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Category-related activation for written words in the posterior fusiform is task specific

Joseph T. Devlin¹, Matthew F. S. Rushworth^{1,2}, and Paul M. Matthews¹

¹Centre for Functional Magnetic Resonance Imaging of the Brain, Department of Clinical Neurology, University of Oxford, U. K.

²Department of Experimental Psychology, University of Oxford, U.K.

Abstract

Category-related brain activations have been reported in the posterior fusiform gyri when people view pictures of tools and animals, but only a single study has observed this pattern when the stimuli were words, rather than pictures. Here we replicate these category effects with words and provide evidence that distinctive patterns of activation are task-specific. The results suggest that category-related activation in the posterior fusiform gyri can be driven either “bottom-up” by visual processing of images or “top-down” by word processing.

Keywords

category-specificity; written words; visual form processing; posterior fusiform gyri; fMRI

Introduction

Certain categories of objects elicit specific patterns of brain activity. Relative to natural objects such as animals and fruit, tools evoke activations in the posterior middle temporal gyrus, an anterior intraparietal region, and the ventral premotor cortex within the left hemisphere (Chao & Martin, 2000; Devlin et al., 2002; Gerlach, Law, & Paulson, 2002). The opposite contrast shows activation in the anterior medial temporal poles, bilaterally (Devlin et al., 2002; Mummery, Patterson, Hodges, & Wise, 1996; Mummery, Patterson, Hodges, & Price, 1998). These activation patterns are independent of the modality of the input, with pictures or words yielding essentially the same results. Moreover, the anatomic distribution of activations is largely consistent with lesion locations in patients with so-called category-specific semantic deficits. Preferential impairments for man-made objects are often associated with large left fronto-parietal infarcts while deficits for natural objects are typically associated with the bilateral anterior temporal lesions of herpes simplex encephalitis (Gainotti, 2000). Category-related activations for both tools and animals also have been reported in the posterior fusiform gyri (Chao, Haxby, & Martin, 1999), a region not typically associated with semantic deficits in neurological patients.

Chao *et al.* (1999) found that pictures of tools activated the medial bank of the posterior fusiform gyrus, bilaterally while pictures of animals activated a more lateral region on the convexity of the gyrus. Similar patterns also were found in 6 out of 8 subjects when the stimuli were written words. Several studies have since replicated these category-related

activations for pictures, but not for words (Chao, Weisberg, & Martin, 2002; Price, Noppeney, Phillips, & Devlin, 2003; Whatmough, Chertkow, Murtha, & Hanratty, 2002). For example, Price *et al.* (2003) found that for picture naming, word-picture matching, and semantic attribute decisions on pictures there was activation for animals and fruit relative to man-made objects in lateral posterior fusiform areas. In contrast, when the stimuli were written words rather than pictures, the activation was not present – in fact, there was less activation for animals than tools in these areas. The authors argued that the posterior fusiform gyri may be primarily engaged by visual form processing and thus the category effects may simply reflect the well known structural differences between natural and man-made categories which are present in images but not written words (Humphreys, Riddoch, & Quinlan, 1988). On the other hand, if a task requires detailed semantic elaboration, then it is possible that category-related activity may still be present in the posterior fusiform even for written word stimuli due to recurrent efferents from higher order association cortices. In other words, category-related activation in the posterior fusiform gyri may be driven either “bottom-up” by visual processing of images or “top-down” based on word processing.

In order to test this hypothesis, we used a 2×2 factorial design which crossed stimulus category (man-made versus natural) with task (semantic versus perceptual decisions). For both tasks, a word appeared in the centre of the screen below a horizontal reference line (see Figure 1). In the semantic task, participants decided whether the word referred to a man-made or natural item. This required instantiating a sufficiently detailed semantic representation in order to classify the item correctly, which presumably includes information about the item's physical properties, its functions (biological or otherwise), as well as any other associated information (Devlin, Gonnerman, Andersen, & Seidenberg, 1998; Moss, Tyler, Durrant-Peatfield, & Bunn, 1998; Rapp & Caramazza, 1993; Rips, Shoben, & Smith, 1973). Indeed, physical attributes such as form, colour, and shape play a prominent role in the semantic representations of concrete objects such as those used in the present study (Warrington, 1975; Warrington & Shallice, 1984). So while it is not necessary to visualize the referent in order to perform the semantic judgement task, generating an internal conceptual representation will presumably engage a diverse network of cortical regions involved in processing semantic information. In contrast, the baseline condition in this experiment was a perceptual task in which participants judged whether the written word was longer or shorter than the reference line. In this case, the task could be performed solely on the basis of the visual information present in the stimulus and did not require access to internally generated representations. Consequently, we expected category-specific activations in the posterior fusiform gyri during the semantic, but not the perceptual, task, i.e. we predicted a Task $\times$ Category interaction.

