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Research Report

Task-related laterality effects in the lateral occipital complex

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ABSTRACT

Using functional imaging, we investigated the effects of two different tasks on activation in the lateral occipital complex (LOC). Alternating blocks of intact and scrambled objects were presented. In one task, subjects responded when an object repeated (matching task). In a second task subjects silently named objects (naming task). Identical objects (tools, animals and letters) were presented for both tasks. A relative measure of the number of voxels activated in LOC in left and right hemispheres was calculated for each task across a range of thresholds. Also the effects of task demands on category specific areas in LOC were examined. The object matching task resulted in proportionally more activity in the right hemisphere. The object naming task resulted in proportionally more activity in the left hemisphere, most prominently in the anterior portion of LOC. Effectively, changing the task changed the lateralization of activation to intact objects in LOC. In contrast, changing the task did not change the lateralization of category-specific activations. The results suggest that there are task-related top-down influences on the activation of neural populations in LOC as a whole, but the lateralization of category-specific regions in LOC is independent of task demands and may reflect bottom-up processing.

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1. Introduction

There is evidence to suggest that neural activations in the ventral visual cortex are modulated by top-down influences. For example, the influence of attention on the activation of neurons throughout the visual cortical hierarchy has been widely researched in both humans and primates (Hillyard et al., 1998; Kastner and Ungerleider, 2000; Treue, 2001; Morrone et al., 2002; Treue, 2003; Murray and Wojciulik, 2004). Less well-known are the top-down effects of task demands on the neural populations in the ventral visual cortex. Given that objects contain a wealth of visual information and task performance may only require processing a subset of this information, it is possible that different tasks

recruit different neural populations. In this study, we compared activation patterns in the lateral occipital complex (LOC), an object sensitive region in the occipital cortex, in response to a picture matching and a picture naming task. Given that language processing in most right handed people is specialized to the left hemisphere, we wanted to find out whether hemispheric asymmetries would occur in LOC depending on whether one task recruited language processes more heavily than the other. We also examined the influence of task demands on activations produced to specific categories of objects.

Naming an object requires the integration of perceptual, semantic and phonological processes and activates a network of interconnected cortical regions including bilateral occipital,

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temporal, left inferior temporal, left inferior frontal, left pre-central, left basal ganglia, left premotor, and anterior cingulate cortices and left insula cortices (Damasio et al., 1996; Martin et al., 1996; Chao et al., 1999; Moore and Price, 1999b,a; Okada et al., 2000; van Turennout et al., 2000, 2003). A common finding in these studies is the preponderance of activation throughout the left hemisphere in response to object naming. A recent PET study by Price et al. (2005) identified those regions involved in perceptual, semantic and phonological processes of object naming. As expected, processes associated with name production generated activation mostly in the left hemisphere. Semantic and perceptual processes generated mainly bilateral activation.

LOC is involved in the perceptual processing of objects. It has been argued that LOCs role in object recognition is of a general purpose shape analyzer and is not involved in representing conceptual information about objects (Grill-Spector et al., 2001; Tyler et al., 2004). In support of this argument, Malach et al. (1995) did not find any difference in activation to familiar compared to unfamiliar objects in LOC (see also Kanwisher et al., 1996). However, there is evidence that the left fusiform gyrus (portions of the fusiform gyrus lie within LOC) is responsive to semantic manipulations (Simons et al., 2003) and responds more strongly to meaningful objects compared to nonsense objects (Zelkowitz et al., 1998; Gerlach et al., 2002; Vuilleumier et al., 2002).

More recently, Tyler et al. (2004) investigated basic level naming (e.g. naming an object as a 'donkey' or 'hammer') and domain level naming (naming the domain to which an object belongs to such as 'living' or 'manmade'). Both of these tasks produced more activation in the left fusiform area (relative to the right) compared to fixating a blank screen. Similar findings of increased activation in the left hemisphere to object naming were found by Moore and Price (1999b) with higher activation in left anterior and left posterior fusiform area to object naming compared to object viewing. In addition, Joseph (2001) reported that viewing, matching and naming tasks recruited different regions of the occipital temporal cortex. This evidence combined with the evidence that the left fusiform is sensitive to semantic manipulations suggests that neural populations in LOC may well respond differently depending on whether a task recruits semantic/language processes or not.

Also of interest, a number of studies have found a lateralized pattern of category-specific activation in the ventral visual pathway (Martin et al., 1996; Chao et al., 1999; Gerlach et al., 2002; Whatmough et al., 2002). Chao et al. (1999) contrasted activations to animals and tools on three tasks (viewing, matching and naming). They found that animal stimuli more commonly produced activation in the right superior temporal sulcus. In contrast, tool stimuli more commonly produced activation in the left middle temporal gyrus. Okada et al. (2000) found a similar pattern of lateralization to the naming of animals and tools. If activation associated with these categories is semantically driven then it is expected that there will be differences in the pattern of activation depending on whether the task requires semantic information or not.

