Note

Negative priming in naming of categorically related objects: An fMRI study

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Abstract

Ignoring an object slows subsequent naming responses to it, a phenomenon known as negative priming (NP). A central issue in NP research concerns the level of representation at which the effect occurs. As object naming is typically considered to involve access to abstract semantic representations, Tipper (1985) proposed that the NP effect occurred at this level of processing, and other researchers supported this proposal by demonstrating a similar result with categorically related objects (e.g., Allport et al., 1985; Murray, 1995), an effect referred to as semantic NP. However, objects within categories share more physical or structural features than objects from different categories. Consequently, the NP effect observed with categorically related objects might occur at a structural rather than semantic level of representation. We used event related fMRI interleaving overt object naming and image acquisition to demonstrate for the first time that the semantic NP effect activates the left posterior-mid fusiform and insular–opercular cortices. Moreover, both naming latencies and left posterior-mid fusiform cortex responses were influenced by the structural similarity of prime–probe object pairings in the categorically related condition, increasing with the number of shared features. None of the cerebral regions activated in a previous fMRI study of the identity NP effect (de Zubicaray et al., 2006) showed similar activation during semantic NP, including the left anterolateral temporal cortex, a region considered critical for semantic processing. The results suggest that the identity and semantic NP effects differ with respect to their neural mechanisms, and the label "semantic NP" might be a misnomer. We conclude that the effect is most likely the result of competition between structurally similar category exemplars that determines the efficiency of object name retrieval.

1. Introduction

The aim of this study is to further explore whether the phenomenon of negative priming (NP) in object naming involves access to semantic representations. The original NP paradigm introduced by Tipper (1985) involved presenting an object as a distractor to be ignored on a prime trial, then presenting it as a target to be named on a subsequent probe trial. Prime–probe pairs that did not involve repeated or related objects served as experimental controls. Naming responses to the previously ignored objects were slowed compared to unrelated objects. Later, the effect was referred to as identity NP, due to the repetition of objects as both distractors and targets (Fox, 1995). Analogous NP effects have since been demonstrated across a wide range of experimental tasks and stimuli (e.g., location NP; for reviews, see Fox, 1995; May et al., 1995).
A central issue in negative priming research concerns the level of representation at which the effect occurs. Nearly all models of object naming assume perceptual, semantic, syntactic, phonological and articulatory processing stages (see Humphreys and Forde, 2001). In order to explain the classic NP effect, Tipper (1985) (also Tipper and Driver, 1988) proposed ignored objects access their abstract semantic representations. According to Tipper, these representations are subjected to an inhibitory attentional mechanism, slowing subsequent responses to them (see also Houghton and Tipper, 1994). To support this interpretation, Tipper (1985) (Experiment 3) demonstrated slower naming responses to targets that were categorically related to ignored objects (e.g., presentation of a picture of a cat as a distractor on a prime trial, compared to ignoring an unrelated prime such as a trumpet). This finding was replicated by several studies (e.g., Allport et al., 1985, Experiments 4 and 5; Murray, 1995; although see Damian, 2000), and has since been referred to as conceptual or semantic NP (Fox, 1995). Typically, the semantic NP effect is slightly smaller (~30 msec) than the identity NP effect (~50 msec) (e.g., Allport et al., 1985, Experiment 5; Tipper, 1985, Experiment 3).

The use of categorically related distractors was for some time considered as an important means of testing the hypothesis that identity NP operates at a semantic level of representation (Fox, 1995). However, objects within categories share more physical or structural features than objects from different categories (e.g., Cree and McRae, 2003; Gale and Laws, 2006; Shapiro and Olson, 2005). Consequently, the NP effect observed with categorically related objects could have been located at a structural (or featural) rather than semantic level of representation. After a decade of NP research, two separate reviews of the empirical data arrived at opposing conclusions about a semantic locus for the effect: May et al. (1995) concluded in favour of a semantic locus “rather than... a specific perceptual, featural” (p. 40) level, while Fox (1995) considered it to be “far from well established” (p. 155). Excepting Damian (2000), behavioural researchers have not addressed the issue for a decade, perhaps due to the complexity of the processes associated with object recognition and naming.

