemisphere also found no main effect of hemisphere, $F(1, 10) = 2.18$, $p = 0.17$, and no interaction between region and hemisphere ($F < 1$, $p = 0.67$). The amount of laterality in the left and right hemispheres did not differ in either the inferior or superior IPS ($t_s < 1.34$, $p_s > 0.2$), confirming the lack of hemispheric asymmetry as was reported in the fMRI response amplitude measures.

A Inferior IPS



B Superior IPS

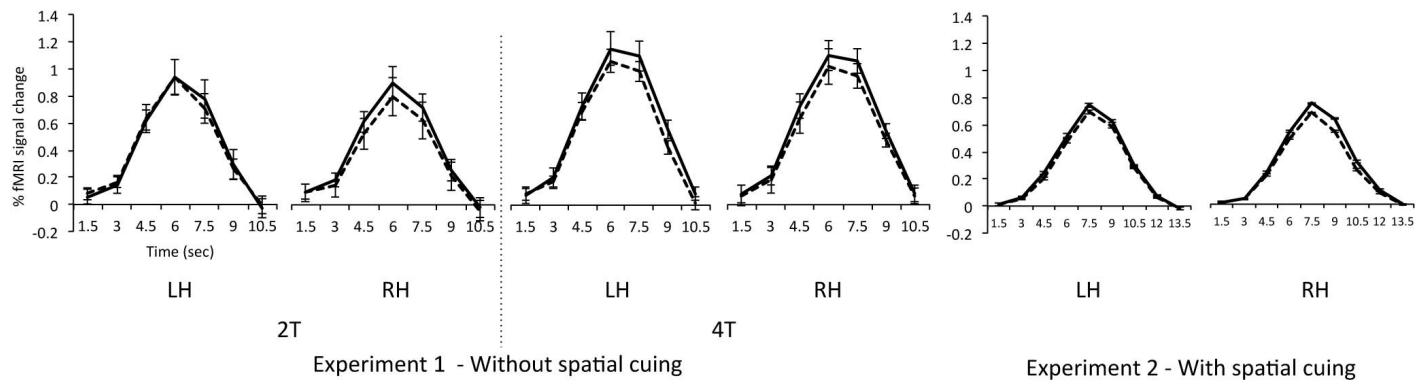


Figure 3. fMRI time courses in (A) the inferior IPS and (B) the superior IPS from Experiments 1 and 2. Solid and dotted lines indicate fMRI response amplitudes to contralateral and ipsilateral targets, respectively. In both experiments, an event-related design was used with each trial lasting 6 s. Error bars indicate within-subject standard errors of the means. LH = left hemisphere; RH = right hemisphere; 2T = target set size two trials; 4T = target set size four trials.

As with the response amplitude measures, there was a significant effect of brain region, $F(1, 10) = 17.19$, $p = 0.002$, with the inferior IPS showing greater laterality than the superior IPS. This is consistent with previous studies reporting location-based encoding in the inferior IPS and feature-based encoding in the superior IPS (Xu & Chun, 2006, 2009). No other main effects or interactions were significant ($F_s < 1$).

Overall, with both response amplitude and laterality index measures, although both the inferior and superior IPS revealed significant laterality, neither showed hemispheric asymmetry in the amount of laterality exhibited. This applied to both the small and large display set sizes used. These results differed from previous findings showing the existence of hemispheric asymmetry (Corbetta, Miezin, Shulman, & Petersen, 1993; Heilman & Van Den Abell, 1980; Mesulam, 1981, 1999; Nobre et al., 1997; Szczepanski et al., 2010) and results showing that hemispheric asymmetry may be obtained in a VSTM task at a large but not at a small display set size (Sheremata et al., 2010).

Experiment 2: VSTM task with spatial cuing in an event-related design

In Experiment 1, because target shapes appeared unpredictably in either hemifield, participants could not anticipate target locations. Previous studies that have reported hemispheric asymmetry have cued participants in advance to the specific hemifield in which the targets would appear (Sheremata et al., 2010; Szczepanski et al., 2010; Vandenberghe et al., 2005). It is thus possible that the deployment of top-down attention to a specific hemifield in anticipation of the upcoming target processing rather than target processing in a specific hemifield per se evokes hemispheric asymmetry in parietal regions. This possibility was tested here.

In Experiment 2, participants were asked to perform a VSTM task similar to that of Experiment 1. Critically, at the beginning of each trial, they were cued to attend to the hemifield in which the targets would appear. Thus, participants were able to deploy their attention to the cued hemifield in advance. To encourage biased spatial attention to the target-present hemifield during the delay

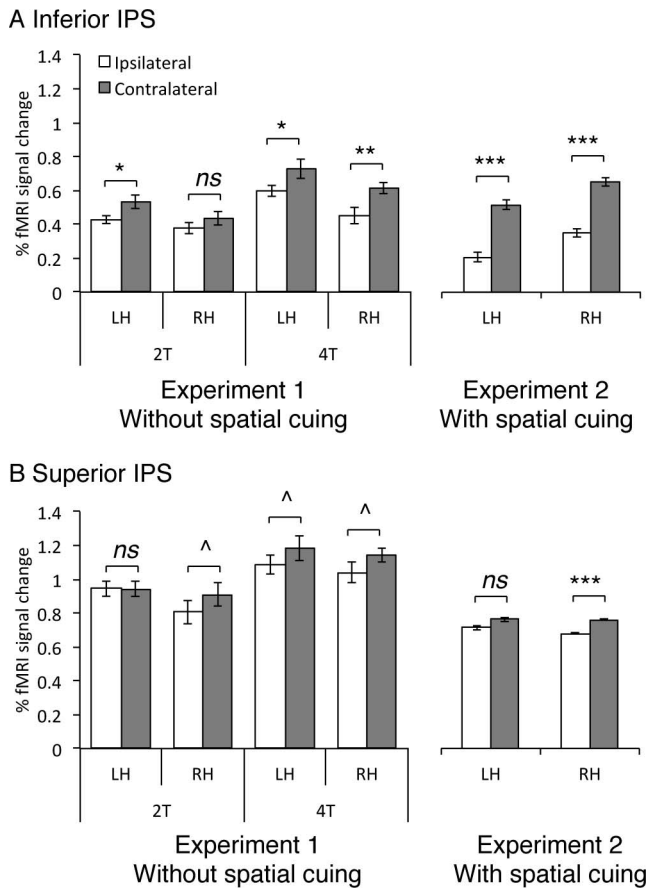


Figure 4. fMRI response amplitude measures in Experiments 1 and 2 from (A) the inferior IPS and (B) the superior IPS in each hemisphere. Error bars indicate within-subject standard errors of the means. LH = left hemisphere; RH = right hemisphere; 2T = target set size two trials; 4T = target set size four trials; [^] $p < 0.1$; * $p < 0.05$; *** $p < 0.01$.

period, test shapes were shown in the same hemifield as the target shapes. Because VSTM capacity for the black shapes used here was less than three (see behavioral results from Experiment 1), to streamline the design of Experiment 2, only set size three displays were included in the VSTM task.