Method

Twelve adults (6F, 6M) aged 21 to 33 participated in the experiment. All were right handed, native English speakers with no personal or family history of epilepsy or any other neurological condition. Each gave written informed consent after the experimental methodology was explained. The experiments were approved by the Local Research Ethics Committee.

There were 50 trials of each task. Half of the words referred to man-made items (e.g. “axe”, “canoe”, “pillow”) while half were natural items (e.g. “apple”, “cat”, “rain”). All of the stimuli were highly familiar, concrete nouns matched across category for rated familiarity (mean for man-made vs. natural: 530 vs. 530, $t_{45} < 1.0$), written frequency (18 vs. 25, $t_{41} < 1.0$), number of letters (5.3 vs. 5.5, $t_{48} < 1.0$), and number of syllables (1.6 vs. 1.7, $t_{48} < 1.0$) (Coltheart, 1981). There was a trend for man-made items to be rated as less concrete than natural items (592 vs. 606, $t_{36} = 2.0$, $p = 0.06$). The same stimuli were used in

both tasks so that any differences between tasks could be unambiguously associated with the tasks rather than the stimuli. To avoid biasing the result with repetition priming effects, stimulus repetitions were counterbalanced across tasks. On average, word repetitions were separated by 105s.

In the scanner, a mixed block and event-related design was used. Tasks were blocked in an ACBC fashion with semantic (A) and perceptual (B) decisions separated by 13 seconds of rest (C). Stimuli were presented for 500ms with 2700ms of blank screen between trials for an inter-trial interval of 3.2s. Stimuli were presented out of phase with data acquisition to ensure an unbiased sampling of the haemodynamic response (Price, Veltman, Ashburner, Josephs, & Friston, 1999). Within each of the task blocks, 10 trials were presented and the items were pseudorandomly ordered. During the session 150 T2*-weighted images were collected. An additional 4 dummy volumes were collected at the start of the session to allow for T1 equilibrium before the test trials began. In total, the scanning session lasted 7.5 minutes. The data from this experiment form a subset of a study of task differences reported previously (Devlin, Matthews, & Rushworth, 2003).

Scanning was carried out using the Varian-Siemens 3 Tesla MRI scanner at the Functional Magnetic Resonance Imaging of the Brain (fMRI) Centre in Oxford. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage head radio-frequency coil tuned to 127.4 MHz. A gradient-echo EPI sequence was used for image collection (TR 3s, TE 30ms, 64 × 64 resolution, 256mm × 256mm FOV). 25 slices were employed to cover the brain with 5mm slice thickness and in-plane resolution of 4mm. An automated shimming algorithm was used to reduce magnetic field inhomogeneities (Wilson et al., 2002) and a TE of 30ms jointly optimized BOLD contrast-to-noise and image signal-to-noise while minimizing intra-voxel de-phasing.

Functional images were realigned (Friston et al., 1995) to correct for small head movements using the Statistical Parametric Mapping software (SPM99, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk/spm99). Translation and rotation corrections did not exceed 2.3mm and 2.5°, respectively for any of the participants. The mean image created by the realignment procedure was used to determine the parameters for transforming the images onto the MNI mean brain. The normalization parameters were then applied to the functional images (Ashburner & Friston, 1997; Ashburner, Neelin, Collins, Evans, & Friston, 1997). Finally, each image was smoothed with a 5mm at full-width half-maximum (FWHM) Gaussian filter. The SPM software was used to compute a random-effects analysis using the general linear model. Trials were modelled as events and the stimulus train was convolved with a “canonical” HRF (Friston et al. 1994; Glover 1999) which was used in all subsequent linear contrasts. Temporal derivatives were included to better fit regional deviations in timing and thus reduce unmodelled variance; they were not used in any contrasts. The interaction between Task and Category was computed by contrasting Natural > Man-made for the semantic task with Man-made > Natural in the perceptual task. Because the interaction is two-tailed, the regional BOLD response in each condition was plotted to determine the direction of the interaction. All analyses were limited to the posterior fusiform gyri bilaterally using four *a priori* regions-of-interest (ROIs) based on previously published findings. Chao *et al.* (2002) reported activation for Animals > Tools at -38 -58 -10 and +36 -58 -10 while the reverse contrast revealed activation at -25 -57 -7 and +22 -57 -5. Each of these coordinates served as the centre of a spherical volume with a 10mm radius which was used to restrict the search space. Given the specificity of the search space, the statistical threshold was set to $p < 0.05$, uncorrected.