Recently, we investigated whether the classic identity NP task involved semantic access using event related functional magnetic resonance imaging (fMRI; de Zubicaray et al., 2006). Given converging evidence from computational modelling, lesion and neuroimaging studies supporting a role for the anterolateral temporal cortex (ATC) in representing abstract semantic information, we hypothesised that this region would be involved in the classic NP effect, if it involved semantic access as Tipper (1985) originally proposed. For example, lesions and neurodegenerative disorders affecting the ATC produce a profound impairment of semantic knowledge (Gainotti, 2000; Lambon Ralph et al., 2001; Mummery et al., 2000). Neuroimaging studies have demonstrated left-lateralised activation in this region consistently during object naming (see Price et al., 2005) and during a range of tasks requiring semantic access, including abstract word reading (Sabsevitz et al., 2005), synonym judgements on abstract concepts (Noppeney and Price, 2004), and narrative speech comprehension (Crinion et al., 2003). As the ATC receives multiple inputs from modality-specific sensory cortices, Rogers et al. (2004) therefore considered it as a candidate region for encoding amodal semantic representations in their connectionist model. Our fMRI data showed increased left ATC activation that was positively correlated with the magnitude of each subject’s identity NP effect, a finding that we interpreted as being consistent with a semantic locus (de Zubicaray et al., 2006).

In this study, we investigate whether the NP effect observed in object naming with categorically related distractors also involves access to abstract semantic representations (Allport et al., 1985; Murray, 1995; Tipper, 1985), or occurs at a more peripheral structural/perceptual processing level. Structural similarity effects in object recognition were among the first phenomena to be studied with functional neuroimaging. These studies revealed reliable activation in the fusiform gyrus, particularly during naming tasks (see Joseph, 2001, for a meta-analysis and review of the early literature). While considerable effort was devoted initially for investigating putative category-specific effects in this region, more recent work has emphasised the role of a more widely distributed conceptual system not organised by category (for a review, see Gerlach, 2007). Studies on repetition priming – a form of positive priming in which responses to repeated objects are facilitated – have typically shown reduced fusiform cortex responses. These studies also reported reduced fusiform responses to perceptually different exemplars of previously presented objects, albeit inconsistently (e.g., Eddy et al., 2007; Koutstaal et al., 2001; Simons et al., 2003; Vuilleumier et al., 2002, 2005). Investigations with classification/categorisation tasks have shown that posterior-mid fusiform cortex in particular appears to be engaged by structural overlap or visual competition between exemplars within categories (e.g., according to their shape configuration, Gerlach et al., 2006; Joseph and Gather, 2003; Rogers et al., 2005). More recently, using positron emission tomography (PET) Rogers et al. (2006) have shown that fusiform cortex is activated when discriminating objects at the intermediate level (e.g., for the general category of “vehicles”, between a CAR and BUS), whereas lateral ATC is activated when discriminating objects at a relatively specific level (e.g., between various makes of cars) where conceptual knowledge is of greater assistance.

Consequently, if negative priming with categorically related objects involves access to semantic representations (Allport et al., 1985; Tipper, 1985), fMRI should reveal activation in the left ATC consistent with the results of our previous identity NP study (de Zubicaray et al., 2006). If it depends instead on the structural similarity of the categorically related objects, then this process should engage the fusiform cortex. Additionally, a more general question that this experiment addresses is whether the neural mechanisms responsible for NP are comparable across the two tasks, irrespective of the locus of the

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1 The focus of the present study is the level of representation at which NP occurs in object naming. Whether NP involves the operation of inhibitory attentional or other episodic retrieval mechanisms has been discussed elsewhere in detail (see reviews by Fox, 1995; May et al., 1995 and Tipper, 2001) and is not the focus of the present study.

2 Distractors are in italics while targets are in capitals.
effect. This was accomplished using a sparse fMRI experimental design that interleaved image acquisition and behavioural trial presentation (for an overview, see Gracco et al., 2005).

