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Distinct anatomy for visual search and bisection: a neuroimaging study

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Abstract

Individuals with spatial neglect following brain injury often show biased performance on landmark bisection tasks (judging if a single item is transected at its midpoint) and search tasks (where they seek target(s) from an array of items). Interestingly, it appears that bisection deficits dissociate from other measures of neglect (including search tasks), and neglect patients with bisection deficits typically have more posterior injury than those without these symptoms. While previous studies in healthy adults have examined each of these tasks independently, our aim was to directly contrast brain activity between these two tasks. Our design used displays that were interpreted as landmark bisection stimuli in some blocks of trials and as search arrays on other trials. Therefore, we used a design where low-level perceptual and motor responses were identical across tasks. Both tasks generated significant activity in bilateral midfusiform gyrus, largely right lateralized activity in the posterior parietal cortex, left lateralized activity in the left motor cortex (consistent with right handed response) and generally right lateralized insular activation. Several brain areas showed task-selective activations when the two tasks were directly compared. Specifically, the superior parietal cortex was selectively activated during the landmark task. On the other hand, the search task caused stronger bilateral activation in the anterior insula, along with midfusiform gyrus, medial superior frontal areas, thalamus and right putamen. This work demonstrates that healthy adults show an anatomical dissociation for visual search and bisection behavior similar to that reported in neurological patients, and provides coordinates for future brain stimulation studies.

Keywords

spatial neglect; line bisection; cancellation; visual search; parietal cortex; landmark task

Introduction

Spatial neglect is a common consequence of right hemisphere injury, with patients classically failing to respond to information on their left side. Two of the most popular paper-and-pencil methods for assessing this deficit are cancellation tasks (where the

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participant is asked to mark target items in a cluttered array of distractors) and bisection tasks (where the individual marks the midpoint of the line). While each of these tasks requires exploratory motor movements, similar effects are observed with variants of these tasks that attempt to isolate the perceptual components: the landmark task (where an individual reports if pre-bisected lines are segmented at their midpoint, Harvey et al., 1995) and effortful visual search tasks (where the participant reports if a target item is present or absent in a cluttered display). Despite clear differences in the visual appearance of the test materials as well as in the cognitive demands of performing the tasks, bisection and cancellation tasks are often used interchangeably to assess neglect with considerable success. However, while some patients exhibit biased performance on both bisection and cancellation tasks, many only exhibit biases on cancellation tasks (Ferber and Karnath, 2001). This dissociation has been interpreted as suggesting that some of the regions critical for accurate cancellation performance are not required for unbiased bisection. Support for this notion comes from a series of studies that demonstrate that individuals with bisection deficits have more posterior injury than those without these deficits (Binder et al., 1992; Rorden et al., 2006; Verdon et al., 2010). Our aim was to use neuroimaging in healthy adults to validate this effect and provide a more accurate understanding of the brain regions involved with these tasks.

Brain imaging studies in healthy adults can help identify brain regions involved in perceptual processing. Seminal work by Fink et al. (2000, 2001) demonstrated that landmark tasks activate the posterior parietal cortex (PPC). Çiçek et al. (2009) extended this by demonstrating that both landmark and bisection tasks cause activation in the PPC. In addition, there is clear agreement that visual search tasks engage the PPC (for review, see Corbetta and Shulman, 2002). A study by Himmelbach et al. (2006) identified activity in the superior temporal gyrus (STG) during a visual search task where participants scanned a cluttered array for a very infrequent target (the letter A). One elegant feature of this analysis is that the search was conducted with overt eye movements, similar to the typical tests used with stroke patients, whereas most prior imaging studies have required participants to maintain fixation. However, this feature may also explain why Himmelbach and colleagues did not detect any PPC activity: their statistics contrasted active visual search with control tasks where the individuals made similar overt eye movements. Specifically, there is clear evidence that the dorsal attentional network (PPC and FEF) is similarly activated during covert peripheral attention and eye movements (de Haan et al., 2008). Further, Himmelbach et al. did not examine activity related to bisection tasks, so it is difficult to determine if their temporal lobe effect dissociates between the search and bisection tasks.