Behavioral results

As in Experiment 1, separate VSTM capacities were calculated for the attend-left and attend-right trials. Average K values were not different between the two types of trials ($t < 1$, $p = 0.95$; mean K and SD were 2.4 ± 0.33 and 2.41 ± 0.36 for the attend-left and attend-right trials, respectively).

fMRI results

fMRI response amplitude measures: To examine the presence of hemispheric laterality and asymmetry, a three-way ANOVA with region, hemisphere, and

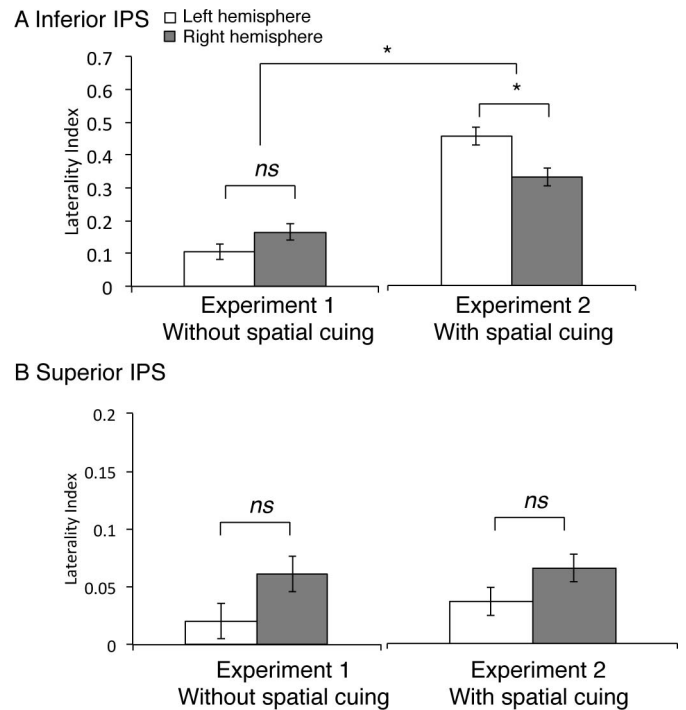


Figure 5. Laterality indices in Experiments 1 and 2 from (A) the inferior IPS and (B) the superior IPS in each hemisphere. Set size two and four trials were averaged together as laterality indices did not differ between these two trial types. Laterality was present in both regions with the inferior IPS showing greater laterality than the superior IPS. Hemispheric asymmetry was not observed in Experiment 1 in either region. However, hemispheric asymmetry emerged in the inferior IPS in Experiment 2 when the target-present hemifield was cued in advance to allow participants to bias their attention to that hemifield. Error bars indicate within-subject standard errors of the means. * $p < 0.05$; ns = nonsignificant.

hemifield as factors was conducted on the peak fMRI response amplitudes obtained (Figure 4A, B). Overall, the main effect of hemifield, $F(1, 8) = 69.34$, $p < 0.001$, was significant, but the interaction between hemifield and hemisphere was not ($F < 1$, $p = 0.426$). Thus, across the inferior and superior IPS, although laterality was present, hemispheric asymmetry was not. Additional comparisons also revealed a main effect of region, $F(1, 8) = 24.74$, $p = 0.001$, with the superior IPS showing a higher response amplitude than the inferior IPS, and an interaction between hemifield and region, $F(1, 8) = 16.19$, $p = 0.004$, with the inferior IPS exhibiting greater laterality than the superior IPS.

Further analyses within each IPS ROI revealed that both regions showed laterality (main effect of hemifield, $F_s > 18.59$, $p_s < 0.003$). Although the inferior IPS showed a main effect of hemisphere, $F(1, 8) = 8.36$, $p = 0.02$, hemisphere did not interact with hemifield in either ROI ($F_s < 1$, $p_s > 0.37$).

Laterality index: To examine laterality and hemispheric asymmetry in detail, a laterality index was calculated for each IPS ROI in each hemisphere. There was a main effect of region, $F(1, 8) = 12.75$, $p = 0.007$, with the inferior IPS showing greater laterality than the superior IPS (Figure 5A, B). The main effect of hemisphere was marginally significant, $F(1, 8) = 3.58$, $p = 0.095$.

Importantly, the interaction between hemisphere and region was significant, $F(1, 8) = 5.49$, $p = 0.047$. This was driven by the presence of significant hemispheric asymmetry in the inferior IPS, $t(8) = 2.33$, $p = 0.048$, but not in the superior IPS, $t(8) = 1.21$, $p = 0.25$.

To directly compare between Experiments 1 and 2, a mixed-design ANOVA was conducted in each region with experiment as a between-subjects variable and hemisphere as a within-subject variable. This analysis was done after excluding participants who took part in both experiments, making participants in the two experiments unique (two and one participants were removed from Experiments 1 and 2, leaving nine and eight participants in Experiments 1 and 2 in this analysis, respectively). This analysis revealed a significant hemisphere by experiment interaction in the inferior IPS, $F(1, 15) = 6.74$, $p = 0.02$ (Figure 5A). No such interaction, however, was found in the superior IPS ($F < 1$, $p = 0.639$, Figure 5B). These results show that hemispheric asymmetry emerged in the inferior IPS when attention was directed to the target hemifield in advance in Experiment 2. Such attention-driven emergence of hemispheric asymmetry was absent in the superior IPS. Additional comparisons revealed that laterality was greater in Experiment 2 than Experiment 1 in inferior but not superior IPS, $F(1, 15) = 10.598$, $p = 0.005$ and $F < 0.1$, $p = 0.661$, respectively.

Thus, as in Experiment 1, laterality was found again in both ROIs in Experiment 2 with laterality being greater in the inferior than the superior IPS. Critically, hemispheric asymmetry emerged in the inferior IPS with the cuing paradigm with laterality being greater in the left than the right hemisphere. Such emergence of hemispheric asymmetry, however, was absent in the superior IPS. Comparison between Experiments 1 and 2 further confirmed that hemispheric asymmetry emerged in the inferior IPS but not in the superior IPS when spatial visual attention was biased toward the target-present hemifield.