Given that LOC is known to be sensitive to objects (Malach et al., 1995; among many others; Kanwisher et al., 1996; Grill-

Spector et al., 1999, 2001, 2003) and identifying objects involves language processes, our study used functional imaging to investigate the effects a naming and a matching task had on the fMRI response in two sub-divisions of LOC. If LOC was sensitive to language processes, we expected more activation in left LOC for the naming task compared to the matching task. We examined both the anterior and posterior portions of LOC as Simons et al. (2003) found that only the left fusiform was sensitive to semantic manipulations involving language. We also examined the effects of the matching and naming tasks on the lateralization of category-specific areas in LOC by contrasting activations to three categories (animals, tools and letters).

2. Results

To identify object-sensitive brain areas, we presented our subjects with intact 2-D black and white line drawings of objects (animals, tools and letters) alternating with scrambled versions of the same images. In one sequence of three scans, subjects performed a matching task where they pressed a response key whenever they saw two-identical images, either intact or scrambled, in a row. In a second sequence of three scans, subjects silently named the same objects and passively viewed the scrambled objects.

The analysis of the fMRI response was performed on two subdivisions of LOC, namely LO (lateral occipital area) and pFs (posterior fusiform area), as illustrated in Fig. 1. To measure

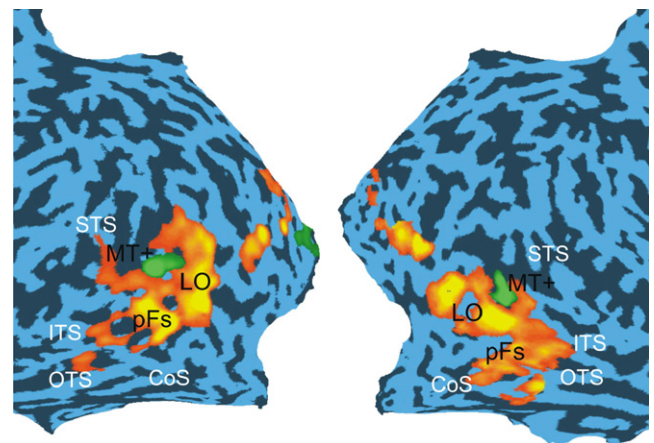


Fig. 1 – The fMRI response in two subdivisions of LOC. Both areas were defined functionally as a set of contiguous voxels with significantly stronger activation ($p < 10^{-4}$) to intact versus scrambled objects. Area LO (lateral occipital area) was located posterior and lateral to MT+ (mean Talairach co-ordinates: right LO: -41.8 ± 4 , -72.3 ± 8 , -3.4 ± 5 , left LO: 41.3 ± 2 , -78 ± 6 , -1.85 ± 3) and area pFs was located anterior to MT+, ventral to LO in the posterior to mid-fusiform gyrus, extending also into the occipitotemporal sulcus (mean Talairach co-ordinates: right pFs: -38.3 ± 5 , -58.4 ± 5 , -15.4 ± 5 , and left pFs: 37.3 ± 3 , -59.9 ± 9 , -14.6 ± 5) (STS=superior temporal sulcus, ITS=inferior temporal sulcus, OTS=occipital temporal sulcus, CoS=calcarine sulcus).

the relative contributions of the two hemispheres, a ratio of activated voxels (laterality index) was calculated for each individual subject (Golby et al., 2001; Hasson et al., 2003). We chose a 'regions of interest' approach, which is not suitable for random effects analysis for the reasons outlined by Saxe et al. (2006; for argument see Friston et al., 2006). The laterality index measured the relative contribution of activation in the left (LH) and right (RH) hemispheres in response to objects that repeated (matching task) or objects that were named. A weighted average of the number of voxels activated to intact objects in the right minus that in the left hemisphere was calculated for each subject in each task:

$$(RH - LH)/(RH + LH)$$

The laterality index ranged between 1 and -1 , where positive values meant more voxels activated in the right hemisphere and negative values meant more voxels activated in the left hemisphere (Golby et al., 2001; Hasson et al., 2003). We calculated the laterality index independently for each ROI and for each subject at five consecutive thresholds (range— $p < 10^{-13}$ to $p < 10^{-28}$). This range of thresholds was chosen as it produced the most consistent activation for all subjects in both tasks in both subdivisions of LOC. The criteria were that consecutive increases in the threshold would produce consecutive decreases in the number of voxels activated in each ROI and that subjects showed active voxels in each of the ROIs.