Our aim was to directly compare the activations observed in neurologically healthy adults while performing a landmark task with the same displays observed during visual search. We specifically chose a 'serial' search task rather than a 'parallel' search task where the targets pop out since this feature is found in all popular cancellation and search tasks used with neglect, and patients with unilateral injury resulting in neglect without additional confounds (such as visual field cuts) as well as patients with simultanagnosia following bilateral injury show remarkably intact performance on preattentive search tasks (Esterman et al., 2000; Karnath et al., 2000). A novel aspect of our paradigm is that we kept the perceptual stimuli and the motoric responses identical between these two tasks. This is important, as it allows us to get a pure measure for task related differences. A second important design decision was to require participants to conduct both tasks without eye movements, in order to rule out the possibility that these tasks might elicit different fixation patterns, which could directly cause different patterns of brain activation.

Based on work with neurologically impaired individuals, we predicted that regions near the superior and middle temporal cortex would show more activation to a visual search task than

a bisection task. A second clear prediction was that the bisection task should elicit strong responses in the PPC, though we were agnostic as to whether this region would be task specific: as reviewed, some studies have implicated the PPC in bisection while others have implicated it in visual search, though it is unclear whether these studies refer to the same or different parts of the PPC.

Methods

Participants

Twenty-six young adults (18 female, average age 23.9 years, range 18-38 years) from the Georgia Tech/Georgia State University community participated in the study after giving informed consent following a procedure approved by the local institutional review board. All had normal or corrected-to-normal vision and reported no history of neurological conditions. Data from an additional five subjects was excluded from further analysis due to poor performance on both tasks ($n = 1$), excessive ($>3\text{mm}$) or stimulus-locked head movement during data collection ($n = 3$), or equipment malfunction (projector focus problems, $n = 1$).

Stimuli

The novel stimuli used in this study enabled us to evaluate the neural correlates of a visual search task and a landmark task using perceptually identical stimuli that required identical motoric responses (see Figure 1). On each trial, a black bar was presented on a grey background. The bar was 12 degrees of visual angle wide and 3 degrees high. To prevent participants from using the fixation cross as a cue to the center of the bar, the bar was never horizontally centered on the screen but appeared at four equally frequent positions on the screen, with its center positioned 2.5 degrees above and either 1 degree left, 0.5 degrees left, 0.5 degrees right, or 1 degree right of the fixation cross. A white line (3 degrees long and 0.13 degrees wide) was positioned vertically to divide the bar into two pieces. The white line divided the bar at the center on 50% of the trials, and appeared 0.4 degrees to the left or right of center on the remaining half of the trials (equally divided). In addition, eight white O or Q-like stimuli were positioned within the black bar on each trial, four to the left of the dividing line and four to the right. Although we did not manipulate set size, previous studies have shown that this stimulus set shows set size effects and requires effortful visual search, with or without eye movements (Zelinsky & Sheinberg, 1997). Each shape was 1 degree in diameter and was positioned so that it was in one of 22 pre-determined positions that were more than 3 degrees but less than 6 degrees from the fixation cross. On 50% of trials, all shapes were Q-like (had a vertical crossbar located at the 12'o'clock position), while on the other 50% of trials, one of the Q-like shapes was replaced with an "O" shape without the crossbar. Half of the time the "O" appeared in one of the eleven positions to the left of the bisecting bar and half the time it was to the right, occurring equally frequently in all positions. The remaining shapes were pseudorandomly assigned to the remaining positions so that four stimuli always appeared on each side of the dividing line and no more than two stimuli were vertically or horizontally adjacent on each side.

On each trial, participants were asked either to judge whether the dividing line was centered or off-center in the bar ("bisection" task) or to judge whether an "O" shape was present or absent among the Q-like shapes ("search" task). Participants reported their judgment by pressing one of two buttons on an MRI compatible button box held in the right hand. 'Present' and 'Centered' responses were mapped to one button and 'Absent' and 'Off-Center' responses were mapped to the other button. Participants were required to make these judgments without moving their eyes from the central fixation cross to control for possible differences in natural eye movement patterns across the two conditions. Within a session,

each display (defined by the combination of bar, line, and shape positions) occurred exactly twice, once in the bisection condition and once in the search condition. Counterbalancing ensured that the position of the bisection line (left, center, or right) provided no information about the presence, absence, or position of the “O” shape and vice versa.

Data acquisition

Functional data were collected using a Siemens Trio 3T MRI scanner equipped with a twelve-channel receive-only head coil, using an EPI pulse sequence with the following scan parameters: repetition time (TR) 1920 ms, echo time (TE) 30 ms, flip angle 90 degrees, 64×64 matrix, 192×192 mm field of view (FoV), GRAPPA parallel imaging with acceleration factor PE = 2. Thirty-six axial slices aligned with the A-P plane were collected in interleaved order with a 20% slice gap, leading to an effective voxel size of $3 \times 3 \times 3.6$ mm. In addition, a 3D anatomical image was acquired for each participant using a T1-weighted MP-RAGE sequence (TR = 2250 ms, TE = 4.18 ms, TI = 900ms, 256×256 matrix, 256×256 mm FoV, 176 slices, voxel size $1 \times 1 \times 1$ mm) with parallel imaging (GRAPPA, acceleration factor PE = 2).