Across the two experiments, probes were presented at target locations in Experiment 2 and at fixation in Experiment 1. This was done to encourage participants to attend to the entire visual field in Experiment 1 and to the cued visual field in Experiment 2 throughout a given trial. One might argue that the difference in the probing procedure might have changed the task demands across the two experiments and resulted in the failure to find asymmetries in Experiment 1. However, a previous VSTM study (Xu & Chun, 2006) showed

that whether or not the probe was shown at fixation or target locations produced very similar responses in behavior and in the inferior and superior IPS.

Additionally, responses from the superior IPS, which tracked VSTM information encoding and storage demand, did not exhibit any difference in laterality or hemispheric asymmetry across the two experiments.

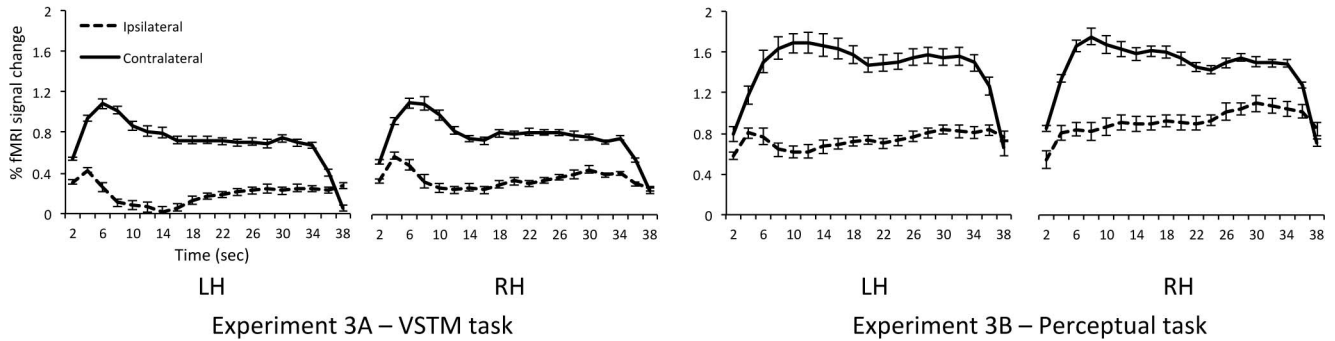
This suggests that whether or not a center or peripheral probe was used had a minimal impact on task demands but a greater impact on the allocation of top-down attentional resources, which, in turn, determines the emergence of hemispheric asymmetry.

Experiments 3A and 3B: VSTM and perceptual tasks with spatial cuing in a block design

Experiment 3A was designed to replicate and examine the hemispheric asymmetry observed in the inferior IPS in Experiment 2 in greater detail. First, to increase the amount of top-down spatial attention to the target-present hemifield, a block design was used. Within a block of trials, targets were always presented in the same hemifield and a cue was provided throughout the block to remind participants of the target-appearing hemifield. This allowed participants to direct their attentional resources to the relevant hemifield in advance. If inferior and superior IPS are indeed controlled by different attentional mechanisms, then even with a much stronger attentional engagement provided by a block design, hemispheric asymmetry would still only emerge in the inferior but not the superior IPS.

Second, in addition to the VSTM task used in Experiments 1, 2, and 3A, in Experiment 3B, a demanding perceptual task was used. Previous studies reporting strong hemispheric asymmetry often employed a task with minimal VSTM involvement, such as target detection, attentional orienting, or passive viewing. As such, one could argue that tasks involving VSTM may not show strong hemispheric asymmetry as activations from the VSTM retention period (which may not be lateralized) could wash out any hemispheric asymmetry that likely exists, accounting for some of our null findings in Experiments 1 and 2. However, this argument is not entirely valid as Sheremata et al. (2010) were able to observe significant hemispheric asymmetry at a large display set size using a VSTM paradigm. Nevertheless, to test this possibility in Experiment 3B, a demanding perceptual task with minimal VSTM involvement was used. In this perceptual task, participants were shown a rapid succession of displays, each containing three target shapes, and were asked to detect displays in which two of the three shapes were identical (occurring in 10% of the trials).

A Inferior IPS



B Superior IPS

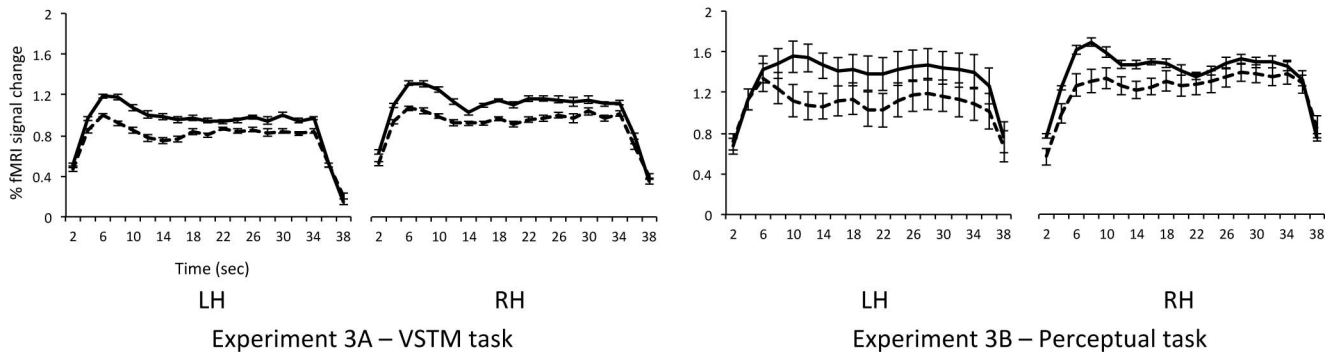


Figure 6. fMRI time courses in (A) the inferior IPS and (B) the superior IPS from Experiments 3A and 3B. Solid and dotted lines indicate fMRI response amplitudes to contralateral and ipsilateral targets, respectively. In both experiments, the target-present visual field was fixed within a block of trials that lasted 32 s. Error bars indicate within-subject standard errors of the means. LH = left hemisphere; RH = right hemisphere.

Behavioral results

In Experiment 3A, the average K estimates for the attend-left and attend-right trials were 2.34 ± 0.34 and 2.32 ± 0.46 , respectively, and they did not differ from each other ($t < 1$, $p > 0.80$). In Experiment 3B, the average target detection accuracy was $82.42\% \pm 11.42\%$ in the perceptual task. Due to technical errors, target detection accuracies in Experiment 3B were not recorded separately for the attend-left and attend-right blocks.

fMRI results

fMRI response amplitude measures: Figure 6 shows the time courses of the fMRI responses. As in Experiments 1 and 2, to examine the presence of hemispheric laterality and asymmetry, a three-way repeated-measures ANOVA was conducted on fMRI responses with brain region, hemisphere, and hemifield as factors separately for the VSTM and perceptual tasks. This revealed a main effect of hemifield (i.e., laterality) in both tasks ($F_s > 94.38$, $p_s < 0.001$), replicating what was observed in Experiments 1 and 2 (Figure 7A, B). Main effect of hemisphere was significant in the VSTM task, $F(1, 11) = 5.97$, $p = 0.033$, but marginally

significant in the perceptual task, $F(1, 11) = 3.775$, $p = 0.078$.