2.1. Picture matching followed by naming

Fig. 2 shows activation in LOC averaged across all subjects in response to intact objects when performing the matching task and when silently naming. It can be seen that for the matching task activation is predominantly localized to the right hemisphere. In contrast, the naming task produces more bilateral

activation, suggesting an increase in left hemisphere activation in response to naming compared to the more perceptual task of matching. These shifts in the lateralization of activation were quantified using the laterality index. In Fig. 3 the laterality indexes for each subject in each region are shown. It is clear that the majority of subjects show more voxels activated in the right hemisphere in response to the matching task (white points). When silently naming the same objects (black points), there was a relative increase in the number of activated voxels in the left hemisphere compared to the right hemisphere. To quantify this difference in the relative contributions of hemispheric activation in response to the two tasks, a repeated measures two-way ANOVA with the factors of Region (LO and pFs) and Task (matching, object naming) was performed. The dependent measure was the laterality index for each subject in each region. There was a main effect of Task, where the laterality index was more positive for the matching task and more negative for the naming task, $F(1,9)=25.5$, $p=.0007$. The fact that there was no main effect of Region or interaction between Region and Task indicates that there was no reliable difference between the two regions LO and pFs. Separate paired t-tests were performed on the laterality indexes for each region confirming that the matching task produced relatively more activation in the right hemisphere and object naming produced relatively more activation in the left hemisphere in LO ($t(1,9)=5.2$, $p=.0006$), and pFs ($t(1,9)=4.2$, $p=.0025$).

The effects of the matching and object naming tasks on fMRI % signal change were also assessed. For each scan, we extracted the fMRI response by averaging the data from all activated voxels within the pre-defined ROIs. We then averaged the signal time course across each condition (task and hemisphere) from each scan independently for each subject. A three-way repeated measures ANOVA was per-

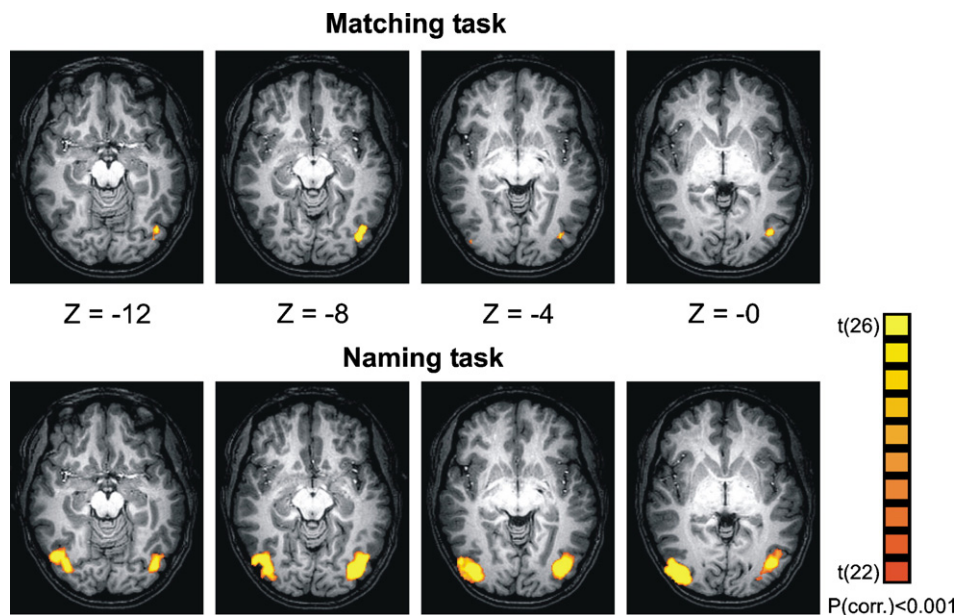


Fig. 2 – Activations for the matching and naming tasks averaged across all subjects. The orange areas represent regions showing greater activation for intact objects compared to scrambled objects in both the matching and naming tasks. Note that for the matching task, activation is predominantly localized to the right hemisphere and there is increased activation in the left hemisphere for the naming task relative to the matching task.