Procedure

Prior to entering the scanner, participants practiced the landmark bisection and search tasks while their eye movements were visually monitored by the experimenter. The experimenter verbally corrected participants when eye movements were detected. By the end of the practice block (80 trials each of landmark and search), all participants were able to perform both tasks accurately while maintaining fixation on the central fixation cross, ensuring that neither differences in overt eye movements between conditions or initial learning effects would lead to differences in brain activity during the functional runs.

Following initial structural image collection, participants completed four experimental runs inside the scanner, with the beginning of each run synchronized with the scanner data acquisition by an optical trigger signal. Each run lasted 10 minutes and 40 seconds and contained eight blocks each of landmark and search tasks. Ten trials were presented within each 30-second task block. The visual bar stimulus was visible for 2s, with a 1s inter-trial interval. A central fixation cross was continuously present on the screen throughout the block. Ten seconds of rest separated each task block, during which subjects were instructed which task to perform on the next block by means of a single word (“bisection” or “search”) centrally presented during the rest period. Stimulus presentation was controlled by E-Prime v 2.0 software and displayed on a rear-projection screen by a projector (Avotec Silent Vision 6011). Participants viewed the screen through an angled mirror mounted on top of the head coil as part of a magnet-compatible eyetracking system (Avotec RE-5701). The experimenter continuously monitored fixation via the tracker’s eye camera during image acquisition, and participants were reminded of the importance of maintaining fixation between sessions. Compliance was considered excellent.

Data Analysis

Functional data were analyzed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>) using Automated Analysis scripts (<http://www.cambridgeuroimaging.com/>). The first four volumes of each run were discarded to remove T1 saturation effects (not including two initial volumes that are automatically discarded prior to reconstruction by our scanner). Remaining volumes were motion-corrected to the first retained volume of the first run. T1 anatomical images were coregistered to the mean functional image and linear and nonlinear transformations were applied to match the T1 image to the SPM8 T1 template. The resulting transform was applied to the coregistered functional data to bring it into alignment with the template, followed by smoothing with an 8mm FWHM Gaussian kernel. Data were high-

pass filtered with a 128s filter. In addition to the two regressors of interest (search task and bisection task), subject-level models contained ten regressors of no interest (six regressors related to head movement and four session-level regressors.) Subjects' individual T-maps from relevant contrasts of interest were submitted for group-level analysis. Data were thresholded at $p < 0.05$, corrected for multiple comparisons using random field theory.

Results

Behavioral Results

While the physical stimuli were identical for both tasks, participants' speed and accuracy at making the landmark bisection and search judgments differed slightly. Participants were more accurate (bisection: 71.9%, search: 68.2%; $t(25) = 2.38$, $p < 0.05$) and faster (bisection: 951.5 ms, search: 1117.8 ms, $t(25) = 9.72$, $p < 0.001$) in the bisection task than the search task. We also continuously monitored gaze fixation during scanning to ensure that they did not make saccades away from the fixation cross while the stimulus display was present. Participants' eye movements were monitored via the coil-mounted eye camera throughout the experiment to detect target-directed saccades. All participants were judged by the experimenter to have excellent gaze fixation for both search and bisection tasks.

Imaging Results

Because both the bisection and search tasks were performed on identical perceptual displays and required the same motor response, any differences in brain activity reflect task-specific attention, calculations, and decisions as opposed to perceptual, spatial, or motoric components of the displays or responses. Consequently, when both the bisection and search tasks were compared to a fixation baseline, largely overlapping activations emerged in primarily right-lateralized posterior parietal cortex, left-lateralized primary motor cortex (consistent with right-handed responses), and bilateral inferior frontal and occipital areas (Figure 2, top panel). All whole-brain analyses reported here were thresholded to correct for familywise error at $p < 0.05$ with a cluster size of 10 voxels ($t > 5.89$).