To assess the degree of hemispheric asymmetry, the interaction between hemisphere and hemifield was examined. In the main analysis, this interaction was marginally significant in the perceptual task but not in the VSTM task, $F(1, 11) = 3.84$, $p = 0.076$ and $F(1, 11) = 1.65$, $p = 0.22$, respectively. Analyses within each ROI revealed that in the perceptual task, this interaction was marginally significant in the inferior IPS, $F(1, 11) = 3.889$, $p = 0.074$, but not in the superior IPS, $F(1, 11) = 1.49$, $p = 0.24$. In the VSTM task, this interaction was not significant in either ROI ($F_s < 1.44$, $p_s > 0.255$). Besides these effects, there was also a main effect of brain region in the VSTM task, $F(1, 11) = 11.37$, $p = 0.006$, due to higher responses in the superior than the inferior IPS. This effect was not observed in the perceptual task, $F(1, 11) = 1.35$, $p = 0.27$.

When the two tasks were directly compared, the perceptual task elicited overall higher fMRI responses than the VSTM task: main effect of task, $F(1, 11) = 26.18$, $p < 0.001$. Across the two ROIs, task also interacted with hemifield, $F(1, 11) = 70.28$, $p < 0.001$, indicating that laterality was modulated by task.

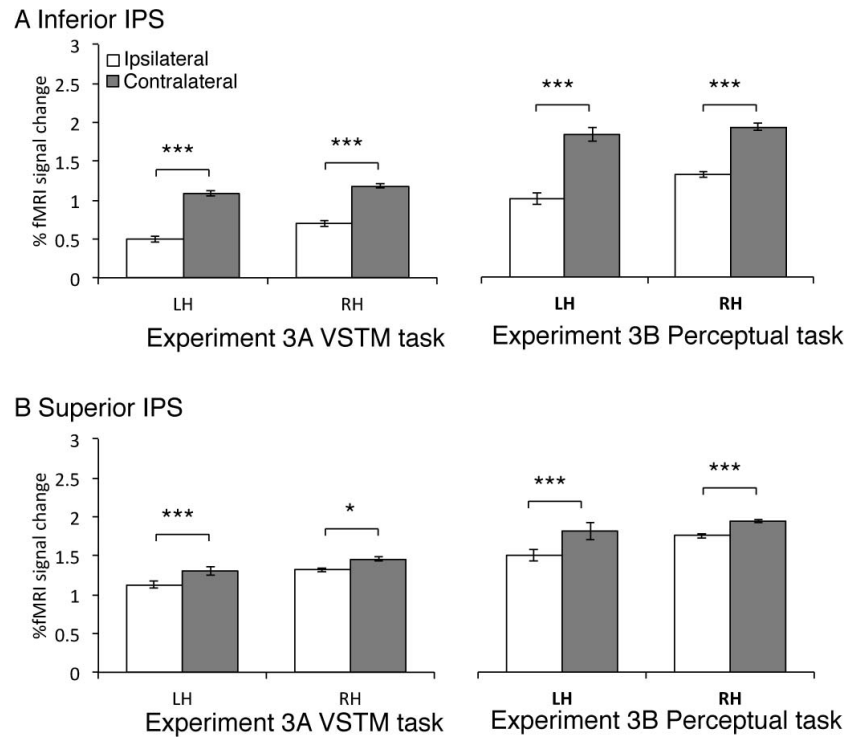


Figure 7. fMRI response amplitude measures in Experiments 3A and 3B in (A) the inferior IPS and (B) the superior IPS in both a VSTM and a perceptual task. Error bars indicate within-subject standard errors of the means. LH = left hemisphere; RH = right hemisphere; * $p < 0.05$; *** $p < 0.001$.

Laterality index: To better examine hemispheric asymmetry, as was done in Experiments 1 and 2, the laterality index was calculated for each ROI in each hemisphere. In both the VSTM and the perceptual tasks, there was a main effect of region ($F_s > 57.07$, $p_s < 0.001$) with the inferior IPS showing greater laterality than the superior IPS (Figure 8A, B). There was also a significant main effect of hemisphere in both tasks ($F_s > 4.89$, $p_s < 0.049$), indicating the presence of hemispheric asymmetry. Comparisons within each ROI revealed that this hemispheric asymmetry was present only in the inferior IPS in both tasks, $t(11) = 2.5$, $p = 0.029$ and $t(11) = 3.83$, $p = 0.003$, respectively, for perceptual and VSTM tasks. The superior IPS did not show asymmetry in either task ($t_s < 0.164$, $p_s > 0.12$). Hemispheric asymmetry was significantly greater in the inferior than the superior IPS in the VSTM task, $F(1, 11) = 7.118$, $p = 0.022$, but not in the perceptual task, $F(1, 11) = 2.726$, $p = 0.127$.

Direct comparison between the VSTM and perceptual tasks revealed a main effect of task, with greater laterality in the VSTM than perceptual task, $F(1, 11) = 8.33$, $p = 0.015$. Task showed a significant interaction with region, $F(1, 11) = 17.11$, $p = 0.002$, mainly due to the presence of greater laterality in the VSTM than in the perceptual task in the inferior IPS, $F(1, 11) = 13.016$, $p = 0.004$, but not in the superior IPS, $F(1, 11) = 2.5$, $p = 0.14$. Task, however, did not interact with

hemisphere across the ROIs ($F_s < 2.5$, $p_s > 0.14$). When the inferior IPS was analyzed alone across the two tasks, task still did not interact with hemisphere ($F < 1$, $p = 0.621$), showing that the presence of hemisphere asymmetry in the inferior IPS was not modulated by task.