2. Methods

2.1. Participants

Fifteen healthy adults (five female, mean age 24 years, SD = 5.2) participated in the study. All were right-handed and native speakers of English with normal colour vision and normal or corrected-to-normal visual acuity. All gave informed consent in writing and were compensated for participating. The experimental protocol was conducted with the approval of the University of Queensland’s Medical Research Ethics Committee.

2.2. Materials

Like the classic identity NP task, the semantic NP task involves superimposed pictorial stimuli presented in two conditions: one in which ignored and named objects are categorically related (semantic ignored) and other involving unrelated objects (control) (Allport et al., 1985; Tipper, 1985).

Stimuli were 25 line drawings of common objects selected from the Snodgrass and Vanderwart (1980) corpus. Although previous studies designated their categories and exemplars on an intuitive or ad hoc basis (e.g., Allport et al., 1985; Damian, 2000; Murray, 1995; Tipper, 1985), we selected objects equally from five categories (vehicles, fruit, musical instruments, clothing and animals) according to the empirically derived norms provided by Cree and McRae (2003) (provided in Appendix). Prime and probe displays comprised two superimposed pictures: the target (red) and distractor (green). Within prime displays, each target was unrelated to the ignored distractor. This was also the case within the probe displays. For the semantic ignored condition, the ignored distractors in the prime display were categorically related to the following probe target, whereas in the control condition they were unrelated. The average associative strength from target to distractor objects in the semantic ignored condition was .08 according to the Nelson et al. (2004) word association norms (distractor to target strength .07). Structural feature similarity ratings for the distractor–target object pairings were derived from the semantic feature production norms provided by McRae et al. (2005), using the visual-form and surface property label from their brain region taxonomy (range 0–4 shared features). Distractor–target object pairings were not repeated within the two conditions, while identical target pictures were used across conditions, requiring the same naming responses. A pattern mask was also created by superimposing fragments of several pictures.

2.3. Apparatus

Stimuli were presented by a PC that also recorded the naming responses digitally (sampling rate 11 kHz). Stimuli were enlarged and back-projected onto the centre of a luminous white screen that the participants viewed through a mirror mounted on the head coil, and subtended approximately 10° of visual arc when each participant was positioned for imaging. Naming responses in both conditions were recorded using a custom positioned MR-compatible microphone. Naming latencies to probe trials were measured using conventional voice-key software, while the filtered audio files were referred to for scoring of responses.

2.4. Procedure

Prior to positioning in the scanner, participants were familiarised with the set of experimental pictures by viewing them separately on a computer screen in random order, with the appropriate name printed beneath. The dimensions of the pictures including background were approximately 10 cm wide by 10 cm high. A practice block of 25 trials in which each target picture was paired with an unrelated distractor was then presented, with instructions to name the red picture as fast and as accurately as possible while attempting to ignore the green picture. Any errors were corrected by the experimenter.

Following positioning in the scanner (a procedure lasting several minutes), the experimental block consisting of 50 trial pairs in each of the two conditions, semantic ignored (25, in which prime distractor and probe target objects were categorically related) and control (25, in which prime distractor and probe target objects were unrelated), was administered during scanning according to the following sequence: a crosshair was presented first for 500 msec, followed by an identical blank period, then superimposed prime target/distractor pictures were presented for 500 msec eliciting a naming response. Following this, a pattern mask was presented for 250 msec, after which a blank interval of 1000 msec was inserted. Probe target/distractor pictures were then presented in an identical manner. A further blank interval of 11 sec then ensued, in which a single image volume was acquired, resulting in a total trial duration of 16 sec (see Fig. 1). Following Damian (2000), trial pairs were presented in pseudorandom order such that targets on adjacent trials did not share the same picture name.