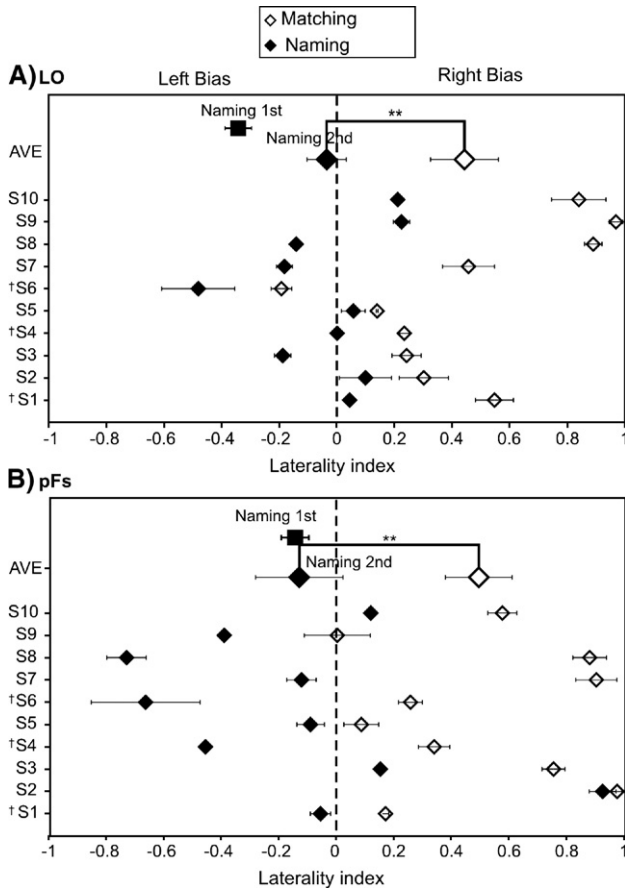


Fig. 3 – Individual laterality indices for matching and naming objects. The laterality index results were averaged across 5 thresholds (range— $p < 10^{-13}$ to $p < 10^{-28}$) for each subject in each region. (A) In LO, the majority of subjects show relatively more activated voxels in the right hemisphere in response to the matching task (white points). When naming the same objects (black points), there was a relative increase in the number of activated voxels in the left hemisphere relative to the right. (B) In pFs the majority of subjects shifted from predominantly right hemisphere activation in the matching task to more left hemisphere activation in the naming task. Also included are the average laterality index results for 5 subjects that performed the naming task before the matching task. In both LO and pFs, Naming First shows a left hemispheric bias in activation. Note: ** indicates $p < .01$ and bars denote \pm standard error and † denotes pilot subjects.

formed on the % signal change in each Region (LO, pFs), in each Hemisphere (right, left) and each Task (matching, object naming). There was a main effect of Task with higher fMRI responses to object naming compared to the matching task $F(1,9)=36.6, p=.0002$ (Fig. 4). There were no other statistically significant effects. However, from Fig. 4 one can see that in both LO and pFs the matching task produced more activation in the right hemisphere compared to the left hemisphere. This difference was supported statistically, $F(1,9)=5.4, p=.04$.

As a control experiment, we ran 6 subjects with the silent naming task first and the matching task second. The average

laterality index results for these subjects are plotted in Fig. 3. In LO (lateral occipital area), all six subjects showed more activation in the left hemisphere relative to the right with silent naming and in pFs (posterior fusiform area) five out of six subjects also showed more activation in the left hemisphere relative to the right. As expected subjects found it difficult to suppress the names of the objects in the matching task once they had been primed in the silent naming task. In LO, four out of five subjects showed more activation in the left hemisphere relative to the right. In pFs three out of five subjects also showed more activation in the left hemisphere compared to the right.

2.2. Category specific effects

To examine the effects of task demands on the lateralization of category-specific areas, we contrasted activations to the three object types in both tasks. Fig. 5 shows the number of voxels activated in each region and hemisphere as well as the proportion of those voxels displaying a preference for tools (blue), animals (red), or letters (green). It is evident that there was little category-specific activation in the lateral occipital complex as a whole. The majority of voxels in both hemispheres and both ROIs were activated equally for all object types. For those voxels that did show category-specificity, an asymmetrical pattern of activation can be discerned. The majority of voxels activated by tools were lateralized to the left and the majority of voxels activated by animals were lateralized to the right. The pattern was the same regardless of whether subjects performed the matching task or the object naming task. Fig. 6 plots the laterality index for each subject in the two regions that showed the majority of activated voxels for tools (pFs) and animals (LO). We did not analyze the category-specific activation in the other two regions (tools (LO) and animals (pFs)) as the data were less consistent across all subjects in these regions. Regardless of task, the majority of voxels activated by tools in pFs were lateralized to the left ($t < 1,$