Despite the low-level similarity of the two tasks, several brain areas show task-selective activations when the tasks are directly compared (Figure 2, bottom panel). Significant activations for the Bisection>Search contrast emerged in superior parietal cortex, particularly in the right hemisphere. This activation is primarily posterior to the postcentral sulcus and above the intraparietal sulcus but does extend into the postcentral sulcus (Figure 3). When compared to rest, however, neither task showed significant activation in superior parietal cortex. This may be due to larger variability in resting activation levels or to differential deactivation. A less conservative statistical threshold ($p < 0.001$, uncorrected) shows a trend toward deactivation during the search condition relative to rest (mean beta value -0.35 , SD 1.25). However, there is positive activation in the bisection versus rest contrast (mean beta value 0.44, SD 1.15). Other significant areas of activation for the Bisection>Search contrast (Table 1) appeared in lateral occipitotemporal cortex and pre- and postcentral gyri (primarily right-lateralized). In the Search>Bisection contrast, we did not observe differential activation for the two tasks in the superior temporal gyrus but neighboring areas in the anterior insula and operculum areas were significantly active bilaterally, along with thalamus, right putamen, bilateral (but primarily left-lateralized) midfusiform areas, and superior frontal areas near supplementary motor cortex extending into the cingulate gyrus.

Discussion

The present study confirmed the hypothesis of distinct neural correlates for visual search and landmark task bisection behavior. Several brain areas showed task-selective activations when the two tasks were directly compared. By using identical displays for landmark and visual search tasks, we attempted to control for differences in perceptual and motor components of the two tasks while isolating brain areas responsible for their differential cognitive and attentional processes. However, while our perceptual stimuli were identical, the tasks do make very different demands on visual perception. One could in principle argue that there are multiple differences between these tasks, making it difficult to disentangle which task differences drive which differences in brain activity. For example, one could argue that overt eye movements are perhaps harder to suppress in the search task, where foveation may help discriminate local features. Our aim here was to closely mimic popular tasks used in clinical diagnosis of neglect, and while we concur that these tasks make different demands, our main finding is an anatomical division that is consistent with the findings of neurological patients.

Our primary prediction was that regions near the superior and middle temporal cortex should show more activity during search tasks than when making bisection judgments. We did not observe differential activation for the two tasks in these areas but neighboring areas in the insula, operculum, medial prefrontal cortex, and right basal ganglia did demonstrate this pattern. However, we concede that the region identified in our imaging study (centered in the anterior insular cortex, AIC) appears to be more medial than typically reported for lesions in spatial neglect (e.g. Karnath et al. 2004, 2011), for visual search tasks in which overt eye movements are performed (Himmelbach et al. 2006), and for the disruption of visual feature search by TMS (Ellison et al. 2004, Schindler et al. 2008). While there are case reports of neglect and/or extinction where the only observable injury is to the insula (e.g. Manes et al., 2004), it is possible that these injuries also include perfusion deficits to more lateral regions. However, given that one of the primary goals of this study was to examine the neural correlates of bisection and search behavior in the absence of differences in the visual displays or overt motor responses required by the tasks, both the landmark and visual search tasks differ considerably from the canonical versions used in previous neurophysiological and neuroimaging investigations. While the controlled displays permit us to be confident that the patterns of brain activity are not the result of low-level differences, the deviations from conventionally used stimuli (thicker, visually cluttered bars for bisection, spatially restricted search arrays, and eye movement constraints, amongst others) make it difficult to assess the implications of null effects or inconsistencies with previous research with this study alone.

Therefore, one of the major findings of our study was that visual search causes more activation of the AIC as well as the medial prefrontal and anterior cingulate cortex relative to bisection (following convention, we refer to these latter two neighboring areas as the ACC). There is a long history of using neuroimaging to examine parallel and serial search (e.g. Corbetta et al., 1995, Leonards et al., 2000). Recent work by Fairhall et al. (2009) reviews this literature and presents a new paradigm designed to decouple effortful serial and parallel search from overt (with eye movements) versus covert (while fixation is maintained) shifts of attention. Overall, the pattern of activations resulting from our covert search task (compared to rest) are quite similar to their main effect of serial search (their Figure 4), including frontal eye fields, lateral prefrontal cortex, frontal operculum, and intraparietal sulcus extending to lateral occipital cortex. Importantly, they also found that covert serial search tasks resulted in increased activation in the insula. In addition, Craig (2009) reviews numerous studies using a wide range of tasks that demonstrate that AIC and ACC activity is typically coupled. Craig notes that this network is activated by attentional tasks, cognitive

choices, and tasks that attempt to isolate awareness of movements and perception, leading him to suggest that the AIC engenders human awareness. While we did see selective activation of this network for search relative to bisection, we certainly do not suggest that this is the sole function of this module. One explanation may be that our search task typically includes response conflict (e.g. both targets and non-targets compete for alternate motoric responses), as well as a conflict between exploration and the need to inhibit previously attended items. This explanation fits nicely with studies that show this network is involved in tasks that invoke response inhibition (Swainson et al., 2003; Wager et al., 2005).