2.5. fMRI data acquisition

For each participant, a single time series of 52 whole brain images were acquired with an optimised gradient echo, echoplanar imaging (EPI) sequence (36 axial 3.5 mm slices with 1 mm gap, 3.6 mm² voxels; TR 3 sec; TE 30 msec; flip angle 60°; McMahon et al., 2004) on a 4.0 T Bruker Medspec system equipped with a transverse electromagnetic (TEM) head coil (Vaughan et al., 2002). A point-spread function (PSF) mapping sequence was acquired prior to the EPI acquisitions to correct geometric distortions in the time series data (Zeng and Constable, 2002). Naming trials were interleaved with image acquisition to capture the estimated peak blood oxygen level dependent (BOLD) signal response to task-related neural activity and permit overt responses within the scanner without affecting the image quality (Gracco et al., 2005). For each trial, no field gradients were applied allowing for prime and probe stimuli to be presented and the participant’s response, then applied for image acquisition 4 sec after presentation of the probe. A single whole brain image was then acquired within a TR of 3 sec, coincident with the probe trial’s estimated
peak BOLD response. Head movement was limited by foam padding within the head coil. In the same session, a magnetisation prepared rapid acquisition gradient echo sequence was used to acquire a high-resolution 3D T1-weighted image (MPRAGE; 256^3 matrix; .9 mm^3 voxels).

2.6. Image analysis

The first two volumes from the fMRI time series were discarded, and the remaining images’ motion corrected using INRIAlign (Freire et al., 2002). A mean image was generated from the realigned and the realigned data series were regrouped such that the images from each condition were treated as a single epoch and trials meeting exclusion criteria removed (see Section 3.1). The resulting images were analysed using statistical parametric mapping software (SPM2; Wellcome Department of Imaging Neuroscience, Queen Square, London, UK). The mean image from each participant was spatially normalised to the SPM2 EPI template image in MNI atlas space, and the non-linear transformations were applied to the realigned and regrouped time series images. Normalised volumes were then resampled to 3 mm^3 voxels and smoothed with an isotropic Gaussian kernel (full width half maximum = 9 mm). Statistical analyses were conducted in two stages of a mixed effects model. Two epoch types corresponding to the experimental conditions were modelled as effects of interest with delta functions representing each epoch onset, and convolved with a basis function consisting of a single finite impulse response (FIR) encompassing the epoch length. High- and low-pass filtering were not applied, due to the rearranging of the time series data and use of long TR (see de Zubicaray et al., 2006). Linear contrasts were applied to each participant’s parameter estimates at the fixed effects level then entered in a group level t-test in a second-stage random effects analysis. Resulting t-values were transformed into corresponding Z-scores.

To assess our hypotheses, we adopted a sensitive region of interest (ROI) approach. This involved defining separate anatomical ROIs for the left and right anterior temporal and fusiform cortices within MNI atlas space using automated anatomical labelling and wfu_pickatlas software (Maldjian et al., 2003; Tzourio-Mazoyer et al., 2002). The ATC ROIs were edited manually according to the anterior y coordinate-based subdivision of the temporal cortex specified by Indefrey and Levelt (2004) (see de Zubicaray et al., 2006, Fig. 2). Further, we defined spherical ROIs (radius = 10 mm) in the left parietal cortex and right supplementary eye field (SEF) based upon the peaks of activation revealed by the exploratory whole brain analysis in our original identity NP study, to determine whether any of these regions were shared with the semantic NP effect as one might expect for a common NP mechanism. All of the ROI results are reported using alpha thresholds of .05 small volume corrected (SVC) for multiple comparisons using the false discovery rate (FDR) method (Genovese et al., 2002).

Fig. 1 – Diagram showing the sequence for presentation of prime and probe stimuli. Image acquisition occurred 4 sec after presentation of the probe, with a TR of 3 sec.
as implemented in the wfu_pickatlas toolbox (Maldjian et al., 2003). Finally, we conducted an exploratory whole brain analysis using an alpha threshold of .001 (Z > 3.09, uncorrected for multiple comparisons) and a spatial extent threshold of .05 (uncorrected).

3. Results

3.1. Behavioural data

Any trials in which probe target naming responses were incorrect or omitted, or if the corresponding prime was misnamed or omitted, were classified as errors and omitted from the RT analyses. Table 1 shows the mean RTs and error percentages for the two conditions. Planned contrasts between conditions were performed using paired t-tests. As expected, percent error rates differed significantly between semantic ignored and control conditions [t(14) = 2.8, p < .05], as did naming latencies [t(14) = 5.43, p < .001].