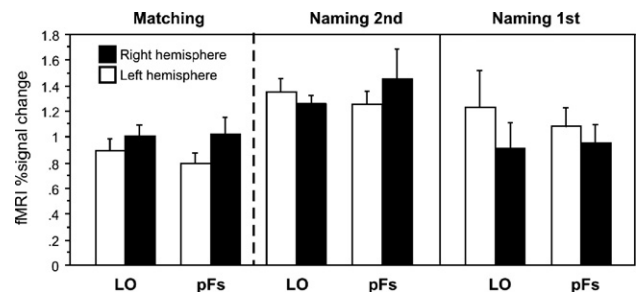


Fig. 4 – The percent signal change in the fMRI response for matching and naming objects in the right (black bars) and left hemispheres (white bars) in each subdivision of LOC. Across LO and pFs, there was more activation overall for silent naming. However, there was a small increase in right hemisphere activation when matching objects. Object naming showed no differences in the amount of signal change in either LO or pFs when naming was performed after the matching task. But when naming was performed first there was increased % signal change in the left compared to the right hemisphere ($F(1,4)=23.69, p=.01, 5$ subjects).

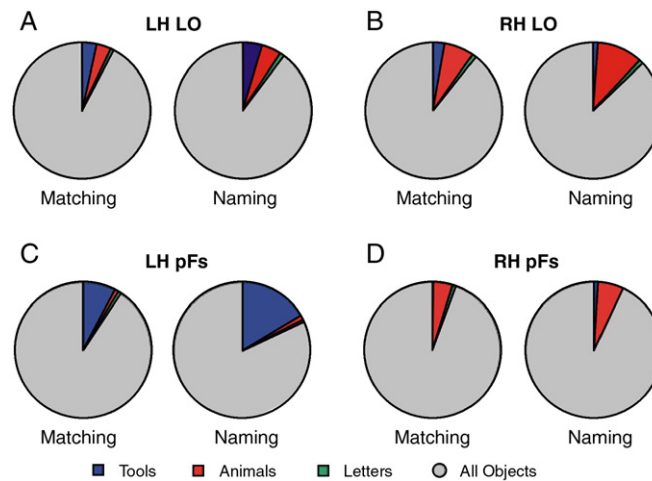


Fig. 5 – The percentage of voxels in each hemisphere in each subdivision of LOC which shows a preference for a specific category of objects in the matching and naming tasks. (A) Right hemisphere LO, (B) Left hemisphere LO, (C) Right hemisphere pFs, (D) Left hemisphere pFs. In each graph, the pie as a whole represents the total number of voxels in each ROI, and the colored pie pieces represent the number of voxels within each ROI that show a preference for a specific category of objects (Tools > Animals + Letters = blue, Animals > Tools + Letters = red, Letters > Tools + Animals = green). Overall the graphs indicate a consistent preference for animals (red) in the right hemisphere, particularly in LO, and a consistent preference for tools (blue) in the left hemisphere pFs region. Despite these trends, the vast majority of voxels in each ROI show no category specific preferences (grey regions).

Figs. 5C and D) and the majority of voxels activated by animals in LO were lateralized to the right ($t < 1$, Figs. 5A and B).

3. Discussion

Our findings suggest that LOC is sensitive to the top-down influences associated with task demands. When matching objects there was relatively more activation in the right hemisphere. In contrast, naming an object produced a relative increase in activation in the left hemisphere resulting in a more bilateral distribution of activation. This shift towards left hemisphere activation was most consistent in the anterior region of LOC, pFs. This suggests that there are task-related top-down influences on the activation of neural populations in LOC as a whole, but that the anterior ventral portion is more sensitive to the top-down effects of object naming. Interestingly, the leftward shift in activation produced by naming relative to matching did not impact the lateralization of category-specific areas suggesting that the localization of these areas is independent of task demands.

The increased extent of activation in left pFs in response to naming compared to matching supports previous findings that the left fusiform cortex is sensitive to semantic content and to object naming. In particular [Simons et al. \(2003\)](#) found that the left fusiform was more sensitive to the names of objects coupled with their pictures than the right fusiform. [Gerlach et al. \(2002\)](#) argued that increased activation in the left fusiform may be related to re-entrant processing from higher order areas that represent stored object knowledge (see also [Humphreys et al., 1997](#)). Naming an object involves

encoding the visual properties of the object and then accessing various stores of knowledge so that the object can be recognized (stored structural description and semantic description) and named (phonological description). Even though these different aspects of object naming give rise to activation in different cortical regions ([Price et al., 2005](#)), evidence from neuroimaging ([Damasio et al., 1996](#); [Chao et al., 1999](#); [Moore and Price, 1999b](#); [Okada et al., 2000](#); [van Turennout et al., 2003](#); [Tyler et al., 2004](#)) and neuropsychological studies ([Warrington and Shallice, 1984](#); [McCarthy and Warrington, 1988](#); [Iorio et al., 1992](#); [Humphreys et al., 1999](#); [Lambon Ralph et al., 2001](#)) suggests that these cortical regions function dynamically as an interconnected network.