Results

Behavioural data from one subject was not collected due to a hardware failure. The remaining data are summarized in Table 1. A 2×2 ANOVA with independent factors of Task (semantic, perceptual) and Category (man-made, natural) revealed a main effect of Task on reaction times (RTs) indicating that participants were significantly faster with perceptual than semantics decisions ($F_{1,10}=22.2$, $p=0.001$). There was no main effect of category ($F_{1,10}<1$) nor a significant interaction ($F_{1,10}=1.5$, n.s.). There were no significant main effects nor interactions in the accuracy data (all $F<1.3$, n.s.).

In the functional imaging data, the interaction between Task and Category produced a pattern of activation in the posterior fusiform gyri similar to that observed previously for pictures of tools and animals. This is illustrated in Figure 2 and the details are presented in Table 2. Orange indicates regions where words for natural objects were more active than words for man-made items in the semantic task, and this effect was significantly larger than the same contrast in the perceptual task. Note that this pattern was only observed in the left lateral fusiform gyrus. In the right lateral fusiform, there was no interaction between Task and Category, but there was a main effect of Natural > Man-made (shown in white). Blue indicates regions where words for man-made items produced greater activity than words for natural objects for the semantic task and this effect was significantly larger than the man-made – natural contrast in the perceptual task. In fact, there was also an increase in BOLD signal for natural items during the perceptual task which contributed to the overall interaction in the medial fusiform regions bilaterally. Even so, the pattern of results in the semantic task matched those seen in previous studies, namely a medial advantage for man-made relative to natural items and the opposite pattern more laterally. For each fusiform region, the bar plots indicate the mean contrast of BOLD signal per region illustrating the interaction (in three cases) and the main effect (in one case).

Discussion

Previous studies have found category-related activations in the posterior fusiform gyri for pictures of tools and animals (Chao et al., 1999; Chao et al., 2002; Price et al., 2003; Whatmough et al., 2002), although only a single study has observed this pattern when the stimuli were words, rather than pictures (Chao et al., 1999). The results of the current study are the first replication of the category effect with words. In addition, our results demonstrate that this pattern of activation is task-specific, at least when the stimuli are written words.

A potential criticism of this work is that due to the low statistical threshold used to identify the effects of interest, the fusiform activations may simply be false positives (Type I errors). For this to be true would require random fluctuations in the Z-field to be i) located in the specific region-of-interest, namely the posterior fusiform gyri, with ii) a medial-to-lateral change in sign that was iii) bilaterally symmetric across hemispheres and iv) corresponded to the pattern seen in several previous studies (Chao et al., 1999; Chao et al., 2002; Price et al., 2003; Whatmough et al., 2002). Although this possibility cannot be entirely ruled out, we consider the combination of factors necessary to produce these results unlikely to occur by chance. The same cannot be said for the areas of activation in Figure 2 outside of the ROIs, however, and these are indeed likely to be Type I errors. As a consequence, we do not consider these activations further.

The semantic categorisation task used here evoked a pattern of category-related activity in the posterior fusiform gyri using words rather than pictures as input. But what aspect of our semantic task engaged the fusiform gyri? One proposal is that semantic representations are

stored in occipito-temporal regions and that access to these representations will lead to category-related activity in this region (Chao et al., 1999; Chao et al., 2002; Martin & Chao, 2001). The main reason to question this interpretation, however, is that not all semantic tasks produce this pattern of activation. Neither semantic attribute decisions (e.g. “Is it larger than a kiwi”) nor a category fluency task (“Name all the land animals you can in 20 seconds”) yielded category-related activity in the posterior fusiform gyri, although both tasks evoked category-related activation in other brain regions (Mummary et al., 1996; Mummary et al., 1998; Phillips, Noppeney, Humphreys, & Price, 2002). If semantic representations are stored in posterior fusiform regions, why do some studies find category effects here while others do not? And why are these effects most prominent for pictures but not for words? One possibility is that these effects may be specific to the categories of animals and tools given that several studies using fruit and tools, for instance, did not report similar effects (Mummary et al., 1996; Mummary et al., 1998; Phillips et al., 2002). Price *et al.* (2003), however, showed that pictures of fruit activated the same lateral posterior fusiform areas as pictures of animals relative to tools. Similarly, the current study found that words referring to fruit and vegetables (as well as other items occurring in nature) activated the same region relative to man-made items. These results suggest that although category-related activation in the posterior fusiform may be strongest when contrasting animals and tools, they are not limited to these categories. Another possibility is that pictures may lead to larger effects than words and thus the lack of activation for words may be due to insufficient statistical sensitivity. Although pictures may generate larger rCBF and BOLD signals than words in this region, Price et al. (2003) showed that activation for words in the posterior fusiform regions was not simply reduced relative to pictures, but was in the opposite direction. Thus, neither the stimulus categories nor statistical sensitivity can account for different activation patterns seen across studies.