A repeated measures ANOVA was next conducted with the naming latencies during the semantic ignored condition to determine whether these were influenced by the structural similarity of the distractor–target object pairings according to the McRae et al. (2005) feature norms. This revealed a significant main effect of structural similarity [F(4, 14) = 4.975, p < .05], with more structurally similar items producing longer NP RTs. Fig. 2 shows the mean RTs according to number of shared structural features.

Table 1 – Mean naming latencies (RT, msec) and percent (%) errors according to experimental condition

<table>
<thead>
<tr>
<th>Condition</th>
<th>RT</th>
<th>% errors</th>
</tr>
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<tbody>
<tr>
<td>Control (unrelated)</td>
<td>816.7 (79)</td>
<td>1.6 (2.9)</td>
</tr>
<tr>
<td>Categorically related</td>
<td>845.6 (68)</td>
<td>5.9 (5.8)</td>
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SDs are given in parentheses. RT = reaction time; SD = standard deviation.

3.2. fMRI data

Of the ROIs interrogated, only the left posterior-mid fusiform cortex showed a significant activation increase for the contrast of semantically ignored and control conditions (peak x, y, z: −39, −63, −12; Z = 3.72, p < .05, small volume corrected) and is shown in Fig. 3a. None of the other ROIs reached nor showed a trend toward statistical significance in either direction. In order to determine whether the left posterior-mid fusiform activation observed was related to the structural similarity of the categorically related distractor–target object pairs in the semantic ignored condition, we entered the similarity ratings from the McRae et al. (2005) feature norms as a regressor in an additional fixed effects analysis of each participant’s fMRI data, then entered the resulting contrast images in a group level t-test in a second-stage random effect analysis. This again revealed a significant effect in the left fusiform cortex ROI within 3 mm of the previously identified peak (peak x, y, z: −39, −63, −9; Z = 3.04, p < .05, small volume corrected).

The whole brain exploratory analysis revealed the left fusiform activation increase and one additional large cluster of voxels extending throughout the insular-opercular cortex (peak x, y, z: −36, −6, 21; Z = 3.75, p < .001, uncorrected) (Fig. 3b). No significant activation was observed for the opposite contrast (control > semantic ignored). To determine whether the activation peaks observed in these regions were related directly to the semantic NP effect, bivariate correlation analyses were conducted with the mean percent BOLD signal responses extracted from each participant and the magnitude of their individual NP effect (calculated as the difference between their mean RTs in the semantic ignored and control conditions). Mean percent BOLD signal responses were extracted from clusters of significant voxels using Marsbar software (Brett et al., 2002; http://marsbar.sourceforge.net). These analyses revealed a positive correlation with the fusiform cortex activation that approached significance (r = .43, p = .053) and a significant negative correlation with the insular-opercular cortex activation (r = −.45, p < .05).

4. Discussion

The aim of the present study was to determine whether the NP effect associated with naming categorically related objects involves access to central abstract semantic representations or more peripheral, structural representations. We expected the former to manifest as increased activation in the lateral ATC, given converging evidence from neuroimaging, lesion and computational modelling implicating this region in encoding of semantic representations, and our prior finding of increased activation in this region during the identity NP effect in object naming. As objects within categories share more physical or structural features than objects from different categories, we considered an alternative explanation that the effect might be due solely to structural representations being accessed within fusiform cortex. Using event related fMRI, we found that the “semantic” NP effect in object naming activates the left posterior-mid fusiform cortex as well as an
opercular–insular cortical region. Further, none of the regions that showed activity during the identity NP effect in our previous study demonstrated similar activation with categorically related objects.