Further comparisons between experiments were done using a mixed-design ANOVA with experiment as a between-subjects variable. Participants who took part in more than one experiment were removed from these between-experiment comparisons. These comparisons revealed that the amount of hemispheric asymmetry in the inferior IPS was significantly greater in Experiments 3A and 3B than in Experiment 1 ($F_s > 10.54$, $p_s < 0.005$) but was not different from that in Experiment 2 ($F_s < 1$, $p_s > 0.686$). This provided further confirmation that hemispheric asymmetry emerged in the inferior IPS only when biased top-down visual attention was deployed in Experiments 2, 3A, and 3B but not when biased attentional deployment was absent in Experiment 1. In the superior IPS, a marginally significant hemisphere by experiment interaction was observed between Experiments 1 and 3B, $F(1, 17) = 4.22$, $p = 0.056$. However, as the superior IPS did not show any significant hemispheric asymmetry in any of the experiments reported here, this suggests that, although the biggest increase in attentional modulation (from an uncued event-related VSTM task in Experi-

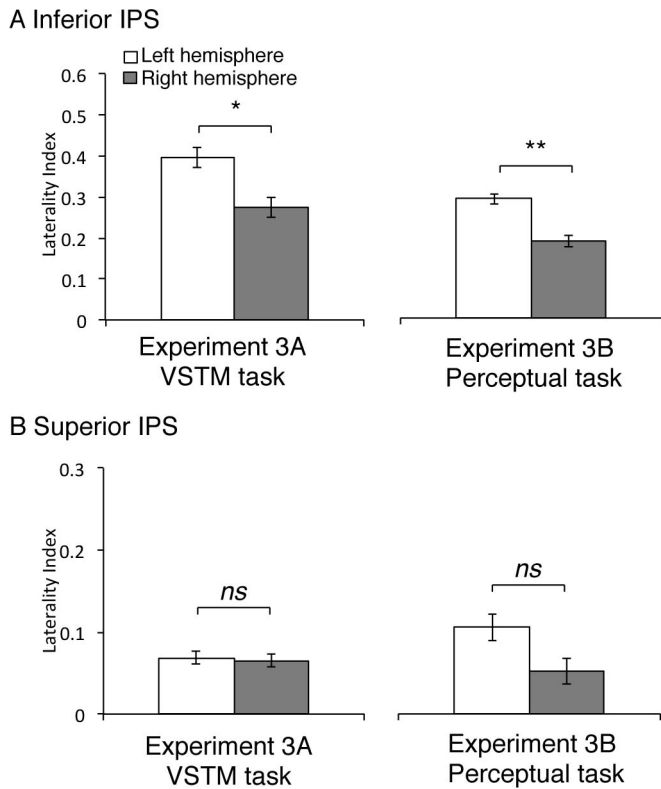


Figure 8. Laterality indices in Experiments 3A and 3B from (A) the inferior IPS and (B) the superior IPS. With the target locations cued in advance by fixing the target-present hemifield within a block of trials in both a VSTM and a perceptual task, hemispheric asymmetry was again found in the inferior IPS but not in the superior IPS, replicating the results of Experiment 2. In both tasks, laterality was also greater in the inferior than the superior IPS, consistent with the results from Experiments 1 and 2. Error bars indicate within-subject standard errors of the means. LH = left hemisphere; RH = right hemisphere; * $p < 0.05$; ** $p < 0.01$.

ment 1 to a cued block design perceptual task in Experiment 3B) was enough to modulate the overall hemispheric asymmetry in the superior IPS, it was still not sufficient to produce a significant hemispheric asymmetry in this brain region. This suggests that the superior IPS is not subjected to the same kind of attentional control as the inferior IPS.

In further analyses, the amount of laterality present was compared across experiments. In the inferior IPS, laterality was greater in Experiments 3A and 3B than in Experiment 1 ($F_s > 6.642$, $p_s < 0.03$) and greater in Experiment 2 than in Experiment 3B, $F(1,16) = 5.646$, $p = 0.03$, but did not differ between Experiments 2 and 3A, $F(1, 16) = 1.33$, $p = 0.266$. In the superior IPS, laterality did not vary significantly across experiments ($F_s < 2.5$, $p_s > 0.133$) except that Experiment 3B showed greater laterality than Experiment 1, $F(1, 17) = 4.857$, $p = 0.042$.

In sum, with a block design, laterality was again observed in both parietal regions in this experiment as it was in Experiments 1 and 2. Importantly, consistent with the findings from Experiment 2, when the top-down attentional bias was deployed through cuing, hemispheric asymmetry was observed in the inferior but not the superior IPS. This cuing-induced hemispheric asymmetry in the inferior IPS did not seem to be modulated by task and was present equally strongly in both the VSTM and perceptual tasks.

Relationship between the strength of laterality and hemispheric asymmetry across the three experiments

Across the three experiments, it seemed that hemispheric asymmetry tended to emerge when laterality was strong. For example, laterality in the inferior IPS was stronger in Experiment 2 than Experiment 1, $F(1, 15) = 10.598$, $p = 0.005$, and stronger in the inferior than the superior IPS in Experiment 2, $F(1, 8) = 12.75$, $p = 0.007$. Correspondingly, hemispheric asymmetry emerged in the inferior IPS in Experiment 2 but not in the inferior IPS in Experiment 1 or in the superior IPS in Experiment 2.

To take a closer look at the relationship between laterality and hemispheric asymmetry, taking advantage of the variability of these two measures across individual observers, a correlation analysis was performed between the strength of laterality (the average of the left and right laterality) and hemispheric asymmetry (the difference between the left and right laterality) across the observers in each experiment. In Experiment 1, this correlation was not significant in the inferior IPS ($r = -0.439$, $p = 0.177$) and marginally significant in the superior IPS in the opposite direction ($r = -0.6$, $p = 0.051$). In Experiment 2, this correlation was marginally significant in the inferior IPS ($r = 0.602$, $p = 0.086$) but not in the superior IPS ($r = 0.329$, $p = 0.388$). In Experiment 3, this correlation was marginally significant in the inferior IPS in the VSTM task ($r = 0.548$, $p = 0.065$) but not in the perceptual task ($r = 0.317$, $p = 0.315$) and was not significant in the superior IPS in either task ($r = 0.265$, $p = 0.406$ and $r = 0.074$, $p = 0.818$, respectively, in the VSTM and perceptual tasks).

These results show that when laterality was strong in the inferior IPS in Experiments 2 and 3, there is a hint that the strength of hemispheric asymmetry tends to positively correlate with the strength of laterality. To examine this further, the unique observers across all three experiments in the VSTM task were combined, and a new correlation was performed. Indeed, in the inferior IPS, the results showed that the strength of hemispheric asymmetry significantly correlated with the strength of laterality ($r = 0.599$, $p = 0.001$). Such a

correlation was not found in the superior IPS ($r = -0.099$, $p > 0.96$). Given that laterality was significantly lower in the superior than the inferior IPS in all three experiments ($F_s > 12.75$, $p_s < 0.01$), these results suggest that hemispheric asymmetry may only emerge when there is a sufficient amount of laterality present.