Interestingly, we also found evidence that LO is sensitive to the effects of naming. Relative to the matching task, there was a shift in the laterality index towards the left. This contrasts to the findings of [Simons et al. \(2003\)](#) who found no sensitivity to their semantic manipulation in LO, and [Vuilleumier et al. \(2002\)](#) who found no difference in the fMRI response to real and nonsense objects in area LO. To our knowledge, there are no neuroimaging studies that have reported a lateralization of activation in the lateral occipital area in response to naming objects. The difference in findings could simply be related to differences in measurement. Unlike this study, previous neuroimaging studies that report lateralized effects in response to naming objects did not calculate the extent of activation.

Although the lateralization of activation clearly changed in LOC in response to silent naming, we did not see the same pattern in measures of the fMRI percentage signal change in our ROIs. This finding was unexpected as previous studies have found differences in the left fusiform for naming ([Moore](#)

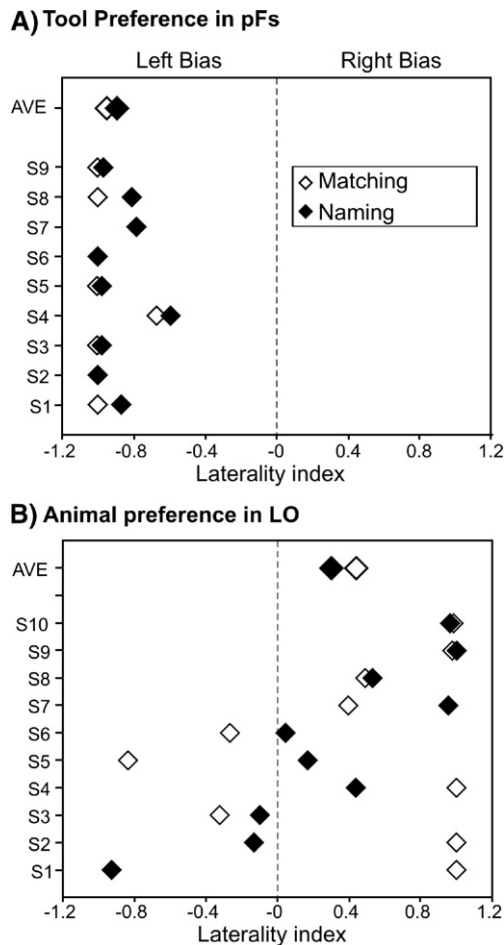


Fig. 6 – The effects of the matching and naming tasks on the lateralization of category-specific areas. (A) The ratio of voxels activated in the left and right hemisphere for each subject in response to the matching task (white points) and naming task (black points) in regions that showed a preference for tools (pFs). (B) The ratio of voxels activated in the left and right hemispheres for each subject in response to the matching and naming tasks in regions that showed a preference for animals (LO). Note that regardless of task, the majority of voxels activated by tools were lateralized to the left and the majority of voxels activated by animals were lateralized to the right.

and Price, 1999b; Smith et al., 2001; Tyler et al., 2004). It is possible that repeated exposure to the same objects ameliorated differences in the fMRI response between the left and right hemispheres, particularly for the naming task. The scans involving naming objects always occurred after the matching task scans to avoid priming a naming response during the task. This meant that in the naming task subjects had been exposed to the same images at least 12 times. In support of this argument, van Turrenot et al. (2000, 2003) reported that activity in occipitotemporal regions decreased as object naming became more efficient with repetition. They showed similar levels of activation in both hemispheres after more than one exposure. Indeed, we found that when subjects named the objects before the matching task, the fMRI

response was higher in both left LO and pFs compared to right LO and pFs.

In contrast to naming objects, the matching task produced a greater extent of activation in the right hemisphere in both subdivisions of LOC relative to the left hemisphere. The fMRI response was also higher in right LOC compared to left LOC in the matching task. Unlike naming, matching one object to a subsequent object does not require access to stored conceptual knowledge. Behavioral studies have shown that the right hemisphere is more sensitive to alterations in the visual form of stimuli and demonstrates superior shape processing (Marsolek, 1995, 1999; Koivisto and Revonsuo, 2003). Neuroimaging studies have found less fMRI adaptation in the right fusiform cortex compared to the left fusiform cortex for repeated presentations of different exemplars of the same object category than repeats of the same exemplar (Koutstaal et al., 2001; Simons et al., 2003). These results suggest that the right fusiform cortex is more sensitive than the left fusiform cortex to variations in the visual form. In addition, Vuilleumier et al. (2002) found that the right fusiform was more sensitive to changes in viewpoint than the left fusiform. The results of these studies and ours suggest that the right fusiform plays a greater role in processing specific visual form information about objects.