The present results offer a possible resolution to the debate concerning whether the NP effect observed with categorically related objects is located at a structural rather than semantic level of representation (Fox, 1995; May et al., 1995). Recent neuroimaging studies have shown that posterior-mid fusiform cortex activation is driven primarily by structural overlap between members of categories (e.g., Joseph and Gathers, 2003; Rogers et al., 2005). For example, Joseph and Gathers (2003) reported activation in the left mid fusiform cortex at \((x = -48, y = -63, z = -18)\) during matching of structurally similar 3D shapes, while Rogers et al. (2005) reported left posterior fusiform activation at \((x = -46, y = -62, z = -16)\) for animals and vehicles categorised at an intermediate level of specificity. The activation peak we observed at \((x = -39, y = -63, z = -12)\) corresponds well with the results of these studies. Rogers et al. (2005, 2006) attributed increases in fusiform activation observed with intermediate level categorically related objects to competition between structurally similar representations that takes longer to resolve, an effect referred to as “visual crowding” (Gale and Laws, 2006). Joseph and Gathers (2003) found that left mid fusiform cortex responses were modulated by RT during shape matching. The positive correlation found between the magnitude of each individual’s NP effect and their left fusiform cortex activation observed in the identity NP task (de Zubicaray et al., 2006) can be considered prima facie evidence that the two paradigms do not share common neural mechanisms. A recent study by Rogers et al. (2006) provides a potential explanation. In their study, left anterolateral temporal cortex was more likely to be activated when discriminating objects at a relatively specific level (e.g., between various makes of cars) where amodal conceptual knowledge is of greater assistance. Conversely, fusiform cortex was more likely to be activated when discriminating objects at the intermediate level (e.g., for the general category of “vehicles”, between a CAR and BUS) where perceptual features are more relevant. This is in keeping with the proposal that the form of representations at the source of NP effects differs flexibly according to the goals of the task at hand (Tipper, 2001), or as Fox (1995) put it succinctly “ignored stimuli are analysed to the level of representation required by the task” (italics added) (p. 153). This suggests that the label of “semantic” or “conceptual” NP following from the use of intermediate level categorically related objects might be a misnomer (cf. Allport et al., 1985; Murray, 1995; Tipper, 1985), as the task appears unlikely to involve “central” or amodal semantic access to the same extent as the identity NP task, nor share the same ancillary processes (e.g., inhibition, episodic retrieval; see Tipper, 2001). Behavioural researchers had assumed that the use of categorically related distractors enabled them to test the hypothesis that identity NP operates at a semantic level of representation (May et al., 1995; although see Fox, 1995), while sometimes acknowledging the potential confound of within-category structural similarity. Thus, neuroimaging data can be a useful supplementary source of evidence to corroborate assumptions concerning cognitive processes targeted in behavioural investigations (de Zubicaray, 2006).