Correlation between laterality and behavioral performance across the three experiments

Previous studies have shown that hemispheric asymmetry in the parietal cortex correlates with an individual participant's behavioral bias in a spatial attention task (Szczepanski & Kastner, 2013). To examine whether or not laterality in each hemisphere was correlated with behavior in each experiment, laterality in each hemisphere was correlated with behavioral VSTM performance (K capacity) when the target shapes appeared in the contralateral hemifield (data were not properly recorded in the perceptual task in Experiment 3B, and thus this analysis could not be performed for that experiment). In Experiment 1 with target locations not cued in advance, only the left inferior IPS laterality correlated marginally with VSTM performance ($r = 0.548$, $p = 0.081$). In other words, participants whose inferior IPS showed a greater laterality in the left hemisphere tended to encode more target shapes when they appeared in the right hemifield. However, in Experiments 2 and 3 when target locations were cued in advance, no significant correlation between laterality and behavioral performance was found in either IPS region (all $p_s > 0.149$). Thus, the impact of laterality on behavioral performance was overall relatively weak.

Examinations of the effect of hemispheric asymmetry on behavioral performance also revealed no significant correlation between hemispheric asymmetry and the difference in behavioral performance between the attended left and right trials in either the inferior or superior IPS in all three experiments (all $r_s < 0.17$, $p_s > 0.65$). It thus seems that hemispheric asymmetry had a minimum impact on behavioral performance in our experiments.

Discussion

By varying the amount of top-down attentional bias and using both VSTM and perceptual tasks, the present study investigated hemispheric laterality and asymmetry previously associated with visual information processing in the human parietal cortex. Two specific parietal regions, the inferior and superior IPS, were examined here because of their previously documented

roles in visual object individuation and identification, respectively (see Xu & Chun, 2006, 2009). Overall, our results revealed that although the strength of laterality could be modulated by the deployment of top-down attention in the inferior IPS, it nevertheless is consistently present in both parietal regions regardless of the amount of top-down attentional modulation and task. Hemispheric asymmetry, on the other hand, seems to only emerge in the inferior IPS when the deployment of top-down spatial attention increases laterality sufficiently.

Hemispheric laterality

Whether or not attention was precued to the hemifield in which the targets would appear, hemispheric laterality was observed in both the inferior and superior IPS across a variety of experimental manipulations employed in the present study, including in both a VSTM and a perceptual task and with both an event-related and a blocked design. This indicated that laterality is likely an intrinsic characteristic of visual information processing in the human parietal cortex, due perhaps to the wiring and physical structure of the brain.

Nevertheless, a change in the allocation of attention and a change in task both modulate laterality in the inferior IPS. Specifically, laterality was greater in the inferior IPS with rather than without the top-down allocation of attentional resources to a particular hemifield. This suggests that attention can further amplify the existing laterality in the inferior IPS. Inferior IPS laterality was also greater in the VSTM than the perceptual task in Experiment 3. This was likely due to a greater response increase in the inferior IPS in the perception than the VSTM task (due to an increased attentional demand in the perceptual task to process the rapid successive presentation of the visual displays) and how the laterality index was calculated (i.e., the difference between the contralateral and ipsilateral responses divided by the sum of these two responses). Meanwhile, neither a change in the allocation of attention nor a change in task modulated laterality in the superior IPS.

Interestingly, the amount of laterality present was not the same across the different parietal regions as greater laterality was observed in the inferior than the superior IPS. This is consistent with previous findings showing location-based encoding in the inferior IPS and feature-based encoding in the superior IPS (Xu, 2007, 2009; Xu & Chun, 2006, 2009). Because the inferior IPS participates in object selection and individuation via location, a topographic representation of the visual input and thus a strong preference to the contralateral hemifield would be beneficial. Such a

requirement, however, is not critical for feature encoding, resulting in weaker laterality in the superior IPS. Consistent with our findings, Robitaille et al. (2010) also reported in a VSTM study bilateral activation in the superior IPS in a load-dependent manner. Likewise, in patient studies, laterality has also been observed in the posterior IPS but to a lesser degree in the middle segment of the IPS (Vandenberghe, Molenberghs, & Gillebert, 2012).

The strong laterality found in the inferior IPS here is consistent with previous behavioral results showing a bilateral advantage in location-based visual information processing. Alvarez and Cavanagh (2005) reported hemisphere independence during multiple object tracking (MOT) such that twice as many targets could be successfully tracked when they were divided between the left and right hemifields compared to when they were all presented within the same hemifield. A similar bilateral advantage could also be seen in attentional selection (Awh & Pashler, 2000; A. B. Sereno & Kosslyn, 1991) and in VSTM for locations (Delvenne, 2005). Using a recall paradigm, Umemoto, Drew, Ester, and Awh (2010) reported a bilateral advantage in VSTM for orientation. Unlike in MOT, however, this advantage was far from doubling the VSTM capacity for orientation (see also Delvenne, 2005; Xu & Nakayama, 2007). Given that MOT primarily involves location-based encoding and VSTM tasks involve both location- and feature-based encoding, these behavioral results are consistent with the strong and weak laterality observed here in the inferior and superior IPS, respectively.

Another factor that could contribute to the different amount of laterality in the inferior and superior IPS is the size of the receptive field. The inferior IPS in the present study not only overlaps with the IPS but also spans to part of the occipital regions, such as V3A and V3B. Population receptive field (pRF) sizes reported in previous studies have indicated that pRF size in the IPS is larger than that in the occipital region (3° – 6° in the IPS and 0.5° – 3° in V1–V3; Dumoulin & Wandell, 2008; Sheremata & Silver, 2015). Thus, the relatively larger receptive field size of the superior IPS likely enables this brain region to have coverage across the vertical meridian, resulting in weaker laterality in the superior than the inferior IPS.

Studies using event-related potential (ERP) have reported a contralateral delay activity (CDA) that tracks the amount of information encoded in VSTM (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). CDA can usually be measured in parietal electrodes and is believed to originate from the parietal cortex as parietal regions have been linked to VSTM encoding and storage (Todd & Marois, 2004; Xu & Chun, 2006, 2009). The present results suggest that CDA likely originates from the inferior IPS due to

its stronger laterality effect than that of the superior IPS. In an fMRI study, by subtracting ipsilateral from contralateral responses, Robitaille et al. (2010) failed to find in the inferior IPS an fMRI equivalent of the CDA that tracks the number of items retained in a VSTM study. However, the MEG signals obtained by Robitaille et al. (2010) also failed to replicate the ERP findings although the MEG findings still shared some similarities with those of fMRI and ERP. Given differences in the nature and time courses of fMRI, ERP, and MEG signals, direct subtractions of fMRI signals may not generate the exact same measures obtained in ERP and MEG even if the underlying neural mechanisms are identical.