We also found that while both tasks activated the bilateral midfusiform regions, this area was significantly more activated during the visual search task than the landmark task. While this effect was not anticipated, one possible explanation is that the visual search task required the participants to attend to the letter-like local features, and therefore invoked the region that is often referred to as the 'visual word form area', though we note that this region is actually observed for a wide range of tasks (Price and Devlin, 2003).

Unfortunately, our observations and predictions regarding the AIC and ACC will be hard to test with complementary methods such as brain stimulation, as these locations are quite distant from the scalp (brain stimulation is best at targeting cortex near the scalp). In general, the brain imaging and brain stimulation techniques are complementary, as brain imaging can provide whole brain coverage to identify candidate areas involved with a task, whereas brain stimulation can identify which regions are critical for a task. Several recent brain stimulation studies provide some support for the notion that PPC and STG have distinct roles. For example, Oliveri and Vallar (2009) recently demonstrated that stimulation of the right inferior parietal lobe disrupted bisection judgments, whereas the same stimulation applied to the STG did not influence this task. While null results are difficult to interpret (they may not have stimulated at the location or depth of the critical temporal lobe region), this finding is consistent with the pattern observed in patients. Arguably the most influential brain stimulation study in this respect was conducted by Ellison and colleagues (2004) who demonstrated that stimulation of the right PPC interfered with serial search but not feature search, whereas the reverse pattern was observed for the right STG. This work clearly implicates the STG with perceptual processing, though it does not necessarily demonstrate that this region is not equally involved in bisection judgments.

Posterior parietal cortex activation was observed for both tasks, with a larger spatial extent in the right hemisphere. However, superior portions of the right PPC and postcentral sulcus were more active during landmark task performance than during visual search. There is now clear evidence that disruption of the PPC using brain stimulation can influence both visual search (Ashbridge et al., 1997) and bisection (Fierro et al., 2000) tasks. However, no previous brain stimulation study has directly contrasted the precise anatomical locations involved in each of these tasks. Our work provides clear anatomical targets and hypotheses for future brain stimulation studies – suggesting that stimulating superior parietal regions may selectively disrupt a participant's ability to make bisection judgments, whereas more inferior stimulation may disrupt both tasks. This raises an apparent paradox, as our imaging study implicates the right superior parietal cortex with bisection, whereas lesion studies tend to implicate more inferior regions of the parietal cortex (e.g. Binder et al., 1992 ; Mort et al., 2003; Rorden et al., 2006; Verdon et al., 2010). We suggest two reasons for this discrepancy. First, the inferior parietal cortex is more vulnerable to injury (as it is part of the middle cerebral artery territory), leading to a sampling bias (at least as observed on structural scans). Second, at the acute stage, many patients with inferior parietal injury show both line bisection deficits as well as cancellation deficits (Rorden et al., 2006), though dissociations are often seen at subacute stages (e.g. Machado and Rafal, 1999; for review, see Ferber and Karnath, 2001). Seen from this perspective, there is a strong agreement

between our imaging results and the lesion location in such patients, as our neuroimaging shows that both landmark and search tasks activate the inferior parietal sulcus and lateral occipital cortex. Based on this, we can make a series of strong, testable predictions. First, our results suggest that patients with selective injury to the right superior parietal lobe will show selective impairments on bisection/landmark tasks. Likewise, TMS application over this superior region should lead to selective impairments of the bisection/landmark tasks. Finally, we suggest that TMS application to the inferior parietal lobe will disrupt both bisection/landmark as well as search/cancellation tasks.

To conclude, using versions of landmark and visual search tasks with identical perceptual stimuli and motor responses allows us to identify regions that subserve both tasks as well as those regions where activity levels discriminate between these two tasks. Consistent with observations in neurological patients, our findings demonstrate an anatomical dissociation for visual search and bisection behavior in healthy adults. While neuropsychological, fMRI and TMS evidence have suggested involvement of regions near the superior temporal cortex in visual search, we particularly identify a region of the anterior insula and right basal ganglia. Likewise, while prior brain stimulation and brain imaging studies have suggested that portions of the posterior parietal cortex are involved with the landmark and bisection tasks, our study suggests that more superior parts of this region appear to be particularly activated by the landmark task. The anatomical coordinates from this work provide clear targets for future brain stimulation studies.