A related hypothesis suggests that that category-related posterior fusiform activations may be due to structural, rather than semantic, processing. Whatmough et al. (2002) found that the pattern of posterior fusiform activation was not affected by the familiarity of the items. Instead, the effects of familiarity were localized to higher order association areas. Because familiarity was deemed to be a semantic variable, the authors argued that the posterior fusiform activations must be due to pre-semantic (i.e. structural description) processing. This is broadly consistent with results from several visual agnosia patients with occipito-temporal lesions presumably affecting their posterior fusiform gyri (Arguin, Bub, & Dudgeon, 1996; Etcoff, Freeman, & Cave, 1991; Humphreys, Riddoch, & Price, 1997). These patients were impaired in their ability to recognise or classify visual objects but their semantic knowledge of these same items was relatively spared.

By this account, the posterior fusiform gyri process visual form information, which is a subset of a concept's overall semantic representation. Information from both low-level sensory cortices and higher order association regions is used to generate a transient representation in a pattern of neural activity (Arbib & Erdi, 2000; Rumelhart, Smolensky, McClelland, & Hinton, 1986). Thus category-related activation will occur whenever a task involves instantiating information about an object's visual form. This is an integral part of visual object recognition (i.e. processing pictures), but is not required when processing written or auditory words except under special circumstances. Thus it is not surprising that visual imagery tasks, for example, evoke category-related activation in posterior fusiform areas (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999) but it is less clear why only some semantic tasks evoke this pattern. Tasks which focus attention on the overall meaning of a concept rather than a particular attribute may automatically evoke structural form information as part of the larger conceptual representation while attending to a specific attribute such as size, colour, or function may not. Further studies which manipulate the type of semantic processing to written word stimuli are necessary to evaluate this hypothesis. In

addition, new connectivity analysis techniques such as dynamic causal modelling provide the potential to demonstrate whether category-related activations in the posterior fusiform are driven by bottom-up activation for pictures (Mechelli, Price, Noppeney, & Friston, 2003), but top-down processing for words.

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Figure 1.

An illustration of the behavioural tasks. A trial began when a word appeared immediately below a reference line in the centre of the screen for 500 msec. In the semantic task, participants pressed one of two buttons to indicate whether it referred to a man-made or natural object. In the perceptual task, they pressed a button to indicate if the line was longer than the word.

Figure 2.

Category-related activations in the posterior fusiform gyri (arrows). The Category $\times$ Task interactions are shown on a coronal and axial planes through a canonical brain in standard space with the cerebellum removed. Blue regions indicate areas where advantage for man-made items over natural objects was greater in the semantic than perceptual task. Orange areas show areas where advantage for natural objects over man-made items was greater in the semantic than perceptual task. The white region indicates the location of a main effect of natural > man-made in the right lateral posterior fusiform. Below, the mean contrast of BOLD signal is plotted for the semantic (black bars) and perceptual tasks (grey bars) across the four ROIs to illustrate the interactions and main effect.

Table 1

Behavioural results.

	Man-made Objects	Natural Objects
Semantic	815 $\pm$ 54	799 $\pm$ 44
	97.1 $\pm$ 1.1%	96.0 $\pm$ 1.0%
Perceptual	658 $\pm$ 49	691 $\pm$ 57
	96.7 $\pm$ 1.7%	96.0 $\pm$ 1.2%

The top value in each cell is the mean reaction time ($\pm$ SEM) in msec while the bottom value is the percent correct.

Table 2

Imaging results in the posterior fusiform gyri.

	Left posterior fusiform			Right posterior fusiform		
	x	y	z	x	y	z
<i>Interaction</i>						
Man-made > natural for Sem. > Perc. tasks	-24	-54	-10	1.8	+30	-52
						-10
						2.5
Natural > man-made for Sem. > Perc. tasks	-36	-56	-12	3.2		
<i>Simple main effects</i>						
Man-made > natural				+26	-56	-10
						2.2
Natural > man-made	-36	-52	-18	2.4	+36	-66
						-14
						2.8

The simple main effects are only based on the semantic task.