Szczepanski et al. (2010) reported that although cued-to-attend stimuli elicited laterality in all the parietal regions examined, unattended stimuli did not. They argued that laterality only occurs when there is a spatial allocation of attention. Here, in Experiment 1, even without the allocation of attention to any specific spatial location, laterality was still observed. This suggests that parietal laterality may be determined by the direct engagement of the parietal cortex in visual processing rather than location-specific allocation of visual attention.

Hemispheric asymmetry

Prior research has reported hemispheric laterality to be greater in the left than the right parietal region (Heilman & Van Den Abell, 1980; Sheremata et al., 2010; Szczepanski et al., 2010; Vandenberghe et al., 2005). Such asymmetry, however, was not found in the present study in a VSTM task when stimulus location was unpredictable and participants had to attend to both hemifields (Experiment 1). Hemispheric asymmetry, however, did emerge when stimulus location was cued in advance in a VSTM task with an event-related design (Experiment 2) and in both a VSTM and a perceptual task with a block design (Experiments 3A, B). Interestingly, this top-down attention-driven hemispheric asymmetry was found only in the inferior but not the superior IPS. Additional analyses showed that the strength of hemispheric asymmetry significantly correlated with the strength of laterality in the inferior but not the superior IPS. Given that laterality was significantly lower in the superior than the inferior IPS in all three experiments, hemispheric asymmetry seems to only emerge when there is a sufficient amount of laterality present. Overall, these results showed that hemispheric asymmetry in the inferior IPS is not a fixed characteristic of that brain region but rather is modulated by the anticipatory deployment of top-down visual attention to the target-present hemifield.

In Experiment 1, to minimize the amount of attentional cuing, the test probes were presented at fixation, and in Experiments 2 and 3A, to maximize such cuing, the test probes were presented at the same locations as the sample stimuli. One may argue that this could have led to a difference in task demands and explain the failure to find hemispheric asymmetries in Experiment 1. In other words, differences in task demands, rather than the modulation of top-down attentional control, may determine the presence or absence of hemispheric asymmetry. Because of the need to minimize the amount of top-down attentional cuing in Experiment 1, had the test stimuli been presented in the target-present hemifield, it would, in effect, serve as a cue and bias participants' attention during the VSTM delay period. In a study conducted by Xu and Chun (2006), both peripheral probes (experiments 1 and 2) and central probes (experiment 4 in the two off-center presentation conditions) were used, and very similar behavioral performance and fMRI response patterns were observed in the inferior and superior IPS. Thus, exactly how the probe stimuli were presented did not seem to affect task performance. In the present study, the laterality index from the superior IPS did not show any difference between Experiment 1 and Experiments 2 and 3A (no main effect of experiment nor interactions between hemisphere and experiment). This further confirms that the superior IPS is tracking the task load and is not affected by exactly how information is encoded into VSTM. Thus, how the test stimuli were presented would affect the allocation of top-down attentional resources but not the overall task demand.

Although one may argue that a perceptual task may be more attention-demanding than a VSTM task, the amount of hemispheric asymmetry observed in the inferior IPS did not differ between these two tasks (Experiment 3). This indicates that the magnitude of hemispheric asymmetry may be solely determined by the engagement of anticipatory top-down visual attention rather than the amount of attentional effort involved.

Previously with a cuing paradigm, Sheremata et al. (2010) reported hemispheric asymmetry in a VSTM task only when the encoding load was high. Here it seemed that a higher VSTM encoding load by itself was not sufficient to evoke hemispheric asymmetry (Experiment 1). But rather, the engagement of top-down spatial attention was necessary (Experiments 2, 3A, and 3B). With the emergence of hemispheric asymmetry, Sheremata et al. reported laterality in the left but not in the right hemisphere. Here strong laterality in both hemispheres was observed even with the emergence of hemispheric asymmetry. In our study, distractors were not present in any trial whereas in Sheremata et al. color-defined distractors were present both in the attended and the unattended hemifields. Distractor

inhibition in the attended hemifield in Sheremata et al. but not in our study may well account for the discrepancies in the results.

IPS topographic maps are equally prominent in both hemispheres even when biased spatial attentional paradigms were used to localize these maps. This seems to be at odds with the existence of hemispheric asymmetry as hemispheric asymmetry would predict more prominent topographic maps along the left rather than the right parietal IPS regions. Given the overlap between IPS topographic maps and the inferior and superior IPS, a close examination of the results from Experiments 2 and 3 revealed that, even with the presence of hemispheric asymmetry, both hemispheres still exhibited strong laterality in the inferior and superior IPS. This likely enabled the localization of equally prominent contralateral topographic maps along IPS in mapping studies despite the presence of hemispheric asymmetry.

In an attention-cuing paradigm, Szczepanski et al. (2010) found that, although lower IPS topographic regions (IPS1 and IPS2) exhibited significant hemispheric asymmetry, the upper regions (IPS3 to IPS5) did not (they did not examine responses from V3A and V3B). Given that the superior IPS only overlapped about 50% with IPS1 and IPS2 (Bettencourt & Xu, 2011, 2016b) and 50% with IPS3, IPS4, and no topographic regions, it seems that, as a functionally defined parietal region tracking VSTM representations, the superior IPS as a whole does not exhibit hemispheric asymmetry although subregions within it could. As the focus of this study was on examining object processing in functionally defined inferior and superior IPS regions, further studies are needed to document how hemispheric asymmetry observed in some of the IPS topographic maps would be affected when the deployment of top-down spatially biased attention was manipulated as was done in the present study.

In a cuing visual search study, by using a random-effect group analysis and directly contrasting activations between the two hemispheres, Shulman et al. (2010) failed to find hemispheric asymmetry in dorsal parietal regions. However, a group-level analysis might not have properly accounted for the variability that existed across participants and brain regions. Our study and those of Szczepanski et al. (2010) and Sheremata et al. (2010) have all used an individual subject-based ROI approach. With this more sensitive measure, hemispheric asymmetry can be reliably observed.

Why would hemispheric asymmetry emerge with the deployment of top-down visual attention? One possibility is that because right posterior parietal regions participate in the maintenance of attention to specific spatial locations (Malhotra, Coulthard, & Husain, 2009), the deployment of top-down attention increases

response and weakens laterality in right posterior parietal regions. Indeed, a population-receptive hemifield in the right parietal regions has recently been shown to enlarge and cover the ipsilateral hemifield when spatial attention was directed to the target location (Sheremata & Silver, 2015). However, the present results show that laterality for both hemispheres actually increased rather than decreased in the inferior IPS with the deployment of top-down attention. Hemispheric asymmetry may thus reflect a brain structure asymmetry that can only be observed when the strength of laterality is sufficient. Because attention can boost the strength of laterality, consequently, attention is also able to modulate the strength of hemispheric asymmetry.