It is possible that repeated exposure to the objects in the matching task produced a reduction in the number of voxels activated in the right hemisphere relative to the left. It is fairly well established that repeating stimuli result in a decrease in the fMRI response (Grill-Spector and Malach, 2001; Henson, 2003; Ganel et al., 2006) and this may also reduce the number of active voxels. If this was the case, it would mean that the leftward shift measured by the laterality index for the naming task would be due to a decrease in the number of voxels activated in the right hemisphere rather than an increase in the number of voxels activated in the left hemisphere. While we cannot rule out this interpretation entirely, we think it is unlikely. A control experiment in which subjects did the silent naming task first also showed that there were relatively more active voxels in the left hemisphere compared to the right (see Fig. 3). We also found that fMRI response was higher in the left hemisphere compared to the right (see Fig. 4) when naming came first. These results would suggest that regardless of whether objects are repeatedly named or not, naming produces relatively more active voxels in the left hemisphere compared to the right in LOC.

If the asymmetries observed in this study are due to repetition effects, does this mean that what we are seeing is the product of bottom-up processing? There have been a number of mechanisms put forward to explain the reduction in the fMRI response produced by repeating stimuli, such as neural fatigue, neural sharpening, and neural facilitation (see Grill-Spector et al., 2006, for a review). But to our knowledge, there is no theory claiming that changes to the firing patterns of neurons induced by repetition are produced solely by feed-forward inputs. Furthermore, a purely 'bottom-up' explanation would have to account for the asymmetrical pattern of activations. There is no reason to expect that reductions in activation associated with repeated stimulus presentations in this experiment would occur asymmetrically across the left and right hemispheres, regardless of task (see Ganel

et al., 2006 on differences between adaptation and priming effects). Bottom-up stimulus repetition effects would also have to generate uneven modulations in the fMRI response resulting in a switch from levels of activation that produce more voxels in the right hemisphere for 3 blocks to activation levels that produce an increase in voxels in the left hemisphere for the final 3 blocks. It seems more logical to argue that if the effects we have observed in LOC are due to repetition, they are also driven by top-down processes associated with task demands.

The lateralization of category-specific regions within LO and pFs was unaffected by the tasks. The extent of activation for tools was greater in the left hemisphere for both the matching and naming tasks. The extent of activation for animals was greater in the right hemisphere for both matching and naming tasks. This would suggest that cortical regions showing a preference for a particular object type were not greatly affected by re-entrant processing from higher order areas. It is more likely that the category-specific regions identified in this study were activated by processes responding to fairly low-level structural properties that happened to be shared by a category of objects (e.g. structural complexity or curved versus straight lines). Indeed, a number of other studies have argued that category-related activity in the occipital and the temporal cortex is mediated by shared visual properties of objects rather than their semantic-relatedness (Whatmough et al., 2002; Mechelli et al., 2003; Price et al., 2003; Rogers et al., 2005). For example, Whatmough et al. (2002) presented pictures of tools and animals, some of which were familiar and some of which were unfamiliar. They found distinct category effects in temporal and occipital areas but these regions did not respond differentially to familiarity. Whatmough et al. (2002) concluded that category-specificity in this part of the brain was driven by structural descriptions of objects rather than the 'instantiation' of semantic representations. Also, in this study, we found that across both subdivisions of LOC the majority of activated voxels responded equally to all three object types and showed no specialization for a category of object. This finding is consistent with the argument that LOC holds distributed object representations (Haxby et al., 2001; O'Toole et al., 2005) and indicates that one should be cautious making claims about category-related activity in this region.

The discussion has focused on specific attributes of the two tasks, namely perceptual processing and language/semantic processing. While it is true that language processing provides the most obvious difference between the two tasks and finds the most support in the literature, these tasks do differ along other attributes as well. For example, the matching task is generally considered an easier task than naming. Might task difficulty explain the asymmetry in activation? A paper by Dräger et al. (2004) manipulated the difficulty of a word finding task and found that increased word finding difficulty did not produce increased activation in language-related areas and the lateralization of these areas remained constant (see also Dräger and Knecht, 2002). By this account, it is unlikely that task difficulty in general can account for the task asymmetries we have observed in this study. However, there are other differences such as motor control (key press v sub-vocalization) and decision-making processes (same picture v correct

name) which we accept may also have an influence over the lateralization of task demands as part of a feedback circuit involving LOC.