In conjunction with the novel finding of fusiform cortex activation, the failure to observe significant activation in the left ATC or any other region detected in our previous study of the identity NP effect (de Zubicaray et al., 2006) can be considered prima facie evidence that the two paradigms do not share common neural mechanisms. A recent study by Rogers et al. (2006) provides a potential explanation. In their study, left anterolateral temporal cortex was more likely to be activated when discriminating objects at a relatively specific level (e.g., between various makes of cars) where amodal conceptual knowledge is of greater assistance. Conversely, fusiform cortex was more likely to be activated when discriminating objects at the intermediate level (e.g., for the general category of “vehicles”, between a CAR and BUS) where perceptual features are more relevant. This is in keeping with the proposal that the form of representations at the source of NP effects differs flexibly according to the goals of the task at hand (Tipper, 2001), or as Fox (1995) put it succinctly “ignored stimuli are analysed to the level of representation required by the task” (italics added) (p. 153). This suggests that the label of “semantic” or “conceptual” NP following from the use of intermediate level categorically related objects might be a misnomer (cf. Allport et al., 1985; Murray, 1995; Tipper, 1985), as the task appears unlikely to involve “central” or amodal semantic access to the same extent as the identity NP task, nor share the same ancillary processes (e.g., inhibition, episodic retrieval; see Tipper, 2001). Behavioural researchers had assumed that the use of categorically related distractors enabled them to test the hypothesis that identity NP operates at a semantic level of representation (May et al., 1995; although see Fox, 1995), while sometimes acknowledging the potential confound of within-category structural similarity. Thus, neuroimaging data can be a useful supplementary source of evidence to corroborate assumptions concerning cognitive processes targeted in behavioural investigations (de Zubicaray, 2006).
It is worth noting that one prior behavioural study attempted to address the issue of within-category structural similarity in semantic NP. Damian (2000) constructed a set of pictorial stimuli and had subjects rate them for visual similarity on a five-point scale. In the semantic NP task, two conditions comprising categorically related objects were devised: the first included objects rated as highly similar while the second included objects selected “without regard” for their similarity (p. 849). Damian (2000) failed to find a semantic NP effect during naming of either type of stimuli, in contrast to the earlier studies that had reported robust effects (e.g., Allport et al., 1985, Experiments 4 and 5) including with rotated objects (Murray, 1995). Although Damian concluded his results discounted structural similarity as an explanation for semantic NP effects, he did acknowledge that the categorically related object pairs used in his study were only weakly associated (Murray, 1995). Moreover, a detailed examination of Damian’s stimuli (personal communication, 10 August 2005) revealed some exemplars that, while perhaps intuitive members of categories, are not reliable exemplars according to the empirically derived norms provided by Cree and McRae (2003) (e.g., for furniture, CLOCK; for tools, KNIFE). In the present study, objects were chosen as category exemplars from Cree and McRae’s (2003) norms, and some were strongly associated (e.g., cat–DOG; Murray, 1995). The exploratory whole brain analysis revealed an additional peak of increased activation extending through insular and opercular cortices. While not predicted a priori, this region is activated reliably in language production tasks, particularly those involving object naming (see Indefrey and Levelt, 2004; Kemeny et al., 2006). Lesions to the insular–opercular area are associated with a disorder known as apraxia of speech (AOS; Dronkers, 1996; Ogar et al., 2006), considered an impairment of the motor components of articulation. Both lesion and neuroimaging studies have indicated a relatively specific role for the insular–opercular area in the articulation of syllable sequences (Aichert and Ziegler, 2004; Bohland and Guenther, 2006). Neuroimaging studies of repetition priming in object naming have also revealed increases in left insular activation (e.g., van Turennout et al., 2000, 2003). These increases have been interpreted in terms of a procedural learning mechanism that enables efficient name retrieval via a mental syllabary at the phonetic encoding level (van Turennout et al., 2003; see also Indefrey and Levelt, 2004). The present finding of a significant negative correlation between the magnitude of each individual’s NP effect and their insular–opercular activation can be considered consistent with a name retrieval efficiency account.

Finally, some caveats should be considered when interpreting the current results. For example, the experiment was designed to collect BOLD signal responses corresponding to probe trials. Consequently, our fMRI data cannot address the nature of the initial processes occurring during prime presentation. In addition, it is possible that the BOLD responses post probe presentation reflect some residual contribution of prime processing due to the fixed intervals used between prime and probe displays. We also cannot exclude the possibility that the fusiform cortex activation observed here reflects a contribution of semantic processing during visual object recognition, an interpretation suggested by some earlier fMRI studies of positive priming effects (e.g., Koutstaal et al., 2001; Simons et al., 2003; cf. Eddy et al., 2007; Vuilleumier et al., 2002, 2005). However, our view like that of a number of researchers is that posterior mid fusiform cortex does not mediate access to stored object knowledge per se (Gerlach et al., 2006; Joseph and Gather, 2003; Rogers et al., 2005, 2006).

As we noted in Section 1, object naming is almost universally assumed to involve perceptual, semantic, syntactic, phonological and articulatory processing stages (see Humphreys and Forde, 2001). Consequently, any one or combination of these stages might be critical for performance in a given object naming task. Considering the RT and fMRI data, our interpretation of the NP effect with categorically related objects is that it is most likely the result of competition between structurally similar category exemplars, or visual crowding, that influences the efficiency of name retrieval, rather than an inhibitory or other mechanism operating on central semantic representations (cf. Tipper, 1985). This differs from the level of representation at which the identity NP effect in object naming operates, as that involves access to abstract semantic codes in the left ATC (de Zubicaray et al., 2006).

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### Appendix

**Category labels and stimuli used in the experiment**

**ANIMALS:** cat, cow, dog, horse, mouse.

**FRUIT:** apple, banana, grape, lemon, orange.

**VEHICLES:** bus, car, motorcycle, train, truck.

**CLOTHING:** belt, dress, shirt, sock, tie.

**MUSICAL INSTRUMENTS:** drum, guitar, harp, piano, trumpet.

### References


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