In the present experiments, a strong correlation between VSTM behavioral performance and either hemispheric laterality or asymmetry was not observed. As a VSTM task involves multiple cognitive processes, including selection, encoding, and maintenance, it seems that the influence of hemispheric laterality and asymmetry on behavior was relatively minor in determining the overall VSTM performance in our study.

In a recent study, behavioral hemispheric asymmetry in a VSTM task was reported such that VSTM performance for single-feature objects was better when the stimuli were presented in the left rather than the right visual hemifield (Sheremata & Shomstein, 2014). However, in the current study, there were no behavioral performance differences between the targets presented in the left and right hemifields in all three experiments. Sheremata and Shomstein reported that the behavioral hemispheric asymmetry was found only when the feature-encoding load was right above the individual participant's VSTM capacity. In the present experiments, set sizes between two and four were used, which were either below or near the individual participant's VSTM capacity. Thus, the discrepancy between our study and Sheremata and Shomstein could be due to differences in the VSTM encoding load used in the two studies and the sensitivity of the behavioral asymmetry effect to the encoding load. As the focus of the present study was on measuring laterality and asymmetry in the inferior and superior IPS using fMRI, it was underpowered to examine in detail how laterality and asymmetry may affect behavioral performance in interesting and fundamental ways.

The relationship between IPS topographic maps and the inferior and superior IPS

The goal of the current study was to examine hemispheric laterality and asymmetry in functionally defined inferior and superior IPS involved in object

individuation and identification, respectively. Given that both regions included areas that do not overlap with topographic IPS (see Bettencourt & Xu, 2016b), examining responses in these IPS maps was not optimal for the purpose of the current study.

One may argue that the IPS regions defined by spatial topographic mapping are the most fundamental way of characterizing IPS functions because they are obtained in independent mapping studies and that other ways of delineating IPS functions are based on somewhat arbitrary cognitive tasks and may be considered obsolete in light of these topographic maps. However, this view is rather limited in a number of ways.

First, although location processing is an important aspect of vision, object perception and VSTM are also fundamental and important components of visual cognition with VSTM being an integral part of perception (see a discussion in Xu, 2002). Thus the tasks that have been used to identify the inferior and superior IPS in their differential roles in object selection, encoding, and storage should not be considered as arbitrary cognitive tasks. Rather, they tap into some fundamental aspects of visual cognition that may not be captured by location processing. The same could be said for all the other cognitive tasks that have been associated with the parietal cortex. Before we understand how parietal regions activated by different cognitive tasks are related to each other, it is somewhat premature and prejudiced to argue that IPS topographic maps are the most principled way of understanding parietal function.

Second, IPS topographic maps are defined by functional tasks by drawing observers' attention to specific locations of the visual display in a systematic manner. This is just one instance of how regions in IPS may be defined functionally—no different from how other functional regions have been defined there apart from the usage of different tasks and procedures.

Third, in a macaque monkey fMRI study, it was found that IPS topographic maps colocalized quite poorly with the IPS regions defined by Lewis and Van Essen (2000a, 2000b) according to architectonic subdivisions, such that area LIP only partially overlapped with one of the topographic maps (Arcaro, Pinsk, Li, & Kastner, 2011). In other words, IPS maps do not correspond to architectonically defined macaque IPS regions. In contrast, topographic areas defined in early visual areas such as V1, V2, V3, and V3a showed a high degree of agreement with architectonically defined areas. Without fully understanding the implications of the disagreement between IPS topographic maps and architectonically defined regions in macaques, to the extent that the human IPS topographic maps are also activations obtained from functional localizers just like how other functional subdivisions within IPS are obtained, using these maps as

principled landmarks to assess other functional subdivisions within the human IPS is not fully justified and can be potentially misleading.

Fourth, and most significantly, although the discovery of the IPS topographic regions have generated the excitement that perhaps we could finally characterize parietal function through the existence of these distinctive regions, similar to how ventral visual cortex has been characterized, in reality, however, we are far from achieving this goal. Unlike the topographic regions in the occipital cortex, whose distinctive roles in visual processing have been well-documented, functional distinctions among the IPS topographic regions remain largely unknown (e.g., Konen & Kastner, 2008). This could partially be due to the difficulty in localizing these regions, especially in higher IPS regions. Although this could reflect the need for further methodological improvement in localizing these regions, given the overall strength of the signal, this could also suggest that IPS topographic regions may not be the ultimate way of characterizing all IPS functions. Consistent with this latter view, in a recent fMRI multivoxel pattern decoding study (Bettencourt & Xu, 2016), we found that VSTM decoding from none of the IPS topographic regions consistently correlated with behavioral VSTM performance. In contrast, superior IPS, as defined by its correlation with behavioral VSTM capacity measures from an independent localizer, showed successful VSTM decoding that was correlated with behavioral VSTM performance. Thus, the IPS topographic regions were not sufficient in capturing the VSTM function associated with the parietal cortex. If we had only examined decoding responses from these topographic regions, we would have falsely concluded that none of the IPS regions contributed significantly to VSTM information storage. In a separate line of research, it has also been shown that the IPS topographic maps showed partial and inconsistent overlap with number- and size-defined parietal regions across participants (Harvey, Fracasso, Petridou, & Dumoulin, 2015; Harvey, Klein, Petridou, & Dumoulin, 2013). Again, IPS topographic regions by themselves were insufficient in capturing the IPS's role in number and size processing.

Thus, there exist partially overlapping functional regions involved in different aspects of visual cognition within IPS. Although the IPS topographic regions provide one way to subdivide the IPS based on location processing, the boundaries delineated by these maps do not necessarily capture other functions associated with IPS. Thus our understanding of the functions of the human IPS should not be reduced to studying the IPS topographic maps only. Understanding the response properties of the IPS regions defined by other functional tasks is still critical if we want to fully understand the multiplex nature of IPS and its role in visual cognition.

Conclusion

In sum, the present study shows that both hemispheric laterality and asymmetry were greater in the inferior than the superior IPS, consistent with their respective roles in object individuation and identification. Although the strength of laterality could be modulated by the deployment of top-down attention in the inferior IPS, it nevertheless is consistently present in both parietal regions regardless of the amount of top-down attentional modulation and task. Hemispheric asymmetry, on the other hand, seems to only emerge in the inferior IPS when the deployment of top-down spatial attention increases laterality sufficiently.

Keywords: attention, hemispheric asymmetry, laterality, parietal cortex, visual short-term memory

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Footnote

¹ Averaged eye positions were compared when participants were cued to attend to the left and right hemifields. Participants were excluded if the averaged horizontal eye positions of the left and right attended trials differed significantly from each other. This was a strong indicator that the eye positions have been biased toward the attended hemifield rather than maintained properly at the central fixation.

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