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- Landmark and visual search tasks show an anatomical dissociation in fMRI in healthy adults, even when stimuli are identical
- The landmark task selectively activates superior parietal cortex
- Visual search selectively activates AIC and ACC plus subcortical regions

Figure 1.

A typical stimulus display. Identical physical stimuli were used for both tasks. For this display, participants would respond 'centered' if asked to make a line bisection judgment (as the white line is in the middle of the black bar) and 'present' if asked to make a search judgment (as one of the items is an 'O').

Figure 2.

Statistical maps shown on top of the mean of the normalized structural scans. All maps are thresholded to correct for familywise error ($p = 0.05$, $t > 5.89$, cluster threshold = 10; with color gradients showing range from $t=0$ to $t>8$) and displayed in neurological convention (with the left hemisphere on the left side of the image). Axial slices correspond to Talairach coordinates $Z = -8, 0, 8, 30, 50, 60, 70$. The top row shows regions more active for each task relative to baseline (rest). Note the similarity in activations, reflecting the identical perceptual stimuli and motoric responses. The bottom panel shows the differences between the two tasks, with the search task yielding more activity in the insula, medial frontal gyrus and midfusiform regions, whereas the bisection task leads to more activity in the posterior parietal lobe.

Figure 3. Statistical map for bisection > search (green) and the Juelich atlas (primary somatosensory cortex of Areas 1 and 2 shown in red) overlaid on the rendered group average brain. Voxels in Areas 1 and 2 that are also involved in the bisection > search contrast appear in yellow. Statistical maps are thresholded at a FWE corrected $p = 0.05$ ($t > 5.89$, cluster threshold = 10). While the task contrast clearly includes portions of the primary somatosensory cortex, peak activation for the bisection > search condition is located in the SPL behind the postcentral sulcus and above the intraparietal sulcus.

Table 1

REGION (AAL)	REGION (Juelich)	x	y	z	T	corrected P value
BISECTION > SEARCH						
SPL (RH)	SPL (7PC) 70%	30	-52	67	9.71	< 0.001
		45	-25	61	9.38	< 0.001
		39	-37	55	9.10	< 0.001
SPL (LH)	SPL (7A) 50% (5L) 50%	-24	-49	70	7.33	0.003
		-15	-43	73	6.08	0.034
lateral occipital/temporal (LH)		-54	-64	-2	7.16	0.004
lateral occipital/temporal (RH)		48	-55	1	7.15	0.004
		57	-61	-5	6.47	0.016
insula (RH)	OP3 30%	36	-4	16	7.28	0.003
precentral gyrus (RH)	Area 1 70%	60	-10	37	7.02	0.005
postcentral gyrus (RH)	Area 2 40% IPC (PFt) 40%	60	-25	43	7.00	0.005
postcentral gyrus (LH)	IPC (PFt) 60%	-57	-22	40	6.60	0.012
		-48	-28	37	6.19	0.028
SEARCH > BISECTION						
medial prefrontal		3	14	49	9.32	< 0.001
		-6	14	49	9.10	< 0.001
		12	26	31	7.74	0.001
anterior insula (LH)		-27	26	-2	8.57	< 0.001
anterior insula (RH)		42	26	1	8.54	< 0.001
		30	20	-5	7.46	0.002
midfusiform (LH)	hOC4v 20%	-27	-73	-17	8.89	< 0.001
		-36	-73	-14	8.32	0.001

REGION (AAL)	REGION (Juelich)	x	y	z	T	corrected P value
midfusiform (RH)	hOC4v 30%	33	-67	-8	7.00	0.005
		39	-64	-26	6.83	0.008
basal ganglia (RH)		18	11	1	7.75	0.001
		6	-19	-2	7.24	0.003
		-3	-19	-2	6.93	0.006
basal ganglia (LH)		-12	-7	7	7.71	0.001
IPS (LH)		-27	-82	19	8.06	0.001
IPS (LH)		-18	-64	40	6.78	0.008
frontal eye fields (LH)		-45	-1	34	8.46	<0.001
superior frontal gyrus (RH)		30	44	34	7.40	0.002
cerebellum		-3	-76	-20	8.39	<0.001
		6	-73	-23	7.13	0.004

(*) included for areas with brain coverage and region identified at > 20% probability