To conclude, previous studies have shown that the left ventral region LOC is more sensitive to object naming and semantic manipulations. The present study establishes that LOC as a whole is sensitive to task demands. We found a greater extent of activation (voxel count relatively higher) and higher level (greater fMRI response) of activation in right LOC for the matching task. For object naming, there was an increase in the number of voxels activated in the left, resulting in a more bilateral distribution of activation. Essentially, changing the task changed the lateralization of activation in LOC. Based on the literature, the most obvious explanation for this lateralization is that feedback from higher order areas makes left LOC more responsive to language/semantic and right LOC more responsive to perceptual processes such as the analysis of visual form information. In contrast, task demands did not influence the lateralization of activation for category-specific regions in LOC. We also found that the majority of voxels activated in LOC were not category-specific. This suggests that the small amount of category-specific activity found in LOC may be unrelated to the semantic associations of the category members and may be due to some uncontrolled for low-level visual properties.

4. Experimental procedures

4.1. Participants

Ten healthy right-handed volunteers (5 male, 5 female) participated in this study. All subjects gave written consent and all procedures were approved by the University of Western Ontario Ethics Review Board.

4.2. Functional MRI

Experiments were performed in a 4.0 T Varian Siemens whole-body imaging system. Functional data were collected using a navigator echo corrected T2*-weighted interleaved, two segment, optimized spiral imaging sequence. A 15.5×11.5 cm quadrature radio frequency surface coil placed at the occipital pole was used to improve the signal-to-noise ratio. Data from 3 subjects came from a pilot study with the following parameters: FOV=19.2×19.2 cm; in-plane pixel size 3×3 mm; TE=15 ms; volume acquisition time 2 s; FA=40°; 11 slices; slice thickness 5 mm. The slices were oriented approximately parallel to the calcarine sulcus and included MT+ and the adjacent LOC. Data from the remaining 7 subjects differed only in that we collected data from 17 coronal slices (5 mm thick). The orientation and number of slices were changed to optimize localizing LOC. Functional data were aligned to high resolution inversion prepared 3D T1*-weighted anatomical images of the brain collected immediately after the functional images using the same in-plane field of view. The parameters for the spiral sequence anatomicals were 96 slices, TE=3 ms, TR=50 ms, TI=1300 ms, in-plane pixel size=.75×.75 mm, slice thickness 1.25 mm.

4.3. Experimental protocol

Subjects viewed, through a mirror, images that were back-projected onto a screen. The screen extended 45° horizontally and 20° vertically. In all experiments, the subjects fixated centrally on a stationary dot. To identify object-sensitive brain areas, we presented our subjects with intact 2-D black and white line drawings of objects (animals, tools and letters) alternating with scrambled versions of the same images. Six functional scans were performed with 25 epochs per scan and each epoch was 12 s long. Twelve images were presented in each epoch at 1 s intervals. The 12 images were randomly selected from 16 possible images in each epoch. In one sequence of three scans, subjects performed a matching task where they pressed a response key whenever they saw two-identical images, either intact or scrambled, in a row. There were 3 repeat objects per epoch. In a second sequence of three scans, subjects silently named the same objects and passively viewed the scrambled objects. Similar to the matching task, there were 3 repeat objects per epoch. Subjects always performed the matching task scans before the object naming scan since naming objects produces a 'stroop-like' effect whereby once an object has been named it is difficult to suppress its name on subsequent viewing (Lachman et al., 1980; Bajo, 1988; Macizo and Bajo, 2004). This was corroborated by the results of a control experiment in which subjects performed the silent naming task first and the matching task second (see Results).

4.4. MT+ localizer

To identify brain areas that are sensitive to motion, the display alternated between moving or stationary vertical black bars (height=20°, total display width of 18 bars=40° individual bar width .2°, velocity=4°/s). The moving bars alternately moved from center screen to the edges (temporal movement) or from the edges to center screen (nasal movement). Four functional scans were performed with 18 epochs per scan. Each epoch was 16s long.

4.5. Image analysis and regions of interest (ROIs)

Analysis was carried out using the Brainvoyager 4.9 software. 3D statistical maps were calculated for each subject based on a general linear model. MT+ was defined as a set of contiguous voxels that showed significantly stronger activation ($p < 10^{-4}$) to moving versus stationary bars. LOC was defined as a set of contiguous voxels which showed significantly stronger activation ($p < 10^{-4}$) to intact versus scrambled objects. The thresholds for the ROIs were also corrected for multiple comparisons ($p < .0001$ for LOC and MT+). The analysis of the fMRI response was performed on two subdivisions of LOC, namely LO and pFs, as illustrated in Fig. 1. Category-specific regions were defined functionally as a set of contiguous voxels with significantly stronger activation ($p < 10^{-4}$) using the following contrasts: Animals>Letters+Tools, Letters>Tools+Animals, and Tools>Letters+Animals. Each region of interest was calculated independently for each subject.

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